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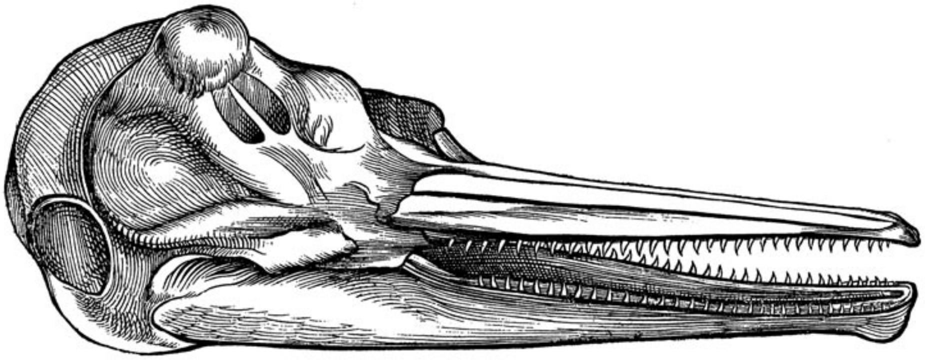

The Therian Skull

A Lexicon with Emphasis on the Odontocetes

J. G. Mead and R. E. Fordyce

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ABSTRACT

Mead, J. G., and R. E. Fordyce. The Therian Skull: A Lexicon with Emphasis on the Odontocetes. *Smithsonian Contributions to Zoology*, number 627, 248 pages, frontispiece, 2 diagrams, 32 figures, 9 tables, 2009. — Cetaceans form one of the most unique groups in the evolutionary history of mammals. They have returned to the sea and modified their tail as an efficient means of locomotion. As they adapted to the limited visibility in the aquatic environment, the odontocetes developed a system of echolocation that resulted in extensive modifications to the skull bones. This made descriptive comparisons very difficult and early anatomists unwittingly composed new terms for anatomical structures that had already been named in other taxa. This made anatomical comparisons, based on the literature, extremely tenuous.

This lexicon is an attempt to remedy that situation in that it provides headwords and definitions for all the terms that have been used in describing the mammal skull and notes the synonymous terms. The lexicon includes the human nomenclature (*Nomina Anatomica*), the veterinary nomenclature (*Nomina Anatomica Veterinaria*) and the nomenclature that is used in descriptive comparative anatomy. The lexicon covers not only extant but extinct mammalian groups and is extensively indexed.

Cover: Detail from Frontispiece, illustration of a dolphin skull (cf. *Delphinus* sp.) presented by Gesner (1560).

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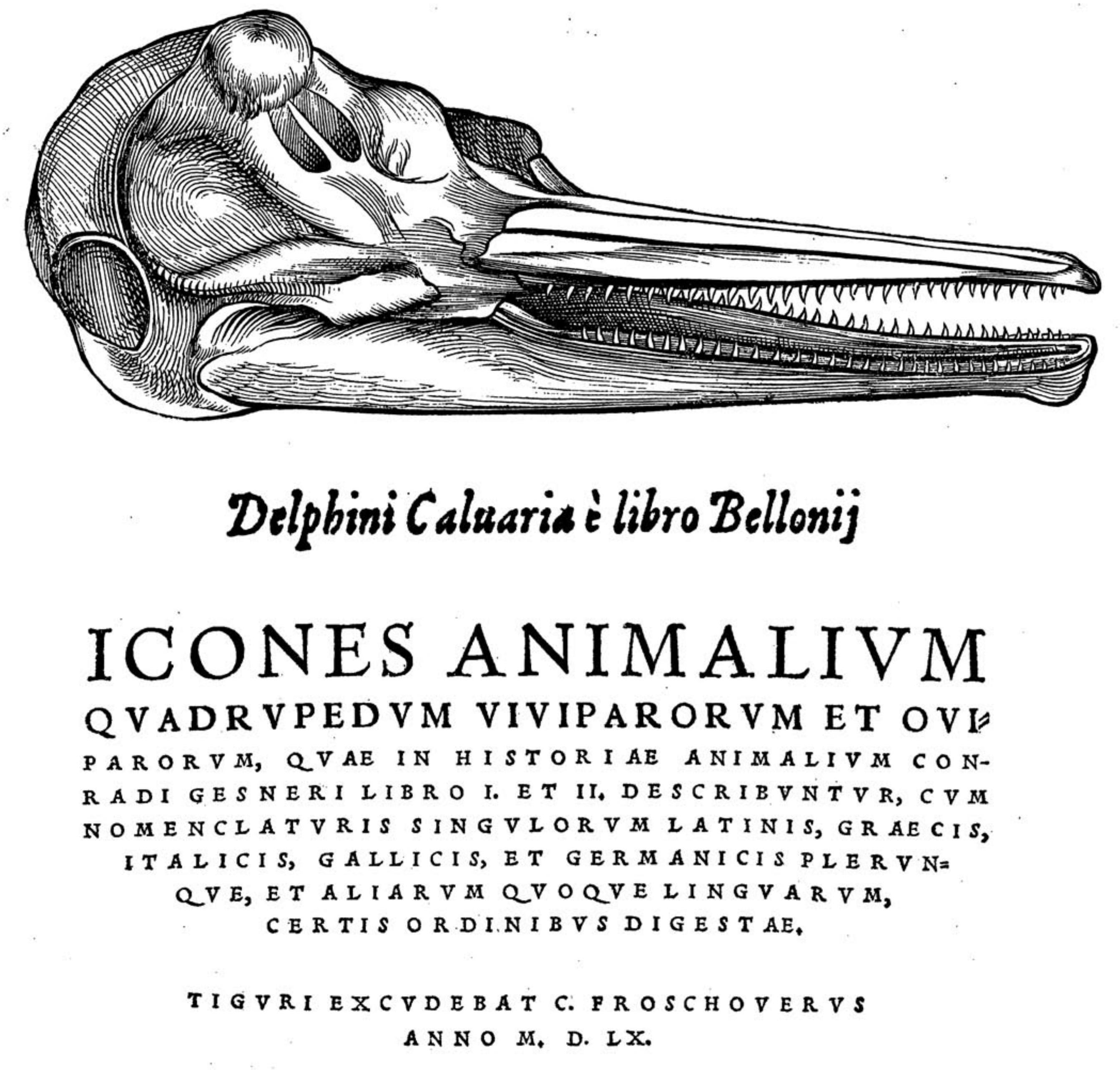
Dedication

The authors dedicate this work to the memory of
Dr. John E. Heyning (6 January 1957–17 February 2007),
who was a colleague in anatomy, a fellow museum curator,
and a valued friend.



Delphini Caluaria è libro Bellonij

ICONES ANIMALIVM
QVADRVPEDVM VIVIPARORVM ET OVIPARORVM,
QVAE IN HISTORIAE ANIMALIVM CONRADI
GESNERI LIBRO I. ET II. DESCRIBVNTVR, CVM
NOMENCLATVRIS SINGVLORVM LATINIS, GRAECIS,
ITALICIS, GALLICIS, ET GERMANICIS PLERVNQVE,
ET ALIARVM QVOQVE LINGVARVM,
CERTIS ORDINIBVS DIGESTAE.

TIGVRI EXCVDEBAT C. FROSCHOVERVS
ANNO M. D. LX.

FRONTISPIECE. Dolphin skull (cf. *Delphinus* spp.) with the caption "*Delphini Calvaria è libro Bellonij*" presented by Gesner (1560:162).

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The Therian Skull: A Lexicon with Emphasis on the Odontocetes

> Because of the perfected adaptation to a completely aquatic life, with all its attendant conditions of respiration, circulation, dentition, locomotion, etc., the cetaceans are on the whole the most peculiar and aberrant of mammals.
>
> —G. G. Simpson (1945:213)

INTRODUCTION

Cetaceans are a highly specialized order of mammals. Anatomists have long been interested in them because they are radically different from other aquatic orders and from terrestrial mammals. Early systematists attempted to describe the differences using terms that were readily available from existing anatomical vocabulary or by creating new terms. Over the years, a literature developed full of vaguely defined or mistaken terminology.

The authors have undertaken this project in an attempt to develop a dictionary that defines terms used to describe osteological landmarks on the skulls of one family of cetaceans, the delphinid odontocetes (dolphins).

One failing of current published anatomical literature dealing with animals other than humans and nondomesticated mammals is an emphasis on the unusual. Detailed descriptions exist for the rare species and nothing for commonplace animals. Thus, little exists for truly comparative analysis. It was with this in mind that the authors set out to create this dictionary. We have attempted to treat every term that pertains to landmarks in the mammalian skull.

The following classic works were used as primary sources: Owen (1866a) on the dwarf sperm whale (*Kogia sima*), Anderson (1879) on the Ganges river dolphin (*Platanista gangetica*) and the Irawaddy river dolphin (*Orcaella brevirostris*), Schulte (1917) on the pygmy sperm whale (*Kogia breviceps*), and Kernan (1918) on the goosebeaked whale (*Ziphius cavirostris*). Other heavily used sources were those of Boenninghaus (1904) on the ear region of odontocetes, Fraser and Purves (1960) on hearing in whales, and van der Klaauw (1931) on the tympanic bulla in fossil mammals.

Several contributions on noncetacean mammals, both living and extinct, were particularly useful to elucidate the origin of cetacean terms, or to identify terms that might be applied to the cetacean skull. Of note are Evans and Christensen (1979) on the domestic dog (see also Evans, 1993), MacPhee (1981) on the primate and insectivore basicranium, Novacek (1986) on leptictid insectivores, and Wible and Gaudin (2004) on armadillos.

HISTORY

As long as humans have been in contact with the sea, there has been an interest in Cetacea. Aristotle, a Greek naturalist philosopher (384–322 BC), was the first author to treat cetaceans biologically. He was familiar with both great whales and dolphins, although it is now impossible to tell how much he knew from first-hand observation and how much was based on conversations with fishermen. Nonetheless, he clearly understood that cetaceans were mammals and that they suckled their young, breathed air, and had hair.

Pliny the Elder, the Roman philosopher and scholar (AD 23–79), was a prolific compiler of natural history. In the preface to his main work, *Naturalis Istoria*, he claimed to

James G. Mead, Division of Mammals, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20013-7012, USA; R. Ewan Fordyce, Research Associate, Division of Mammals, Department of Geology, University of Otago, Post Office Box 56, Dunedin, New Zealand.

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have assembled 20,000 facts from 2,000 books written by 100 authors. Most of the works that Pliny cited have disappeared, but the information extracted has persisted. In the sixteenth century, libraries began to include anatomical works by authors who had first-hand experience with cetacean anatomy. Two ichthyologists, Pierre Belon (1551, 1553) and Guilliame Rondelet (1554), wrote monographs on fish anatomy in which they included cetaceans. Belon (1553:14) illustrated a skull of a dolphin that might have been the specimen that Craigie (1831:45) said Belon found on the shore of the "Cimmerian Bosphorus." Conrad Gesner (1560:162), whom many people style the father of natural history, presented a figure of a dolphin skull with the caption "Delphini Calvaria è libro Bellonij" that looks like the skull that Belon (1553:14) illustrated but in a better state of preparation. We have reproduced Gesner's illustration as the frontispiece of this work. Gesner obtained most, if not all of his information concerning cetaceans from Belon and Rondelet. Edward Tyson (1680) was the first to treat the anatomy of a cetacean in a work devoted solely to that purpose. In 1787 John Hunter presented a paper, "Observations on the Structure and Oeconomy of Whales," to the Royal Society of London. These works dealt primarily with soft-part anatomy, as did others of their time. Hunter and others of his generation had medical training and used terms that were oriented toward human anatomy.

It was not until the classic studies of Georges Cuvier (1769–1832) that scientific interest in the skeleton became widespread. His *Recherches sur les Ossemens Fossiles de Quadrupèdes* (1821–1823) and *Leçons d'Anatomie Comparée* (1835–1846) are seminal academic works.

As more studies were done on a variety of animals, it became apparent that structures were present in nonhuman mammals that were not present in humans, and the body of comparative anatomical terms began to expand. It was with the works of Richard Owen (1804–1892) and William Henry Flower (1831–1899) that comparative studies reached a peak. Flower was the first person to take an evolutionary approach, in the Darwinian sense, to cetacean anatomy. Two works have become classical references: Owen's (1866b–1868) *On the Anatomy of Vertebrates* and Flower's (1885) *An Introduction to the Osteology of the Mammalia.*

When comparative anatomy became a recognized academic field, the vocabulary increased exponentially. Many terms were coined to document diversity of form and to avoid confusion with terms used for human descriptive anatomy. In addition, veterinary anatomy produced terminology that hybridized human and nonhuman mammalian terms. Studies on cetaceans were performed as material became available. Anatomists were dealing with anatomical structures of uncertain origin and function, and studies were not always performed on the freshest of specimens. Some workers, frustrated with the uncertain definitions and homologies of past works, contributed terms that seemed more appropriately descriptive. As a result, cetacean terminology did not develop consistent anatomical standards.

EVOLUTIONARY CHANGES

Cetacean skulls have radically diverged from the skulls of terrestrial mammals. In both suborders of living cetaceans, the skull has been extremely modified in terms of location of external nares, structural modification of middle and inner ear, changes in feeding apparatus, and elimination or reduction of structures. Homology and analogy have always been of concern to evolutionary biologists, and problems have been compounded by differences in terminology. The basic problem is the difficulty in recognizing structures that have a common evolutionary origin.

The topographic changes of cetaceans are obviously the result of aquatic adaptation. Changes in cetacean skulls are best viewed in terms of functional complexes. These complexes include feeding, breathing, sound production, sound reception, and locomotion. Individual changes usually overlap two or more functional areas.

In the head, the rostrum has elongated and the position of the external nares has shifted to a more dorsal position, altering the relationship of the nose to the eye and ear. The ear has become highly modified in response to the aquatic environment. The external ear has disappeared and is represented by vestigial cartilage. The middle and inner ears have become isolated from the surrounding skull bones and have changed their morphology drastically, reducing bony conduction of sound.

In odontocetes, the soft tissue between the mouth and the nose—the upper lip—has become hypertrophied in association with development of the melon and associated musculature and nasal diverticula or epicranial sinuses. The melon is a subdermal structure composed of layers of lipids of differing composition that function in acoustic transmission. Correlated with this change is the differentiation of a number of lipid bodies associated with the lower jaw and ear. The shape of the melon body differs from the external profile of the head, which could reflect sexual or other modes of selection. The melon makes possible the development of impressive foreheads seen in such species as pilot whales, belugas, bottlenose whales, and finless porpoises. The spermaceti organ in sperm whales is derived from different anatomical origins but is possibly functionally similar to the melon. In addition to the melon, the muscles and nasal diverticula associated with the complicated external nasal passage have an effect on the morphology of the underlying bones (Mead, 1975).

The pterygoid bones surrounding the internal nares have become modified to form pterygoid sinuses. The pterygoids have joined ventrally to form the posterior margin of the hard palate. The lamina of the pterygoid has split into lateral and medial portions and has been invaded by an air sinus that is an extension of the middle ear cavity. This sinus system is commonly referred to as the pterygoid sinus system. It consists of a number of basicranial sinuses and bony fossae that may or may not be directly related to the pterygoid sinus. This system has been thoroughly described in a monograph by Fraser and Purves (1960).

The external nares of cetaceans began their posterodorsal migration shortly after they diverged from terrestrial mammals, resulting in changes to the relative positions of the skull bones in both mysticetes and odontocetes. Breathing and, possibly, sound production were two of the factors driving the changes. The rapid exchange of air that is necessary in an active, air breathing, aquatic organism was responsible for simplification of the bony nasal passage, formation of a palatal sphincter, and elimination of nasal turbinates and olfaction in odontocetes.

A new term introduced by Winge (1918) to explain the overall result of the changes was *sammenskudt,* translated by Miller as "telescoping." Subsequently, Miller (1923) used "telescoping" in a paper describing the structural relationships of the skull elements in archaeocetes, mysticetes, and odontocetes. Although neither Winge (1921) nor Miller (1923) defined it, the term "telescoping" has been applied in comparing relationships of bony elements in cetaceans to the overlapping tubes of a telescope. *The Century Dictionary* (Whitney, 1989–1910:[vol. 8]6218) provided this definition: "telescope, v. to drive into one another like the movable joints or slides of a spy glass; as 'in the collision the forward cars were telescoped'; to shut up or protrude like a jointed telescope."

All these adaptations result in extensive changes in the skulls. Cladistic analysis shows that there are four styles of telescoping: (a) facial telescoping in odontocetes, (b) facial telescoping in mysticetes, (c) supraoccipital telescoping in odontocetes, and (d) supraoccipital telescoping in mysticetes. Widening, flattening, and thickening of the occipital bones at the rear of the skull allows for stronger attachment of more muscles associated with locomotion without limb involvement. Facial telescoping in (a) and (b) also involves movement of the nares independent of changes in the maxilla and premaxilla.

Changes in both odontocetes and mysticetes are most dramatic in non-braincase structures. In odontocetes the rostral elements (maxilla and premaxilla) move dorsally and posteriorly over the cranium to form elements of the facial region. In mysticetes the rostrum is expanded anteriorly and the rostral elements do not move back over the cranium. In extant odontocetes the occipital elements move slightly anteriorly so that the parietal is excluded from the dorsal midline by the interparietal and the supraoccipital bones. In mysticetes the external borders of the occipital elements move radically farther anteriorly and the supraoccipital lies far forward of the braincase. The braincase does change, but in more subtle ways. The sum total of changes results in odontocete skulls that are strikingly asymmetrical.

The rostrum or snout is extremely plastic in mammals, with marked evolutionary changes in length and width. Once cetacean teeth had simplified, it was a relatively simple matter to increase the length of the rostrum and number of teeth to form impressive specializations for use in manipulation and feeding.

The entire paranasal sinus complex (frontal, maxillary, and sphenoid sinuses) is lost in living cetaceans, involving the maxilla, frontal, ethmoid, and sphenoid bones. Some of the paranasal sinuses are still present in some archaeocetes (Kellogg, 1936), and it is possible that some cranial foramina in living Cetacea are vestigial and once associated with the paranasal sinuses.

The throat of cetaceans has been modified to form a more efficient food passage for mammals that swallow their food whole. The balaenopterid mysticetes have developed a specialization, the *cavum ventrale*, that permits expansion of the mouth to accommodate the schools of fish and crustaceans on which they feed. The odontocete nasopharynx became modified into a sphincter that holds the larynx and provides a relatively strong continuous air passage between the lungs and the nasal diverticula or epicranial sinuses. This modification is important in providing a mechanism by which feeding and echolocation can take place simultaneously.

In the axial and appendicular elements of cetaceans, there has been considerable change. There has been a tendency to fuse anterior cervical vertebrae. The sacral region has been lost in all living whales and the caudal region has retained the usual mammalian variation in both living and fossil species. Only the thoracic and lumbar series have remained relatively stable in number. The other axial elements associated with the vertebral column (ribs and sternal elements) have varied in number depending on the variation in thoracic count.

Multiplication or reduction has occurred in areas where there are serial elements that are functionally similar. These areas in mammals include the digits of the limbs, the teeth, and the vertebrae and ribs. Cetaceans have not increased the primitive number of digits, but hyperphalangy is widespread. Once the teeth began to simplify, they either increased or decreased beyond the primitive mammalian count of 11 per jaw (total of 44). Mysticetes lost all adult teeth but still have a number of tooth buds in utero. In all odontocete males there is at least one erupted tooth. Females and young of some species remain edentulous, although teeth are present as vestiges. When the number of teeth increased, they became morphologically similar and conical in shape. The La Plata River dolphin (*Pontoporia blainvillei*) represents the most extreme increase, with a total of 242 teeth.

MATERIALS AND METHODS

Protocol for Terms in the Lexicon

The course of cetacean evolution has resulted in skulls in which the homologies with terrestrial mammals and humans are sometimes uncertain. For one cetacean species, the bottlenose dolphin (*Tursiops truncatus*), we have attempted to homologize the osteological landmarks we found with features recognized in *Nomina Anatomica Veterinaria* (3rd edition, ICGVAN, 1983), *Nomina Anatomica* (5th edition, IANC, 1983), and current comparative anatomical usage. That is, we attempted to treat every term that pertains to landmarks in the mammalian skull. We used Schaller (1992) extensively because this work included all the terms that the *Nomina Anatomica Veterinaria* recognized, and we used Feneis (1994) because it did the same for *Nomina Anatomica*. In citing these works we used the following format: publication year:page number.reference number used by the author for the structure in the author's figure (e.g., Schaller, 1992:14.9 for *canalis nasolacrimalis*). We used the 1918 edition of Gray's *Anatomy of the Human Body* in preference to more recent editions because we felt there was a tendency in later editions to reduce the anatomical detail.

In dealing with an anatomical system that has become so changed by evolution as the cetacean skull, we continually found structures that were radically modified morphologically but were homologous with structures in other mammals. If the structure in cetaceans could be satisfactorily derived from another structure in terrestrial mammals, we considered the structures to be homologous.

We generally restricted our observations to the bottlenose dolphin, but wherever enough data were available, we extended the observations to the family level (Delphinidae) or to the suborder (Odontoceti) or order (Cetacea).

We realize that our conclusions will have importance beyond the bottlenose dolphin and should be applicable to the entire order, both fossil and recent. Thus, we took pains to not "paint ourselves into a corner" and considered the situation, where appropriate, in mysticetes and fossil taxa, including archaeocetes.

By "Cetacea" we mean the living Odontoceti and Mysticeti and their close fossil relatives. These represent the crown-group Cetacea or Neoceti—living odontocetes and mysticetes, plus all fossil descendants of their most recent common ancestor. We give only occasional mention of stem-Cetacea, the wholly extinct Archaeoceti.

In the Lexicon, we differentiated the formal Latin terms in the heading by putting them in parentheses. We then used the English term as the preferred term in the text. If there did not appear to be an English term for the structure, we translated the Latin term and put the English term in the heading. We realized that some Latin terms have become universally used (e.g., *sella turcica*) and the English translation (Turk's saddle) would not be an appropriate preferred term, so we have used the Latin. Other Latin terms that we retained as preferred include the *foramen magnum* and *foramina ovale* and *rotundum*.

Priority

In deciding which term to use, we have weighed the earliest usage of a term for a feature, the number of authors who have used the term, the etymological correctness of the term, conflicting and/or ambiguous usage, and whether the term was used in the anatomical standards (*Nomina Anatomica, Nomina Anatomica Veterinaria*). Some historical terms were never used after their proposal and have been forgotten, and new synonymous terms were published much later. In such cases, the older terms might be viewed as *nomina oblita* and not worthy of being resurrected.

For Cetacea it is desirable to use terms that are applied in other mammals unless the feature in Cetacea is so highly modified that the normal mammalian term is misleading; in such cases, we indicate the homology (see, e.g., *tegmen tympani*). We have not adhered strictly to one system or another, nor used strict priority rules, but have provided cross-references and an extensive index.

Where the arguments for and against using a term were equal, we have used Flower's (1885) introduction to the osteology of the Mammalia, which was the first osteological work based on evolutionary thought.

We have not imposed a strict chronological priority system but returned to what most people consider the foundation of modern anatomy, Vesalius' 1543 *Fabrica,* and considered the terms that Vesalius used in the figures for the skull (liber I, capita 6–12). Our research was made easier by Richardson and Carman's translation of Vesalius (Vesalius et al., 1998), particularly the table compiled by Richardson and Carman listing all the identifiable foramina of the head and upper jaw.

In our definitions of the foramina, we have inserted the Latin terms that Vesalius used in his 1543 edition. We felt that it would be valuable as a temporal landmark to demonstrate either the name or phrase that Vesalius used in speaking of the foramina. We also consulted a later edition of Vesalius' osteological work (Vesalius and Sandifort, 1782), and examined Lancisius' publication of Eustachius' plates (Eustachius and Lancisius, 1714). The nomenclature of those plates was supplied by Lancisius and was in vogue at the beginning eighteenth century, not during Eustachius' lifetime (1520–1574). Although Eustachius was a contemporary of Vesalius and did equally detailed work, his results were not published until 1714.

One significant anatomical author antedates Vesalius—Galen. Charles Singer (Galen and Singer, 1956:xviii), in his translation of Galen's work of AD 177, said:

> The Greeks, unlike ourselves, had no classical language from which to draw scientific terms. These they made either by combinations of words, or by giving ordinary words a special meaning, or by using short descriptive clauses. Taking examples from our text, one illustrative of the first method is PERIKRANION, "around the cranium"; of the second is KONARION, "cone-shaped thing," pineal gland; of the third is O TOU BRACHIONOS PROSTHIOS MYS, "the anterior muscle of the arm," biceps. Manifestly these terms were far less distinctive for Greek speakers than are their equivalents for English speakers. It is especially for the description of muscles, vessels, and nerves that the text presents difficulties to the translator. The obstacles to understanding for those ancient readers who did not dissect and had no anatomical figures were insuperable. Until modern times, and until the revival of the practice of dissection and the introduction of representational art, the anatomical works of Galen were almost incomprehensible.

Embryological Terms

Terms included in the Lexicon generally do not include embryological terms unless such names have also been applied to adult cetaceans and other placental mammals considered in our main sources of literature.

Orientation Terms and Terms that Imply Size, Shape, and Proportion

Many orientation terms have become incorporated into names of bony features. For example, terms for the ear include anterior process (of periotic), posterior process (of tympanic bulla), lateral tuberosity (of periotic), and dorsal surface of *pars cochlearis* (of periotic). Some of these terms reflect the orientation of a part as seen in a particular species of cetacean, which could be an extinct species, or the orientation as seen in other placental mammals. Because of evolutionary changes in the orientation of parts of the cetacean skull, a particular structure may no longer face the direction that its name suggests. This is particularly the case for the ear region. Thus, the long axis of the tympanoperiotic complex in many living odontocetes commonly faces somewhat anteromedially rather than anteroposteriorly and, in the extreme case of pygmy sperm whales, *Kogia* spp., the long axis faces markedly anteromedially. In *Kogia* spp., also, the periotic is rotated so that the cerebral surface, which is homologous with the dorsal surface in some other living and many extinct Cetacea, faces dorsomedially.

To aid comparison, and circumvent problems created by variable orientations among species, we used anatomical terms that have an orientation component (e.g., anterior process, posterior process) as if the structures are actually oriented as their name suggests. Such use requires that we separately describe the actual orientation of the part in the broader context of the skull.

The terms "major" and "minor" are preferred over "greater" and "lesser"; we consider that the latter do not create synonyms.

Many names as used originally were hyphenated. In general, we have stripped hyphens except where quoting in the original context.

Descriptive terms such as "angle" and "tubercle" may convey to different readers quite different concepts of profile or degree of development. Where a skull feature consistently has a shape or size that suits such terms as angle or tubercle, we retained the particular term, but in general we prefer to use more generic terms such as "process."

Eponymous Terms

Where they have been in wide use, or are less contentious than certain descriptive terms that do not always apply across a range of species, we accepted eponymous anatomical terms, such as Eustachian tube and Meckel's cartilage.

Usage of Terms

We have gone to more effort in researching the usage of these terms than is obvious from the citations we provided for the terms, but we felt that to give a blow-by-blow account of each term would not be useful.

As an example, the case of the foramina and canals on the maxilla that contain the branches of the infraorbital nerve and vessels deserves some mention. In researching the terms that had been used for the openings, we found antorbital, infraorbital, maxillary, suborbital, and supraorbital, and the canal also had been referred to as antorbital and infraorbital. There was no unambiguous way to refer to these structures, so we felt obliged to coin new terms. We chose the "internal maxillary foramen" for the proximal opening, "external maxillary foramen" for the distal opening, and "infraorbital canal" for the canal. A detailed discussion of our reasoning is provided in the section on the infraorbital canal under "Maxilla."

We use "jugal" because of the confusion with the multiple features that are termed zygomatic; we prefer to use "zygomatic" to refer to the arch rather than the bone.

Absence of Landmarks

It can be difficult to deal with some structures that cetaceans supposedly lack, such as the lacrimal gland and paranasal sinuses. If we were able to locate the osteological features that define the structure in other mammals, we named the feature. A good example of this is the anterior lacrimal crest on the maxilla. In dealing with these cases, we still need studies of the soft anatomy, including histology, to be absolutely certain of the correct term.

Illustrations

One outstanding requirement for a work such as this is adequate illustrations. We have illustrated an intact neonate skull and adult bottlenose dolphin skulls from the standard anatomical views (dorsal, ventral, anterior, posterior, and lateral). We have also provided oblique views in areas where the orthogonal views did not portray a feature adequately. We then illustrated the individual bones in a disarticulated skull of a newborn bottlenose dolphin from all five anatomical viewpoints.

Separate Treatment of Bones Associated with the Ear

As anyone who has looked into the systematic importance of the skull bones realizes, the bones associated with the ear are very important. The importance that we attached to them will be evident by the number of pages in the text and the number of illustrations devoted to them. We felt that these bones constituted an important subsystem and deserved to be treated accordingly.

CRANIOMETRIC LANDMARKS

We have treated all the craniometric terms included in *Nomina Anatomica*, although many of them involved points that could not be found on a delphinid skull. We illustrated those that could be located, and the others are discussed under the bones on which they were located (Table 1).

SPECIMENS USED

We were greatly assisted in this project by having access to an outstanding collection of bottlenose dolphin skulls. We were able to take individual and ontogenetic variation into account when considering the identity of structures. Table 2 gives data on the specimens on which we relied.

For comparative purposes we also used the following specimens from the collections of the National Museum of Natural History: the skull of an adult white-tailed deer (*Odocoileus virginianus*) from Maryland that had been sectioned along the sagittal plane (from the comparative collection, Division of Vertebrate Paleontology); three adult skulls of un-cataloged

TABLE 1. Craniometric points and the bone sections under which they are discussed.

Craniometric point	Term used in this work	Bone
Asterion	Mastoid angle	Parietal
Basion	*Basion*	Exoccipital
Bregma	Frontal angle	Parietal
Clivus	*Clivus*	Basioccipital
Frons	*Frons*	Frontal
Gnathion	*Gnathion*	Mandible
Gonion	*Gonion*	Mandible
Inion	External occipital protuberance	Interparietal
Lambda	Occipital angle	Parietal
Nasion	Occipital angle, sphenoidal angle	Parietal
Occiput	Occiput	Supraoccipital
Ophryon	Frontal angle	Parietal
Opisthion	*Opisthion*	Supraoccipital
Opisthion	Occipital angle	Parietal
Pogonion	*Pogonion*	Mandible
Prosthion	*Prosthion*	Premaxilla
Pterion	Sphenoidal angle	Parietal
Sinciput	Sinciput	Frontal
Vertex	Vertex	Frontal

TABLE 2. Data on specimens of the bottlenose dolphin, *Tursiops truncatus*, in the collection of the United States National Museum of Natural History; CBL = condylobasal length; ? = data not available.

Catalog number	Total length (cm)	CBL (cm)	Sex	Comments
241288	?	?	?	Isolated periotic, no data
241289	?	?	?	Isolated periotic, no data
500851	113	28.2	M	Calf, intact
501197	?	52.6	?	Extremely mature, lacerate foramina filled
504144	106	27.5	F	Vomer
504420	163	37.3	M	Skull, earbones in place
504560	126	31	F	Calf, disarticulated (drawn)
504567	174	37.7	M	Earbones, partially disarticulated skull
550403	202	44.9	M	Good skull (drawn)
550835	106	26.9	F	Calf, intact
550836	?	47.0	?	Sectioned tympanoperiotic
571017	264	50.3	M	Sectioned tympanoperiotic
571036	160	39.3	?	Sectioned tympanoperiotic
571471	203	42.3	M	Good complete skull, disarticulated lacrimal
571622	119	28.9	?	Calf, calvarium removed, occiput good
571643	115	28.4	M	Calf, intact
571695	?	45.7	?	Sagittally sectioned adult skull

potential dog/red wolf/coyote hybrids, (1) broken skull #1299, (2) sagittally sectioned female skull #1221, and (3) intact skull #1266 (from the National Biological Service, U.S. Department of the Interior collections at the USNM); and a human skull (sex unknown) from the Division of Mammals, USNM 301622.

OSTEOLOGICAL RELATIONSHIPS OF THE SKULL BONES

Types of Features

Osteological features found on the bones of the skull consist of either protuberances or lack of bone.

Features Involving a Lack of Bone

alveoli
aperturae
aqueducti
canales
canaliculi
cavitas
fissura
foramina
fossae
fossulae
foveae
hiates
impressiones
incisura
infundibula
labyrinthi
pores
sellae
semicanales
sinuses
sulci
vestibuli

Protuberances

alae
anguli
anuli
apices
arci
bases
bullae
capita
choanae
colla
condyles
corpora
cristae
crura
eminentia
facies
hamuli
juga
laminae
linea
lingula
marginis
meatuses
partes
plana
processes
rami
rostra
septa
spinae
squamata
suturae
symphyses
tegmina
tori
tuber
tubercula
tuberositas

Topographic Relationships of the Bones

Table 3 lists the relationships between the skull bones of a generalized terrestrial mammal (*Canis lupis*) and a delphinid (*Tursiops truncatus*). There is some degree of subjectivity in the relationships because the bony elements are not perfect squares and do not bear purely orthogonal relationships with other elements. When (in our opinion) one element bears an anterolateral relationship to another element, the first element is listed as both an anterior and lateral relationship of the second. When an element bears primarily an anterior relationship to another element, but has a slight lateral relationship, the first element is listed as only an anterior relationship of the second.

Where elements bear only an occasional relationship to one another, the second (relational) element is followed by a question mark (?). When an element does not have any bony relationship in a particular direction *x*, "*x* element" is entered where "*x*" is the direction concerned. For example, the premaxilla does not have any anterior relationships because it is at the most anterior extremity of the skull, hence "anterior element" is entered in the anterior relationship space for the premaxilla. "Midline element" is used where the medial relationships of an element are its opposite half.

We used some soft anatomical structures in this section when we wanted to be certain that there was no osteological contact in that direction. For example "peribullary sinus" is used as one of the lateral relationships of the basioccipital in delphinids to demonstrate that the basioccipital does not contact any components of the temporal.

It soon became clear that orientation is one of our primary problems. Some orientation terms are used as the proper names of structures and, because of the shift of osteological orientation in the cetacean skull, these terms may be misleading. We have dealt with that problem on a case-by-case basis (Table 3).

Cranial Nerves

The cranial nerves form an important part of the anatomy of the skull. Their nomenclature differs, depending primarily on which animal is the subject of study. The following list presents the cranial nerves in order of their exit from the skull. We used

TABLE 3. Topographic relationships between the bony elements of the skull for two mammals. A question mark (?) indicates a bone that sometimes was present in the orientation described and sometimes was absent; orientation for free-standing bones is marked "n/a" (not applicable).

Element and relationship of other elements	Relational elements for skull type	
	Non-cetacean (*Canis*)	Delphinid (*Tursiops*)
Basioccipital Bone		
Anterior	Sphenoid	Sphenoid, pterygoid
Posterior	Exoccipital	Exoccipital
Dorsal	Cranial cavity	Cranial cavity
Ventral	Pharynx	Pharynx
Lateral	Temporal (bulla, petrosal)	Peribullary sinus (parietal)
Medial	Midline element	Midline element
Ethmoid Bone		
Anterior	Nasal cavity	Vomer, pterygoid, palatine?, mesorostral cartilage
Posterior	Sphenoid, cranial	Sphenoid, cranial cavity, nasal cavity (adults)
Dorsal	Frontal, nasal	Frontal (adult), maxilla?
Ventral	Vomer, palatine	Vomer, pterygoid
Lateral	Maxilla, frontal,	Frontal, lacrimal
Medial	Midline element	Midline element
Exoccipital Bone		
Anterior	Temporal	Parietal, squamosal, basioccipital, peribullary sinus
Posterior	Atlas	Atlas
Dorsal	Supraoccipital	Supraoccipital
Ventral	Pharynx	Basioccipital, squamosal
Lateral	Temporal	Parietal, squamosal
Medial	Basioccipital	Basioccipital, contralateral exoccipital
Frontal Bone		
Anterior	Maxilla, nasal, lacrimal, palatine	Maxilla, nasal, lacrimal, palatine
Posterior	Parietal, sphenoid	Interparietal, parietal, sphenoid
Dorsal	Dorsal element	Nasal, contralateral frontal
Ventral	Palatine, sphenoid	Pterygoid, sphenoid
Lateral	Lacrimal, maxilla	Lacrimal
Medial	Contralateral frontal sphenoid	Contralateral frontal, sphenoid
Hyoid Apparatus[a]		
Thyrohyoid	Most distal	Fuses with basihyoid with age
Basihyoid	Midline element, articulates with thyrohyoid distally, ceratohyoid proximally	Articulates via a cartilage (ceratohyoid) with stylohyoid
Ceratohyoid	Paired, articulates with epihyoid proximally	Reduced to cartilage in cetaceans
Epihyoid	Paired, articulates with stylohyoid proximally	Lost or fused with ceratohyal
Stylohyoid	Paired, articulates with tympanohyoid cartilage proximally	Articulates with ceratohyoid distally and paroccipital process proximally
Tympanohyoid	Cartilaginous, articulates with mastoid process of petrosal (periotic)	Fused with posterior process of periotic, lost direct bony connection with rest of hyoid apparatus.
Interparietal Bone		
Anterior	Parietal	Frontal
Posterior	Supraoccipital	Supraoccipital
Dorsal	Dorsal element	Dorsal element
Ventral	Cranial cavity	Cranial cavity
Lateral	Parietal	Parietal, frontal
Medial	Midline element	Midline element
Jugal Bone (*Malar*)		
Anterior	Maxilla	Maxilla
Posterior	Squamosal	Squamosal
Dorsal	Squamosal, lacrimal	Maxilla, lacrimal, squamosal
Ventral	Maxilla	Maxilla
Lateral	Lateral element	Lacrimal
Medial	Squamosal, maxilla, lacrimal	Maxilla, squamosal?

(*continued*)

TABLE 3. (*Continued*)

Element and relationship of other elements	Relational elements for skull type	
	Non-cetacean (*Canis*)	Delphinid (*Tursiops*)
Lacrimal Bone		
Anterior	Maxilla	Maxilla, jugal
Posterior	Frontal, palatine	Frontal
Dorsal	Frontal, maxilla?	Maxilla, frontal
Ventral	Palatine	Jugal
Lateral	Jugal	Lateral element
Medial	Ethmoid	Maxilla, jugal
Mandible		
Anterior	Anterior element	Anterior element
Posterior	Squamosal	Squamosal
Dorsal	Squamosal	Squamosal
Ventral	Ventral element	Ventral element
Lateral	Lateral element	Lateral element
Medial	Contralateral mandible	Contralateral mandible
Maxilla		
Anterior	Premaxilla	Premaxilla
Posterior	Frontal, lacrimal, jugal	Frontal
Dorsal	Palatine, lacrimal	Premaxilla
Ventral	Ventral element	Palatine, lacrimal, jugal, vomer
Lateral	Jugal	Lacrimal, jugal, frontal
Medial	Nasal, frontal, ethmoid, premaxilla, palatine	Premaxilla, nasal, vomer, contralateral maxilla
Nasal Bone		
Anterior	Anterior element	Anterior element
Posterior	Frontal	Frontal
Dorsal	Dorsal element	Dorsal element
Ventral	Ethmoid	Frontal, ethmoid
Lateral	Frontal, maxilla, premaxilla	Frontal, maxilla
Medial	Contralateral nasal	Contralateral nasal
Palatine Bone		
Anterior	Maxilla, ethmoid	Maxilla
Posterior	Sphenoid, pterygoid	Pterygoid,
Dorsal	Vomer, frontal, lacrimal	Maxilla
Ventral	Ventral element	Pterygoid
Lateral	Frontal, lacrimal	Lateral element
Medial	Palatine, sphenoid, vomer	Pterygoid, vomer, maxilla
Parietal Bone		
Anterior	Frontal, alisphenoid	Frontal, interparietal
Posterior	Interparietal, supraoccipital, temporal	Supraoccipital, exoccipital
Dorsal	Interparietal	Interparietal, supraoccipital
Ventral	Alisphenoid, temporal	Alisphenoid, squamosal, exoccipital
Lateral	Temporal	Squamosal
Medial	Interparietal	Alisphenoid (basioccipital)
Premaxilla		
Anterior	Anterior element	Anterior element
Posterior	Maxilla	Maxilla
Dorsal	Nasal	Dorsal element
Ventral	Maxilla	Maxilla
Lateral	Maxilla	Maxilla
Medial	Contralateral premaxilla	Vomer, contralateral premaxilla, mesorostral cartilage
Pterygoid Bone		
Anterior	Palatine	Palatine
Posterior	Basisphenoid	Basisphenoid, basioccipital, ethmoid
Dorsal	Palatine, basisphenoid, ethmoid	Palatine, presphenoid
Ventral	Ventral element	Ventral element
Lateral	Palatine, basisphenoid	Palatine, frontal?
Medial	Basisphenoid, presphenoid	Vomer, palatine, contralateral pterygoid

(*continued*)

TABLE 3. (*Continued*)

Element and relationship of other elements	Relational elements for skull type	
	Non-cetacean (*Canis*)	Delphinid (*Tursiops*)
Sphenoid Bone		
Anterior	Ethmoid, vomer	Ethmoid, frontal, vomer, pterygoid
Posterior	Squamosal, basioccipital	Basioccipital
Dorsal	Ethmoid, cranial cavity	Cranial cavity
Ventral	Vomer, pterygoid	Vomer, pterygoid, basioccipital
Lateral	Parietal, frontal, palatine	Frontal, parietal, squamosal
Medial	Midline element	Midline element
Supraoccipital Bone		
Anterior	Parietal, interparietal cranial cavity	Parietal, interparietal cranial cavity
Posterior	Posterior element	Posterior element
Dorsal	Parietal, interparietal	Parietal, interparietal
Ventral	Exoccipital	Exoccipital
Lateral	Parietal	Parietal
Medial	Midline element	Midline element
Squamosal Bone		
Anterior	Sphenoid	Sphenoid, parietal
Posterior	Exoccipital	Exoccipital, tympanic bulla (falciform process)
Dorsal	Parietal	Parietal, exoccipital
Ventral	Ventral element	Periotic, tympanic bulla, jugal
Lateral	Lateral element	Lateral element
Medial	Basioccipital	Sphenoid, peribullary sinus, parietal, periotic, tympanic bulla
Periotic Bone		
Anterior	Sphenoid	Alisphenoid, squamosal
Posterior	Exoccipital	Exoccipital
Dorsal	Dorsal element	Squamosal, parietal
Ventral	Tympanic bulla	Tympanic bulla, ossicles
Lateral	Squamosal	Squamosal (closely approximated in *tursiops*?)
Medial	Basioccipital	Peribullary sinus
Tympanic Bulla		
Anterior	Anterior element	Squamosal (falciform process)
Posterior	Exoccipital	Peribullary sinus, exoccipital
Dorsal	Petrosal	Periotic
Ventral	Ventral element	Ventral element
Lateral	Lateral element	Squamosal
Medial	Medial element	Peribullary sinus
Auditory Ossicles: Malleus		
Anterior	n/a	Tympanic bulla
Posterior	incus	Incus
Dorsal	incus	Periotic
Ventral	Tympanic membrane	Incus
Lateral	Tympanic membrane	Tympanic membrane, tympanic bulla
Medial	n/a	Incus
Auditory Ossicles: Incus		
Anterior	n/a	Malleus
Posterior	n/a	n/a
Dorsal	n/a	Stapes, periotic (*fossa incudis*)
Ventral	Malleus	n/a
Lateral	n/a	Malleus
Medial	Stapes	n/a
Auditory Ossicles: Stapes		
Anterior	n/a	n/a
Posterior	n/a	n/a
Dorsal	Petrosal	Periotic
Ventral	n/a	Incus
Lateral	Incus	n/a
Medial	Petrosal	n/a

(*continued*)

TABLE 3. (*Continued*)

Element and relationship of other elements	Relational elements for skull type: Non-cetacean (*Canis*)	Relational elements for skull type: Delphinid (*Tursiops*)
Vomer		
Anterior	Premaxilla	Anterior element
Posterior	Presphenoid	Ethmoid, sphenoid, frontal
Dorsal	Sphenoid, ethmoid, palatine	Ethmoid, sphenoid, maxilla?
Ventral	Maxilla, palatine	Palatine, premaxilla, maxilla
Lateral	Maxilla, palatine	Palatine, premaxilla, maxilla, pterygoid
Medial	Midline element	Midline element

[a] For Hyoid Apparatus, first column entries are the relational elements; second and third column entries are the topographical relationships and other relational comments.

Romer (1955) and Gray (1918) for standards. See Appendix A for terms that have been used in the past by various authors.

0	Terminal	VI	Abducens
I	Olfactory	VII	Facial
II	Optic	VIII	Acoustic
III	Oculomotor	IX	Glossopharyngeal
IV	Trochlear	X	Vagus
V	Trigeminal (ophthalmic, maxillary, mandibular)	XI	Accessory
		XII	Hypoglossal

GUIDE TO LEXICON ENTRIES

In the sections below, we describe and illustrate the skull as disarticulated bones to expose details that are hidden in an articulated skull. The technique is useful when dealing with isolated bones, as paleontologists frequently do.

The individual bones are treated alphabetically, and details of the bones' features are then also covered in alphabetical order. This method has obvious drawbacks, particularly in dealing with structures that are on more than one bone. We have provided numerous cross-references and an extensive index to help minimize confusion.

Twenty-two bones or bone groups are presented (the groups include the auditory ossicle and the tympanoperiotic). After the heading for each bone we list the figure(s) in which the bone is illustrated; when multiple figures are listed, the primary figure number is in bold type.

Each bone section begins with a general treatment of the bone, describing peculiarities of its evolution, relationship(s) to other groups of bones, and details of its embryological development. Below this general discussion, the lexicon terms—names for features of the bones—are presented alphabetically (letter by letter) as individual lexicon entries, which are then described in more detail.

Generally these terms are alphabetized by their English name which is then followed by the official Latin term (in parentheses) used in the *Nomina Anatomica* and *Nomina Anatomica Veterinaria*. Exceptions to this include, for example, such Latin terms as *foramen magnum*, which does not have a commonly used English equivalent, or *foramen ovale*, for which the Latin is more commonly used than the English "oval foramen." In these cases the Latin term is listed first without parentheses, and the English term, if known, is provided in parentheses. Also, if we discovered that the original spelling of the term used a diphthong such as æ or œ (which are no longer used), the original spelling is inserted in square brackets.

A symbol before each lexicon entry denotes the standing of the term, its presence or absence in *Tursiops*, and/or the presence or absence of illustrations in this work:

* indicates the feature is present in *Tursiops* and illustrated herein;
\+ indicates the feature is present in *Tursiops* but not illustrated;
– indicates the feature is absent in *Tursiops*;
= indicates the feature is is a synonym of another term.

Definitions are typically arranged as follows (although not every term has all of these constituents):

symbol **anatomical term / alternate term** [original spelling / additional information] (*Latin term*) (author citation) = synonym(s) (Figures)
General definition of the term in mammals.
Definition of the term in the highest taxonomic unit of cetaceans in which we know it occurs.
Cross references ("See . . . ").

In addition, a few nonosteological definitions occur in places where we felt further amplification of structures was essential. Finally, lexicon terms mentioned in other terms' entries are bold to facilitate cross-referencing.

In some cases an author citation is available only for a synonym rather than the entry's term name, thus the citation appears after the synonym in those lexicon entries.

Lexicon

BASIOCCIPITAL BONE

Os Basioccipitalis

FIGURES 3–5, 6B,D,E,G, 7, 28–29, 31A

The basioccipital bone is a midline ossification in the ventral posterior portion of cranium. It does not take part in the occipital condyles but may form a small part of the ventral margin of the *foramen magnum*. The basilar part (*pars basilaris*) of the occipital bone is equivalent to the basioccipital ossification (Schulte, 1917:374, 375, 379, 382, 383, 393, 394; McFarland et al., 1979:8; Schaller, 1992:16; Feneis, 1994:8). The basioccipital bone is also known as the basal process.

The basioccipital is bordered on the posterolateral surface by the exoccipitals; on the anterolateral surface by the parietal and sometimes the alisphenoid; and on the anterior surface by the basisphenoid.

– **basal process** = basioccipital crest

Luo and Gingerich (1999:29, 36, fig. 9, in the archaeocete *Pakicetus*).

See also **falcate process**.

* **basioccipital crest** (Figures 2, 7b–e)

The basioccipital crest in cetaceans is the ventrolateral part of the basioccipital in adults (Fraser and Purves, 1960:29, 38, 39, 41, 42, 44, 45, 47, 66–68, 70–72, 79, 80, 136). This part of the basioccipital is produced into crests. The basioccipital crest also has contributions from the exoccipital medial to the **hypoglossal notch**. The basioccipital crest tends to isolate the tympano–periotic region from the dorsal pharyngeal region and continue onto the pterygoids as the **pharyngeal crest** (Owen, 1866a:35, pl. 13: figs. 2–5'. Schulte (1917) also referred to the basioccipital crest as the otocranial flange (1917:383, 394, 400), the otocranial plate (1917:373), **otocranial process** of Owen (1917:374), the flange of the basioccipital (1917:379, 381), the flange of the occipital (1917:384), the occipital flange (1917:374) and the great flanges of the occipital (1917:374). Owen referred to the basioccipital crest as the otocranial plate (1866a:26, 39), otocranial plate of the **basisphenoid** (1866a:28, 30, 40), and the otocranial plate of the basioccipito-sphenoid (1866a:35). He did not refer to the basioccipital crest in his monograph on comparative anatomy (Owen, 1866b–1868). Barnes and McLeod (1984:13) used the term "lateral tuberosities of basioccipital." Other terms include lateral process of basioccipital (Kellogg, 1936), *processus alaris* or alar process (de Muizon, 1987:5), and **falcate process** (q.v.).

= **basioccipital process** (Fraser and Purves, 1960:13, 77) = basioccipital crest

Fraser and Purves (1960:13, 77) used basioccipital process as a lapsus calami for **basioccipital crest**.

= basioccipital ridge (Fraser and Purves, 1960:48) = basioccipital crest

Fraser and Purves (1960:48) used basioccipital ridge as a lapsus calami for **basioccipital crest**.

– *basion*

See "Exoccipital Bone."

= basisphenoidal otocranial plate (Owen, 1866a:28, 30, 35, 40, pl. 13: fig. 2 [5']) = basioccipital crest

Owen (1866a:35, pl. 13: fig. 2 [5']), in describing the holotype of *Kogia sima*, which has the basioccipital fused to the **basisphenoid**, uses basisphenoidal otocranial plate to refer to the **basioccipital crest**.

*** *clivus*** (Figure 7c)

The *clivus* is the sloping surface between the ***foramen magnum*** and the ***dorsum sellae*** (Gray, 1918:148; Dox et al., 1979:101; Schaller 1992:12.14; Feneis, 1994:8.6a, 30.5; not in Evans and Cristensen, 1979). The *clivus* consists of the dorsal median portion of the basioccipital and the **basisphenoid**, and supports the *pons* and the medulla oblongata.

Tursiops has a normal *clivus*.

*** endocranial sulcus / foramen for the vestibulocochlear nerve [new term]** (Figures 30, 31b)

All odontocetes have the **periotic bone** isolated from the skull and suspended in the **jugular foramen**. The vestibulocochlear nerve runs through a sulcus in the dorsolateral margin of the basioccipital bone. In individuals where the jugular foramen is closed with bony growth, that sulcus becomes a foramen.

See also **cranial hiatus** under "Exoccipital Bone."

= falcate process = basioccipital crest

Falcate process = alar process = **basioccipital crest** (de Muizon, 1987:5); = lateral descending process sensu Kellogg, 1936 (Luo, 1998:276); **falcate crest** (Luo and Gingerich, 1999:29, 36, 41); falcate process (e.g., Schulte, 1916:178; Howell, 1930; Thewissen and Hussain, 2000:142; Uhen, 2004:48, fig. 36; Ichishima and Kimura, 2005:658; Geisler, 2001:42 identified as a synonym for basioccipital crest).

Not to be confused with the falcate process (**falciform process**) of the squamosal bone.

See also **basal process**.

– groove for ventral petrosal sinus (*sulcus sinus petrosi ventralis*)

The groove for the **ventral petrosal sinus** lies on the dorsolateral surface of the basioccipital (Schaller, 1992:16). The groove houses the ventral petrosal sinus and forms the medial portion of the **petrobasilar canal** (q.v. under **periotic bone**) (Evans and Christensen, 1979:134, 794).

The ventral cranial venous sinuses (also called inferior sinuses) have been extremely modified in cetaceans. The ventral petrosal sinus does exist in phocoenids (Boenninghaus, 1904) and probably delphinids as well; but a groove for the ventral petrosal sinus has not been demonstrated in delphinids.

See also **cranial hiatus**, including comment on **foramen for the inferior** (or ventral) **petrosal sinus**.

*** impression for the medulla oblongata** (*impressio medullaris*) (Figure 7a,c)

The impression for the medulla oblongata lies on the dorsal surface of the basioccipital just anterior to the ***foramen magnum*** (Schaller, 1992:16).

The impression for the medulla oblongata in delphinids is a very shallow depression that lies on the dorsal surface of the basioccipital just anterior to the *foramen magnum*. It is more pronounced in older animals (USNM 501197).

= intercondyloid notch

See "Exoccipital Bone."

– laryngeal arcade (Fraser and Purves, 1960:47, 50)

The laryngeal arcade separates the pharyngeal region from the orbital and basicranial regions in cetaceans. The laryngeal arcade consists of the **basioccipital crests**, **pharyngeal crests**, and the free narial margin of the pterygoid bones. It has also been called the basioccipital arcade (Fraser and Purves, 1960:44).

*** muscular tubercle** (*tuberculum musculre*) (Figures 2, 7b)

The muscular tubercles are rough sagittally elongate areas on the basioccipital located medially to the tympanic bullae (Evans and Christensen, 1979:123; Schaller, 1992:16). These tubercles form the area of insertion of the *rectus capitis ventralis* muscle (Evans and Christensen, 1979:315).

The muscular tubercle in *Tursiops* varies between small and lacking.

= odontoid notch (Wible and Gaudin, 2004:143)

In the yellow armadillo (Wible and Gaudin, 2004:143), the odontoid notch is a U-shaped median ventral embayment in the basioccipital between the **occipital condyles**. **Intercondyloid notch** (see "Exoccipital Bone") is an alternative use (Wible, 2003:166; Wible and Gaudin, 2004:143).

See **intercondyloid notch** under "Exoccipital Bone."

– otocrane (Owen, 1866a:26, 29, 30, 35)

Owen used the term "otocrane" to refer to the space surrounding the tympanoperiotic. The otocrane is defined by Whitney (1889–1910:[vol. 5]4175) as "the bony structure of the middle and inner ear of a vertebrate, containing the essential parts of the organ of hearing."

= otocranial process = basioccipital crest

– peribullary sinus

The peribullary sinus is one of the basicranial air sinuses associated with the middle ear and is peculiar to cetaceans. The sinus arises at the posteroventral end of the **pterygoid sinus** and lies between the tympanoperiotic and the **basioccipital crest** (Fraser and Purves, 1960:1, 5, 8–10, 14, 53, 55, 62, 63, 65–74, 76, 77, 79, 80, 84, 100, 102, 136). Unlike some other parts of the pterygoid sinus system in the broad sense, the peribullary sinus generally lacks a distinct fossa. The sinus is limited dorsally by the dura mater. The sinus does not extend to the ventral surface of the tympanoperiotic, but a posterolateral extension of the peribullary sinus (posterolateral sinus) may extend to the **paroccipital process** to form the **posterolateral sinus fossa**.

Fraser and Purves (1960:5) stated:

> Camper (1777) gives reference to Joh. Dan Major as the discoverer of the peribullary sinus in the year 1672, quoting the latter's paper he states "one should know that the petrous bones are not tightly attached to the cranium, but are lying loosely between the flesh and the fat close to the base of the brain and the **occiput**, at the side of the head, in a sinus, which is formed by two processes which do not touch each other."

Dan Major thus antedated Tyson (1680) who, in his "Anatomy of a Porpess," made much the same observation.

* **peribullary sinus fossa** (Figures 7a,c,d, 30)

The **peribullary sinus** is one of the basicranial pterygoid air sinuses associated with the middle ear. In *Tursiops* the peribullary sinus fossa is entirely limited to the lateral surface of the **basioccipital crest**. The fossa begins anteriorly at the area immediately adjacent to the **ventral carotid foramen**. This portion of the fossa is delimited by the moderate crest around the ventral carotid foramen. The fossa then continues posteriorly and is bounded by the dorsal and ventral surface of the basioccipital crest and the **jugular notch**. Fraser and Purves referred to the peribullary sinus fossa as the peribullary space (1960:40, 43, 46–49, 52, 53, 55, 56, 58, 67).

* **pharyngeal crest [new term]** (Figures 2, 30)

The pharyngeal crests in delphinids are the paired crests on the ventral surface of the skull that separate the pharyngeal region from the auditory and optic regions. In *Tursiops* each crest is a continuous structure formed by the **basioccipital crest** posteriorly and the **medial lamina of the pterygoid** anteriorly. The crest ends anteriorly at the **Eustachian notch**, and posteriorly at the **jugular notch**. In some Cetacea, there is an obvious **medial exoccipital crest** posteriorly, medial to the jugular notch.

– **pharyngeal tubercle** (*tuberculum pharyngeum*)

The pharyngeal tubercle is a median triangular area on the ventral surface of the basioccipital just anterior to the **intercondyloid notch** (Evans and Christensen, 1979:123; Schaller, 1992:16). It forms the attachment for the pharyngeal raphe (Feneis, 1994:8).

In delphinids, with the hypertrophy of the palatopharyngeal sphincter (constrictor) (e.g., Fraser and Purves, 1960:20), the relationships in the pharyngeal region have changed. There does not appear to be a pharyngeal raphe or pharyngeal tubercle.

– **pituitary fossa** = hypophyseal fossa

See **basisphenoid**.

* **pontine impression** (*impressio pontina*) (Figure 7a,c)

The pontine impression lies on the anterodorsal (cranial) surface of the basioccipital (Evans and Christensen, 1979:122, 123; Schaller, 1992:16). The pontine impression holds the *pons*.

In *Tursiops* the pontine impression is a very shallow depression just posterior to the ***sella turcica***. It is more pronounced in older animals (USNM 501197).

– **third condyle** (*condylus tertius*)

Robineau (1968) described a third **occipital condyle** in a specimen of *Mesoplodon bidens*. Robson and Van Bree (1972) described the third condyle in specimens of *M. layardii* and *M. grayi*, Casinos and Fillela (1981) described a third condyle in *M. densirostris*, and Ross (1984:222) showed a third condyle to occur consistently in *M. densirostris*. Thus, the third condyle is at least a relatively common occurrence in ziphiids of the genus *Mesoplodon*. It has not been seen in any other cetacean species.

= trans-basicranial ridge

Anderson (1879:428) used trans-basicranial ridge in his table of detailed measurements of the skull of *Platanista*. This ridge is pronounced in a ventral view of an adult *Platanista*, lying just posterior to the spheno-occipital suture. The trans-basicranial ridge extends laterally and then posteriorly to terminate on the **basioccipital crest**. The ridge appears to be homologous with the **muscular tubercle** of the basioccipital, on which the *longus capitis* muscle inserts.

See **muscular tubercle**.

* **tympanic plate of the basioccipital bone** (Figure 7b,d,e)

The tympanic plate is used by Anderson to refer to a process of the basioccipital in *Platanista* (Anderson, 1879:428, 503, 505). The paired tympanic plates are terminated ventrolaterally by the **basioccipital crests**. The tympanic plates are medial to the **tympanic bulla**. This is not to be confused with the **tympanic plate of the bulla**.

The situation is similar in *Tursiops* and other delphinids.

ETHMOID BONE

Os Ethmoidale

FIGURES 1, 3, 4, 8

The ethmoid bone consists of four parts: an anterodorsal median perpendicular plate or perpendicular lamina (mesethmoid); two lateral masses (ectethmoids) covered by the external lamina (*lamina externa*); and a posteroventral midline cribriform plate (*lamina cribrosa*) to which the ethmoturbinates of the lateral masses attach. The mesethmoid forms the osseous nasal septum (Evans and Christensen, 1979:135). Vesalius (1543:23, 25) referred to it as the *octavum capitis os*. Eustachius and Lancisius (1714:112) referred to the *os cristatus* and *processus cristatus* in tabula XLVI, figs. XII–XVI, a reference that is confusing to us; we believe this reference may instead be to the *crista galli*.

In odontocetes, with the lack of development of the features associated with the sense of smell, all parts of the ethmoid are reduced. In *Tursiops* all four elements are present, but the *lamina externa* does not expand to support any development of turbinals. The ethmoid is bounded in the normal mammalian pattern by the vomer anteriorly and ventrally, the frontal dorsally and laterally, and the presphenoid and orbitosphenoid posteriorly. In odontocetes the olfactory nerve (Schulte, 1917:378) is absent and the cribriform plate is imperforate. Mysticetes, on the other hand, have a variably developed olfactory apparatus. A rudimentary *crista galli* is present in both fetuses and adults.

The cribriform plate is posteroventral to the mesethmoid and forms the most posterior element of the ethmoid bone. The cribriform plate forms a part of the anterior wall of the cranium in cetaceans. The cribriform plate is perforated by the olfactory nerve in other mammals and forms the basis for the olfactory epithelium.

De Beer (1937:442), in reference to the mesethmoid, stated, "Contrary to previous notions, it is now clear from Broom's (1926) investigations that the mesethmoid was evolved with the Mammalia, and only some and not all of the orders of the class possess this bone." De Beer then questions its presence in cetaceans. Schulte (1917:372, 384, 385, 387, 388, 390, 400) found it present in *Kogia*. See Kellogg (1926:7) for a discussion of situation of the ethmoid in extant taxa.

The ethmoid lies ventral and medial to the frontals; ventral to the nasals in adults; posterodorsal to the vomer; medial to the orbitosphenoid; anteromedial to the presphenoids; and anterior to the basisphenoid.

– ala cristae galli

The *alae cristae galli* in humans are anterolateral projections of the ***cristae galli*** that are received into corresponding depressions in the frontal bone (Gray, 1918:153).

In *Tursiops* and other odontocetes the *ala cristae galli* is not developed.

– cribriform foramina (*foramina laminae cribrosae*)

Cribriform foramina are formed in the **cribriform plate** for passage of the branches of the olfactory nerve (Evans and Christensen, 1979:137). Vesalius (1543:25) referred to the cribriform foramina as the *cribri instar foraminibus*. Eustachius and Lancisius (1714:112, tabula XLVI, figs. XII, XIV) mentioned the *processus papillares* in connection with the foramina for the olfactory nerve in the cribriform plate.

In *Tursiops* and other odontocetes the cribriform plate appears imperforate. Kellogg (1928:200, 201) said the cribriform plate is imperforate but illustrated a young *Tursiops* in which several foramina can be seen in the ethmoid in the region of the cribriform plate. Schulte (1917:385) interpreted such foramina as being for the nasal not olfactory nerve.

Cribriform foramina have been reported in *Physeter* (Flower, 1868:316), and *Berardius* (Flower, 1872:220). In some mysticetes, particularly balaenopterids where **turbinals** are still present, the cribriform foramina may occur.

*** cribriform plate** (*lamina cribrosa*) (Figure 8a–e)

The cribriform plate is the posterior of the two midline ethmoid ossifications. It is perforated by branches of the olfactory nerve (Gray, 1918:153; Evans and Christensen, 1979:137; McFarland et al., 1979:8; Schaller, 1992:28.29; Feneis, 1994:20.2). The cribriform plate is not to be confused with the *lamina cribrosa* of the sclera (Gray, 1918:1005; Feneis, 1994:354.34). Eustachius and Lancisius (1714:112) referred to it as the *cribriformia ossa*. Vesalius (1543:50) and Vesalius et al. (1998:131) referred to the cribriform plate of the ethmoid bone as the *hac sede in octavo capitis osse multa, sed exigua spectantur foramina, odorum and aeris inn inspirationibus ad cerebrum ingressus nomine, incisa*.

In *Tursiops* and other odontocetes the cribriform plate is well developed though imperforate. A vestigial ***crista galli*** is present on the cribriform plate in both the fetus and the adult.

* ***crista galli*** (Figures 8a,c–d, 28)

The *crista galli* is a small crest on the **cribriform plate** that divides the cribriform plate into right and left fossae for the olfactory lobes of the brain (Gray, 1918:153; Evans and Christensen, 1979:137; Schaller, 1992:28.30; Feneis, 1994:20.3). Vesalius (1543:25) referred to it as the *septum . . . quae cerebri processibus parantur*. It may be the element that Eustachius and Lancisius (1714:112) referred to as the *processus cristatus* (*cristati processus*). In humans it serves for the attachment of the *falx cerebri* (Gray, 1918:153).

In *Tursiops* and other odontocetes the *crista galli* is vestigial.

= dorsal lamina of the ethmoid = roof plate

– dorsal nasal concha (*concha nasalis dorsalis*) = nasoturbinate

The dorsal nasal concha arises dorsally from the posterior part of the **cribriform plate** as well as from the medial part of the **roof plate** (Evans and Christensen, 1979:138).

The dorsal nasal concha is an alternative name for the **nasoturbinate** bone.

In *Tursiops* and other extant odontocetes the **turbinals** are not developed.

*** ectethmoid** = lateral wings of mesethmoid (Figures 8a,c–d, 28)

The question of the presence of separate ectethmoid and **mesethmoid** ossifications in cetaceans is still open to debate. Rommel (1990:33) provided a concise summary of the problem, concluding that supposed ectethmoids could equally arise from frontals and/or from vomer. Schulte (1917:378) mentions the term "ectethmoid" in referring to *Kogia*. His usage of the term is consistent with ectethmoid being synonymous with lateral wings of mesethmoid. Schulte (1917:372, 378, 385) also uses the term "lateral ethmoid."

In referring to the lateral ethmoid, De Beer (1937:443) said, "Since it would seem that this bone has been independently evolved within the class Aves and has not been inherited directly from the fish it should not be called the lateral ethmoid. Perhaps the term 'ectethmoid' may be restricted to mean the ossification in birds, without increasing the nomenclature."

We shall use the term "ectethmoid" sensu Schulte (1917:378, 380, 385, 388), realizing the problems brought up by Rommel. Kellogg (1928:200, fig. 22) illustrated the ectethmoid in a young *Tursiops*.

– ectoturbinates (*ectoturbinalia*)

The ectoturbinates are a division of the **ethmoturbinates**.

The ectoturbinates are absent in *Tursiops* and other odontocetes.

See **ethmoidal labyrinth**.

– endoturbinates (*endoturbinalia*)

The endoturbinates are a division of the **ethmoturbinates**.

The endoturbinates are absent in *Tursiops* and other odontocetes.

See **ethmoidal labyrinth**.

– ethmoid air cells (*cellulae ethmoidales*)

The ethmoid air cells consist of many thin-walled cavities (**paranasal sinuses**) situated in the **ethmoidal labyrinth** and completed by the frontal, maxilla, lacrimal, sphenoidal, and palatine bones (Gray, 1918:998).

In *Tursiops* and other odontocetes the paranasal sinuses are not developed (Fraser and Purves, 1960:5, 75). Paranasal sinuses occur in some extinct cetaceans, as discussed under **frontal sinus** (“Frontal Bone”).

– **ethmoidal bulla** (*bulla ethmoidalis*)

The ethmoidal bulla in humans is caused by the bulging of the **ethmoid air cells** into the nasal cavity (Gray, 1918:995).

This feature is not present in *Tursiops* or other odontocetes because the ethmoid air cells are absent.

– **ethmoidal infundibulum** (*infundibulum ethmoidale*)

The ethmoidal infundibulum is a sinuous passage leading from the middle meatus of the nose to the anterior ethmoidal cells (Gray, 1918:156).

The ethmoidal cells are not developed in *Tursiops* and other odontocetes, so the ethmoidal infundibulum does not exist.

– **ethmoidal labyrinth** (*labyrinthus ethmoidalis*)

The ethmoidal labyrinth forms the principal portion of the lateral mass of the **cribriform plate**. It is composed of delicate bony scrolls or **ethmoturbinates**, which attach to the **external lamina of the ethmoid bone** by basal laminae and attach caudally to the cribriform plate (Evans and Christensen, 1979:137).

In *Tursiops* and other delphinids the ethmoidal labyrinths are not developed. There are structures in the ethmoid of *Platanista* and all the ziphiid genera that could be interpreted as ethmoturbinates. The presence of the olfactory nerves and ethmoturbinals in the mysticetes has been amply demonstrated (Flower, 1866:147; Edinger, 1955; Breathnach, 1960:192). An olfactory apparatus including **turbinals** and associated **paranasal sinuses** was present in archaeocetes (Edinger, 1955), and has been inferred for some archaic odontocetes (Fordyce, 2002). Buhl and Oelschläger (1988) have demonstrated the presence of an olfactory bulb in fetal *Phocoena*.

– **ethmoidal meatus** (*meatus ethmoidales*)

The ethmoidal meatus is that portion of the nasal passages that pass through the ethmoidal conchae or **turbinals** (Evans and Christensen, 1979:513).

In *Tursiops* and other odontocetes the turbinals are not developed and therefore the ethmoidal meatus is not considered as a separate element of the nasal passages.

– **ethmoidal process** (*processus ethmoidalis*)

The ethmoidal process is located on the middle portion of the inferior nasal concha. It ascends to join the **uncinate process** of the ethmoid bone.

In *Tursiops* and other odontocetes the **turbinals** are not developed.

– **ethmoturbinates** (*ethmoturbinalia*)

The ethmoturbinates are a series of bony scrolls attached to the **external lamina of the ethmoid bone.** Posteriorly the ethmoturbinates are attached to the **cribriform plate.** They form the contents of the **ethmoidal labyrinth** (Evans and Christensen, 1979:137).

In *Tursiops* and other extant odontocetes the **turbinals** are not developed in the normal mammalian manner, as discrete bony structures in adults.

See **ethmoidal labyrinth**.

* **external lamina of the ethmoid bone** (Figure 8b–e)

The external lamina of the ethmoid bone lies lateral to the **mesethmoid** and medial to the **orbitosphenoid.** In cetaceans the *lamina externa* does not expand to support any development of **turbinals**.

– **floor plate** = ventral lamina = transverse lamina (*lamina basalis*)

The **external lamina of the ethmoid bone** is divided into dorsal, lateral, and ventral parts. The ventral part is called the floor plate or *lamina orbitalis* (Evans and Christensen, 1979:137).

In *Tursiops* and other odontocetes the external lamina is not subdivided.

* **foramen for the nasal nerve** (Schulte, 1917:378, 385) (Figure 8b)

In the dog the nasociliary nerve (a branch of the ophthalmic nerve) runs anteriorly between the dorsal oblique and medial rectus muscles and enters the cranial cavity by means of the ventral ethmoid foramen (Evans and Christensen, 1979:914), becoming the ethmoidal nerve. The ethmoidal nerve then leaves the cranial cavity through an unnamed foramen in the dorsomedial aspect of the **cribriform plate** (Schaller, 1992:466.4, 7). The ethmoidal nerve contributes branches to the nasal conchae (internal nasal nerves; *ramus nasalis medialis*) and terminates in the external nasal nerves, which are distributed to the skin of the rostrum (Schaller, 1992:466.7).

We unsuccessfully examined Gray (1918), Sisson and Grossman (1953), Evans and Christensen (1979), Schaller (1992), and Feneis (1994) in hopes of finding a named foramen.

Schulte (1917:378, 384, 385) has interpreted the foramina in the ethmoid of *Kogia breviceps* as possibly being for the transmission of the “nasal” nerve. Gray (1918:888) gives the nasal nerve as a synonym for the nasociliary nerve, and we presume that Schulte used it in this sense. The terminal branches of the nasociliary nerve have yet to be studied in sufficient detail in delphinids to permit us to say whether they perforate the ethmoid. In an illustration, we labeled a foramen that appeared in the ethmoid of the newborn animal (USNM 504560) as “Foramen for the nasal nerve?”. This foramen did not appear in any of the adults or calves that we used in this lexicon.

For the fossil odontocete *Squalodon*, Kellogg (1923:46, 47) identified paired foramina at the posterior end of the mesorostral groove as likely for nasal branches of the ophthalmic nerve.

– **fundus of the nasal fossa**

The fundus of the **nasal fossa** is the area occupied by the **ethmoturbinates** (Evans and Christensen, 1979:159).

The fundus of the nasal fossa is absent in *Tursiops* and other odontocetes.

See **ethmoidal labyrinth**.

– **lacrimal process** (*processus lacrimalis*)

The lacrimal process is located on the middle portion of the inferior nasal concha. It articulates, by its apex, with the descending process of the lacrimal bone (Gray, 1918:169).

In *Tursiops* and other odontocetes the **turbinals** are not developed.

– maxillary fossa of the ethmoid bone

The maxillary fossa of the ethmoid bone is a depressed area of the orbital lamina of the ethmoid bone that forms the medial wall of the **maxillary sinus** (Evans and Christensen, 1979:137). The posterolateral portion of the maxillary fossa consists of the anterior part of the **nasal surface of the palatine** bone (Evans and Christensen, 1979:144).

The maxillary fossa of the ethmoid bone is not developed in *Tursiops* or other living cetaceans. It might be present in extinct forms in which **paranasal sinuses** are developed.

Not to be confused with **maxillary fossa** (or **facial fossa**) of the maxilla (q.v.).

– maxillary process of the ethmoid bone (*processus maxillaris*)

The maxillary process of the ethmoid bone is located on the middle portion of the inferior nasal concha. It articulates with the maxilla and forms a part of the medial wall of the **maxillary sinus** (Gray, 1918:169).

In *Tursiops* and other odontocetes the **turbinals** are not developed.

* **mesethmoid** (Figures 8a,c–e, 28, 31a)

The mesethmoid is the most anterior/dorsal midline element of the ethmoid ossification. It forms the ventral portion of the osseous **nasal septum** in most mammals, the dorsal portion being formed by the frontal and nasal bones (Evans and Christensen, 1979:135). Posteriorly the mesethmoid fuses with the **cribriform plate**; Schulte (1917:372, 378, 380, 381, 384–387) used it in this context in *Kogia*.

In a newborn *Tursiops* it has begun developing anteriorly into the mesorostral groove of the vomer, forming a posterior termination of that groove. In adult *Tursiops* it is prolonged dorsally to contact the nasals. The mesethmoid is attached to the **mesorostral cartilage**, which is homologous with the **cartilaginous nasal septum**.

Owen (1866a:27, 30, 37, 38) referred to the mesethmoid as the prefrontal. We use a different concept of the prefrontal (q.v. under frontal bone). Anderson (1879:507) referred to the central portion of the mesethmoid, from which the mesorostral cartilage arises as the central plate of the mesethmoid.

= mesethmoid cartilage

See **mesorostral cartilage**.

* **mesethmoid ridge** (Figure 8a,e)

The mesethmoid ridge in *Platanista* is the ridge of the **mesethmoid** that protrudes anteriorly into the **mesorostral canal** of the vomer. The **mesethmoid cartilage** attaches to the mesethmoid ridge (Anderson, 1879:522).

In *Tursiops* and other delphinids the mesethmoid ridge is low and indistinct.

* **mesorostral cartilage** = mesethmoid cartilage = septal cartilage (Figure 8a,e)

The mesorostral cartilage, **mesethmoid cartilage**, or **septal cartilage** is an anterior extension of the **nasal septum** (Evans and Christensen, 1979:135).

In *Tursiops* and most cetaceans the mesorostral cartilage is a very prominent cartilage that fills the mesorostral groove, which is formed by the vomer and premaxillae. Anderson referred to the mesorostral cartilage as the cartilaginous vomer (1879:527) and the septal cartilage (1879:450, 451, 507); Schulte (1917:380, 384, 385) referred to this structure as the septal cartilage.

– middle nasal concha (*concha nasalis media*)

The middle nasal concha in humans is the ventral part of the labyrinth or lateral mass of the ethmoid (Gray, 1918:156).

In *Tursiops* and other odontocetes the **turbinals** are not developed.

* **nasal fossa** (Schulte, 1917:378, 385–389, 394) (Figure 1)

The nasal cavity in mammals is composed of two nasal fossae (Evans and Christensen, 1979:158; not in *Nomina Anatomica*, *Nomina Anatomica Veterinaria*; Feneis, 1994; Schaller, 1992) containing the nasoturbinates and separated by the **nasal septum**.

The odontocetes have reduced many of the elements of the nasal cavity in their transition to an aquatic life, including the entire loss of the olfactory system. The nasal fossae, sensu Evans and Christensen, in odontocetes are reduced to the portion of the nasal passage that lies adjacent to the nasal septum.

The nasal fossae were also known as the olfactory chambers (Flower, 1885:124).

– nasoturbinal [nasoturbinate] (*concha nasalis dorsalis*)

The nasoturbinal (nasoturbinate; **dorsal nasal concha** of veterinary anatomy) is one of several scroll-like bones that arise dorsally from the posterior part of the **cribriform plate** as well as from the medial part of the **roof plate** (Evans and Christensen, 1979:138). Wible and Gaudin (2004:120) described the nasoturbinal in relation to the ventral surface of the nasal in the armadillo. Uhen (2004:46) described **turbinals** in the archaeocete *Dorudon atrox*.

In *Tursiops* and other extant odontocetes the turbinals are not developed in the normal mammalian manner, as discrete bony structures in adults.

– olfactory foramina (Owen, 1866a:30)

The olfactory foramina transmit the olfactory nerves through the **cribriform plate**.

Odontocetes lack olfactory nerves, and olfactory foramina are not positively identifiable in *Tursiops*.

= orbitosphenoid (Figure 8a–e)

See “Sphenoid Bone.”

= optic canal (Figure 8a–e)

See “Frontal Bone,” “Sphenoid Bone.”

= perpendicular plate (*lamina perpendicularis*)

The perpendicular plate is an anteroventral extension of the **mesethmoid** that divides the anterior portion of the nasal passages into right and left halves (Gray, 1918:154). It forms the base for the **septal cartilage**.

In *Tursiops* and other odontocetes the perpendicular plate is weakly developed as the **mesethmoid ridge**.

See **mesethmoid ridge**.

= presphenoid (Figure 8a,b,e)

See "Sphenoid Bone."

– roof plate (*lamina tectoria*)

The **external lamina of the ethmoid bone** is divided into dorsal, lateral, and ventral parts. The dorsal part is called the roof plate or *lamina orbitalis* (Evans and Christensen, 1979:137).

In *Tursiops* and other odontocetes the external lamina is not obviously subdivided.

– semilunar hiatus (*hiatus semilunaris*)

The semilunar hiatus is a curved cleft caused by the bulging of the **ethmoidal bulla** into the nasal cavity (Gray, 1918:995).

The ethmoidal bulla is not present in *Tursiops* or other odontocetes.

= septal cartilage

See **mesorostral cartilage**.

– side plate (*lamina orbitalis*)

The **external lamina of the ethmoid bone** is divided into dorsal, lateral, and ventral parts. The lateral part is called the side plate or *lamina orbitalis* (Evans and Christensen, 1979:137).

In *Tursiops* and other odontocetes the external lamina is not subdivided, so side plates are not considered as separate elements.

– supreme nasal concha (*concha nasalis suprema*)

The supreme nasal concha is the most dorsal of the rudimentary nasal conchae in humans (Feneis, 1994:20). It is also known as the superior nasal concha (Gray, 1918:156).

No nasal conchae are present in delphinids.

– terminal nerve foramina

The terminal nerve (cranial nerve 0) is difficult to identify in most mammals, although it appears to be a primitive vertebrate character. In humans it unites the anterior perforated substance (*substantia perforata anterior*) in the brain with the olfactory region of the nasal cavity (Feneis, 1994:312.2, 352.27). The function of the terminal nerve in humans is unknown but is presumed to be autonomic (Feneis, 1994:352.27).

The terminal nerve in the dog is grouped, along with the vomeronasal nerve, with the olfactory nerve and is not given separate cranial nerve status (Evans and Christensen, 1979:910; Schaller, 1992:464.5). The terminal nerve is formed by bundles that arise from the vomeronasal nerves as they terminate on the accessory olfactory bulb. They unite to form a trunk that runs caudoventrally on the medial surface of the olfactory tract and "appears to enter the brain substance 1 or 2 cm caudal to the olfactory bulb" (Evans and Christensen, 1979:910). Sisson (1910:440, 772) and Gray (1918:71, 996) have paragraphs on the vomeronasal organ but did not mention the terminal nerve. Flower (1885) and de Beer (1937) did not mention either the vomeronasal organ or the terminal nerve.

Ridgway et al. (1987) dissected the terminal nerve in 14 odontocete cetaceans (13 delphinids, including *Tursiops* and a *Kogia*). They found that fibers of the terminal nerve issue from the brain just anterior to the optic chiasma and leave the cranial cavity through several minute foramina in the **cribriform plate**. They were unable to trace them outside the cranial cavity.

= turbinals

See **ethmoidal labyrinth.**

– uncinate notch (*incisura uncinata*)

The uncinate notch is located posterodorsal to the **uncinate process** of the ethmoid bone in the meatus between the first two **endoturbinates** (Evans and Christensen, 1979:137).

In *Tursiops* and other odontocetes the **turbinals** are not developed, so the uncinate notch does not exist.

– uncinate process (*processus uncinatus*)

The uncinate process is a part of the first **endoturbinate** and of the orbital lamina (lateral lamina) (Evans and Christensen, 1979:137; Feneis, 1994:20.16). This feature of the ethmoid should not be confused with the **uncinate process** (**accessory ossicle**) of the **tympanic bulla** (q.v.).

In *Tursiops* and other odontocetes the **turbinals** are not developed, so the uncinate process does not exist.

– ventral nasal concha (*os conchae nasalis ventralis*)

In most mammals the ventral nasal conchae (**maxilloturbinate**) are a series of scrolls that occupy the anterior part of the nasal cavity and are attached to the *crista conchalis* on the medial surface of the maxilla (Evans and Christensen, 1979: 512).

In *Tursiops* and other odontocetes the **turbinals** are not developed, so the ventral nasal concha does not exist.

EXOCCIPITAL BONE

Os Exoccipitalis

FIGURES 1, 3–5, 6B,C,E, 9, 28,29, 31A

The exoccipitals form part of the posterolateral wall of the cranium. They are paired ossifications that form the occipital condyles on their medial aspects. The exoccipitals are also known as the lateral processes (*partes laterales*) of the occipitals.

The exoccipitals are bounded by the supraoccipitals dorsally, the parietals anterolaterally, the squamosals anteriorly, and the basioccipital anteroventrally.

– anterior basi-occipital angle (Anderson, 1879:502)

Anderson (1879:502), in his description of the skull of *Platanista* made this statement:

> The notch in the skull is converted into a foramen.
> The transverse ridge terminates above the inner border
> of the **paroccipital process** on a line with the anterior
> basi-occipital angle of the bone [exoccipital]; the
> whole of the paroccipital process below that level is
> outside and deeply concave, especially at its lower
> margin, where a distinct pit is formed.

This is the only section in which Anderson used the term, and from this we are unable to make any reliable reference to the anterior basi-occipital angle.

= anterior condyloid foramen (Anderson, 1879:503) = hypoglossal foramen (Gray, 1918:131)

* ***basion*** (Figure 5)

The *basion* is the craniometric point that is located in the middle of the ventral margin of the ***foramen magnum***. The ventral border of the *foramen magnum* in delphinids consists entirely of exoccipitals.

– bullar process of the exoccipital bone (Luo and Gingerich, 1999:29, 41)

Luo and Gingerich (1999:29, 41) described the bullar process of the exoccipital bone in some archaeocetes. The process articulates with the **medial prominence** of the **tympanic bulla**. Luo and Gingerich (1999) also used the apparently synonymous terms "**exoccipital protuberance**" and "**exoccipital contact**." Luo and Gingerich (1999:41) stated that the bullar process of the exoccipital bone is separated by the **jugular notch** from the posterior part of the **basioccipital crest** (basioccipital **falcate process**, in their terminology). However, judging from Luo and Gingerich (1999: fig. 18b), the jugular notch lies immediately posterolateral to the bullar process of the exoccipital bone. The bullar process of the exoccipital bone should not be confused with features of the mammalian tympanic bulla or **periotic bone / petrosal** (e.g., Novaceck, 1986:52; Wahlert, 2000: fig. 1).

In *Tursiops* the **bulla** does not contact the exoccipital and there is no bullar process of the exoccipital bone.

* **cerebellar juga** (Figures 9d, 31a)

The cerebellar juga consists of all the bony internal elevations formed by the sulci of the cerebellum (Evans and Christensen, 1979:157). "**Cerebral juga**" is sometimes used as a general term for all the bony internal elevations formed by the sulci of the brain.

The cerebellar juga are the same in cetaceans as they are in any other mammals.

* **concavity for lobes of the cerebellum** (Figure 9a)

In all mammals there is a concavity on the internal surface of the exoccipital that houses the lobes of the cerebellum.

In *Tursiops* and other odontocetes it lies just lateral and slightly ventral to the ***foramen magnum***.

– condylar canal (*canalis condylaris*)

The condylar canal lies in the **dorsal condyloid fossa**. The condylar canal contains the *sinus condylaris* that communicates with the **transverse sinus** (Evans and Christensen, 1979:122; Schaller, 1992:16.19; Feneis, 1994:8.15). Gray (1918:131) referred to it as the condyloid canal. Vesalius (1543:53; Vesalius et al., 1998:131) referred to the condylar canal as the *non insigniter amplum foramen, quod ab externa calvariae sede, x posteriori nimirum sede capitis occipitii ossis*.

The development of the condylar canal is questionable in *Tursiops*. There are a number of "nutrient foramina" that open into the **condylar foramen** externally and into the **sulcus for the transverse sinus** internally. These may be **dorsal condyloid foramina** (q.v.) in the sense of Wible and Gaudin (2004). It is extremely difficult to probe these and establish whether or not they communicate with one another.

= condylar foramen

See **condyloid foramen**.

= condyloid foramen = condylar foramen = hypoglossal foramen (Flower, 1885:210; Flower and Lydekker, 1891:38, fig. 8; McFarland et al., 1979:8)

Anderson (1879:451, fig. 15) appeared to use this term to refer to the ***foramen magnum***.

See also **hypoglossal foramen**.

= condyloid fossa

See **dorsal condyloid fossa, ventral condyloid fossa**.

* **cranial hiatus** = jugular foramen in part, or posterior lacerate foramen (Figure 31b)

In odontocetes the tympanoperiotic does not protrude into the cranial cavity but is displaced ventrolaterally so that the periotic no longer contributes to a continuous wall of the cranial cavity and is physically separated from dorsally and/or medially adjacent bones. Fraser and Purves (1960) introduced the term "cranial hiatus" for the resulting space between the dorsal or cerebral part of the periotic and the adjacent exoccipital, basioccipital, **alisphenoid**, parietal, and squamosal. Many later authors have referred to the structure but, probably because Fraser and Purves (1960) did not explicitly define the cranial hiatus, concepts of the cranial hiatus vary. To help define the cranial hiatus, consider the statements of Fraser and Purves (1960).

Fraser and Purves (1960:30) commented: "the paths of the [cranial] nerves [on the basicranium] are restricted to three exits, that associated with the **optic infundibulum**, that of the infundibulum of the ***foramen ovale*** and that of the 'cranial hiatus' in the vicinity of the periotic". And about *Grampus*, they commented that "the cranial hiatus is obliterated by secondary bone, except for the foramina of the auditory nerve and the *foramen lacerum posterius*" (Fraser and Purves, 1960:56). We interpret these statements to mean that the cranial hiatus is the confluent path for cranial nerves VII to IX and associated vessels not otherwise in named foramina or canals.

Fraser and Purves (1960:34) commented: "The Mysticeti differ from the Odontoceti in that the tympano-periotic is not completely extruded from the cranial wall—thus there is no cranial hiatus." We interpret this to mean that the cranial hiatus is not developed in Cetacea in which the periotic contributes to the cranial wall in the broad sense.

Fraser and Purves (1960:40) commented, for ziphiids: "In very young specimens there is a cranial hiatus dorsal to the periotic but this is soon occluded by extensions of the bones adjacent to the hiatus." For the sperm whale *Physeter*, they commented (1960:43): "The tympano-periotic bones are excluded from the wall of the cranium and in the specimen examined, no trace of the cranial hiatus remains," and for the porpoise *Phocoena* they said (1960:49): "The cranial hiatus, dorsal to the ear bones is partly filled by osteosclerotic extensions of the basioccipital . . . and parietal." We interpret this to mean that the cranial hiatus may become closed during ontogeny to the extent that it is eliminated.

Finally, Fraser and Purves (1960:63, 64) commented for *Inia* that "the **peribullary sinus** completely surrounds this bone [tympanoperiotic]. As in the previously described species [*Pontoporia*], the centre of the mass represents the air space between the periotic and the skull and coincides with the position of the cranial hiatus." We interpret this to mean that the cranial hiatus is functionally associated with the peribullary sinus.

The term "tympano-periotic hiatus" (Fraser and Purves, 1960:133) may be a lapsus calami.

"Cranial hiatus" has been used since with various meanings. Here, the cranial hiatus is defined as the confluent opening for the **posterior lacerate foramen**, **jugular foramen**, and the **internal acoustic meatus**. The cranial hiatus comprises the enlarged **basicapsular fissure** plus adjacent foramina associated with nerves, with the petrosal sinuses, with the posterior **lacerate foramen**, and with the jugular foramen. In the young animal and in some fossil species, the *foramen ovale* may be confluent with the cranial hiatus.

Tursiops has a cranial hiatus that may become constricted in older specimens by bone outgrowths, producing sulci or endocranial foramina for nerves and vessels, and resulting in distinct endocranial **foramina for the vestibulocochlear nerve** and facial nerve, and posterior lacerate and jugular foramina. The cranial hiatus occurs in most living Cetacea.

Earlier Owen referred to the cranial hiatus as the otocranial vacuity (1866a:30) or the otocranial cavity (1866a:40). Flower (1867:94) gave a lucid description but did not use a formal name. Schulte (1917:374) used the terms **secondary internal auditory canal** and **secondary internal auditory meatus** without definition in a context that suggests cranial hiatus. The cranial hiatus includes the **petrosoparoccipital fissure** of Luo and Gingerich (1999: tbl. 6, #34b), the basicapsular fissure (sensu Luo and Gingerich, 1999), and the basicapsular fenestra (or **basicochlear fissure**) (sensu MacPhee, 1981:4948) of other mammals. Luo and Gingerich (1999:41) used the terms **tympanic cavity** and peribullar cavity apparently to refer to the cranial hiatus. Barnes (1985:3) indicated that the *foramen ovale* might be separate from the cranial hiatus, and (Barnes, 1990:21, #19; 22, #23) indicated that the cranial hiatus is formed by merging of the middle and posterior lacerate foramina. Heyning (1989a:51, character 24) stated that the margins of the cranial hiatus are formed from the squamosal, parietal, and **occipital bones**. Yamagiwa et al. (1999) identified the cranial hiatus in *Grampus* as the "***foramen lacerum***" (for nerves IX, X, XI, and internal jugular vein), not including the exit for the vestibulocochlear and facial nerves. Geisler and Sanders (2003:87) stated that the cranial hiatus is the basicapsular fenestra. Current use suggests that the **piriform fenestra** (q.v.) is also part of the cranial hiatus. Judging from the situation in other mammals (Wible and Gaudin, 2004:131), the cranial hiatus may include the equivalent of the mammalian **foramen for the inferior petrosal sinus**.

See also **jugular foramen** and **endocranial sulcus**.

– **dorsal condyloid foramen** (Wible and Gaudin, 2004:151)

Wible and Gaudin (2004:151) named the dorsal condyloid foramina in the yellow armadillo as the small nutrient foramina that open into the **dorsal condyloid fossa**.

Adult specimens of *Tursiops* have variably developed dorsal condyloid foramina in the dorsal condyloid fossa.

See also **condyloid canal**.

* **dorsal condyloid fossa** (*fossa condylaris dorsalis*) (Figures 5, 9c,e)

The dorsal condyloid fossa lies immediately dorsal to the **occipital condyles** on the exoccipital bone. The fossa provides room for movement of the atlas. The **condylar foramen** is perforated by the condyloid canal, through which an emissary vein passes from the **transverse sinus** (Evans and Christensen, 1979:122). The dorsal condyloid fossa is present and is better developed than the **ventral condyloid fossa** in all cetaceans.

= **exoccipital contact of the exoccipital** (Luo and Gingerich, 1999)

See **bullar process of the exoccipital bone**.

– **exoccipital plate** (Owen, 1866a:35)

Owen uses exoccipital plate (1866a:35) to refer to the contribution of the exoccipital to the **circumnarial basin** (Owen, 1866a:44) or **supracranial basin** (Flower, 1868:314) in *Physeter*.

The exoccipital plate is not developed in delphinids.

= **exoccipital protuberance** (Luo and Gingerich, 1999)

See **bullar process of the exoccipital bone**.

= **falcate crest of the exoccipital** (Luo and Gingerich, 1999:41) = medial occipital crest

Luo and Gingerich (1999:41) mentioned the falcate crest for archaeocetes and archaic odontocetes, but did not define it. Uhen (2004:48) noted an exoccipital contribution to the **falcate process** in archaeocetes.

See **medial exoccipital crest**, **pharyngeal crest**.

* ***foramen magnum*** (Figures 5, 9d,e, 31a)

The *foramen magnum* is bounded by the posteromedial margins of the basioccipital, exoccipital, and **supraoccipital** bones (Gray, 1918:129, 132, 192; Evans and Christensen, 1979:121, 123; Schaller, 1992:16.3; Feneis, 1994:8.3). It transmits the spinal cord. Vesalius (1543:22) referred to the *foramen magnum* as merely the "*foramen*," but in another section he referred to the *foramen magnum* as the *foramen unicum, caeterisque omnibus facile maximum, quod occiptis ossi insinuatur, gratia dorsalis medullae ex cerebro originem ducentis* (Vesalius, 1543:53; Vesalius et al., 1998:131).

The *foramen magnum* is well developed in cetaceans where, in addition to the spinal cord, it transmits branches of the vertebral vascular plexus. That plexus forms the main blood supply to the brain. The *foramen magnum* has also been called the **occipital foramen** (Anderson, 1879:428; Owen, 1866a:34; Schulte, 1917:365).

* **hypoglossal canal** (*canalis hypoglossi*) (*canalis n. hypoglossi*) (Figures 9a,d, 28, 31b)

The hypoglossal canal runs in an anteroventral direction from the floor of the **cerebellar fossa** in the cranial cavity to the **hypoglossal foramen** (Evans and Christensen, 1979:122). The internal opening is not named (Gray, 1918:131; Schaller, 1992:16.18; Feneis, 1994:8.16). Vesalius (1543:53; Vesalius et al., 1998:131) referred to the hypoglossal canal as the *foramen in occipitii osse gratia ervi septimi paris nervorum ceebri incisum*.

In odontocetes the hypoglossal canal is well developed ventrally and somewhat anterolaterally (Schulte, 1917:375).

– **hypoglossal depression**

The hypoglossal depression is a small oval depression into which opens one or more **hypoglossal foramina** in the rodent *Exmus* (see Wible et al., 2005:118).

Tursiops lacks a hypoglossal depression.

* **hypoglossal foramen** (Figure 9b)

The hypoglossal foramen opens on a ridge of bone anterior to the **ventral condyloid fossa.** This foramen forms the opening of the **hypoglossal canal,** which transmits the hypoglossal nerve (Schulte, 1917:379, 401; Evans and Christensen, 1979:122). McDowell (1958:123, 125) cautioned that the hypoglossal foramen should not be confused with the **condyloid foramen** (see also Wible and Gaudin, 2004:175).

In *Tursiops* the hypoglossal foramen is situated on a ridge of bone between the posterior end of the **basioccipital crest** and the **paroccipital process** and opens into the **jugular notch.**

– **hypoglossal fossa**

Novacek (1986:65) said: "Usually the [paroccipital] process is weak where the hypoglossal fossa of the basioccipital is crowded by the large mastoid process and the ventral **occipital condyle.**" We have not found a clear definition for the hypoglossal fossa, and thus cannot identify it in *Tursiops.*

= **hypoglossal notch** = jugular notch

The hypoglossal notch is equivalent to the jugular notch. This term comes from Kernan (1918:384), where he used it for the notch that lies between the **paroccipital process** and the **otocranial process.**

* **intercondyloid notch** (*incisura intercondyloidae*) (Figures 2, 5, 28)

The intercondyloid notch lies between the ventral portions of the **occipital condyles.** It forms the ventral border of the ***foramen magnum*** and consists, in most mammals, of the posteromedial portion of the basioccipital bones (Evans and Christensen, 1979:123). **Odontoid notch** (see under "Basioccipital Bone") is an alternative use (Wible, 2003:166).

The intercondyloid notch is well developed in *Tursiops* and all other cetaceans. The intercondyloid notch is formed by the exoccipital ossifications in *Tursiops.* The exoccipitals fuse posteromedially, preventing the basioccipital from forming part of the margin of the *foramen magnum.*

– **intrajugular process of the exoccipital bone** (*processus intrajugularis*)

The intrajugular process of the exoccipital bone is a spicule of bone that may project into the posterior part of the **jugular foramen** (**jugular notch**) (Gray, 1918:131; Schaller, 1992:16.21; Feneis, 1994:8.21; not in Evans and Christensen, 1979).

The intrajugular process of the exoccipital bone does not appear to exist in *Tursiops.*

– **intraosseous passage**

There is an intraosseous passage between the condyloid canal and the **hypoglossal canal** in dogs (Evans and Christensen, 1979:122). This canal does not appear to be named.

The existence of the intraosseous passage in cetaceans is not demonstrated.

= **jugal notch** [paroccipital notch]

This appears to be a printing error in Rommel (1990). Other authors have referred to it as the jugular notch.

* **jugular foramen** (*foramen jugulare*) [part of the posterior lacerate foramen] (Figures 6b, 30, 31b)

The jugular foramen in the dog is a large aperture in the petro-occipital fissure (Evans and Christensen, 1979:156; Schaller, 1992:12.1). In humans it is subdivided into three compartments (Gray, 1918:181; Feneis, 1994:30.18). The anterior compartment transmits the **ventral petrosal sinus**; the intermediate compartment transmits the glossopharyngeal nerve, vagus nerve, and accessory nerve; the posterior compartment transmits the **transverse sinus** and some meningeal branches from the occipital artery and ascending pharyngeal artery (Gray, 1918:181). McDowell (1958:124) noted that, in some mammals, the **posterior lacerate foramen** (for nerves IX, X, and XI) might also transmit the jugular vein, so that jugular foramen and *foramen lacerum posterius* could be used interchangeably; see also discussion by Wible (2003:176). McDowell (1958) cited Story (1951) as differentiating the nervous *foramen lacerum posterius* from the venous jugular foramen. Vesalius (1543:53; Vesalius et al., 1998:131) referred to the jugular foramen as the *foramen occipitis ossi and temporis ossi commune, ac sexto pari nervorum cerebri, and maiori internae jugularis venae ramo, minoribus soporalis arteriae soboli exculptu.*

In odontocetes the jugular foramen is inferred to be the generally undifferentiated most-posterior part of the **cranial hiatus.** The jugular foramen is normally marked by a sulcus, presumably for the jugular vein, that runs vertically up the face of the exoccipital from the jugular or **hypoglossal notch.** In Cetacea, as in land mammals, the terms jugular foramen and posterior **lacerate foramen** (*foramen lacerum posterius,* q.v.) are commonly interchanged (e.g., McFarland et al., 1979:10). Odontocetes in which the cranium is extremely heavily ossified, with bony occlusion of the cranial hiatus, may have a more-anteriorly placed posterior lacerate foramen for nerves IX, X, and XI that is separate from a distinct more-posterior jugular foramen; we recommend that "jugular foramen" be used only when the bony path for the jugular vein is separate from the posterior lacerate foramen.

= **jugular incisure** = jugular notch

See Schulte, 1917:375 for *Kogia*; Melnikov, 1997:37, for fetal *Physeter.*

* **jugular notch** (*incisura jugularis*) (Figures 2, 9a,b,d,e, 28)

The jugular notch forms the posterior or exoccipital portion of the **jugular foramen** (Gray, 1918:131; Schaller, 1992:12.1, 16.20, 22.26). It lies just medial to the petrous margin of the exoccipital. In delphinids the jugular notch is well developed between the **paroccipital process** and the **basioccipital crest.** The jugular notch is the feature referred to as the **paroccipital notch** (Fraser and Purves, 1960:15, 29, 39) and may be the feature referred to as the paroccipital fissure (Fraser and Purves, 1960:13). The jugular notch has also been referred to as the **jugular incisure** (Schulte, 1917:375; Melnikov, 1997:37).

= **jugular process** (*processus jugularis*) = paroccipital process

For a discussion of the equivalence of the mammalian paroccipital process and human jugular process, see Gray, 1918:131, fig. 129; McDowell, 1958:125, 126; and discussion below under

paroccipital process. Wible et al. (2005:110, 111) noted confusion in the use of the term "paroccipital process."

See also **paracondylar process.**

– jugular tubercle (*tuberculum jugulare*)

The jugular tubercle is an oval eminence that overlies the **hypoglossal canal** in the cranial cavity in humans. It is sometimes crossed by an oblique groove for the glossopharyngeal nerve, vagus nerve, and accessory nerve (Gray, 1918:131).

The jugular tubercle does not appear to exist in *Tursiops*.

= jugulo-acoustic canal (Schulte, 1917:379, 384, 399) = jugular foramen

= lateral occipital fontanelle = mastoid fontanelle (Kernan, 1918:384)

– mastoid fontanelle

The mastoid fontanelles occur at the juncture of the parietal, squamosal, and exoccipital centers of ossification (Gray, 1918:197).

The mastoid fontanelles are closed by the time of birth in *Tursiops*. That area of the skull is one of the most heavily ossified areas in delphinids.

– mastoid margin of the exoccipital (*margo mastoideus*)

The mastoid margin of the exoccipital is that portion of the exoccipital that abuts the mastoid process of the temporal (Sisson and Grossman 1953:48; Schaller, 1992:16.23; Feneis, 1994:8.9).

The **posterior process of the tympanic bulla** does not contact the rest of the skull in *Tursiops* but is closely approached by the mastoid margin of the exoccipitals.

*** medial exoccipital crest [new term]** (Figure 9b,e)

The medial exoccipital crest is the posterior part of the **pharyngeal crest** formed by the exoccipital medial to the **jugular notch** in archaic fossil Cetacea and some living species. Because an exoccipital component is not apparent, the medial exoccipital crest is not distinct in adult *Tursiops*.

See **basioccipital crest** for "falcate crest" and other synonyms; see also **pharyngeal crest.**

– occipital bone (*os occipitale*) (McFarland et al., 1979:10)

The bone forming the base and posterior parts of the skull is sometimes referred to as the occipital bone (McFarland et al., 1979:10). It is composed of separate ossification centers known as the basioccipital, exoccipital, and **supraoccipital**, under which heading we discuss it. Schulte (1917:370), in describing *Kogia*, referred to the supraoccipital and parietal as the "occipital complex."

*** occipital condyle** (*condylus occipitalis*) (Figures 5, 9b,c, 28, 31a)

The occipital condyles are a pair of rounded structures located on the posteromedial ends of the exoccipital bones. They form an articular surface for the first vertebra (atlas) (Gray, 1918:131; Evans and Christensen, 1979:122, 151; Schaller, 1992:16.13; Feneis, 1994:8.14). Vesalius (1543:22, 23) referred to the occipital condyles as *capita occipitii ossis*.

The occipital condyles are well developed in all cetaceans (Schulte, 1917:365, 370).

– occipital fontanelle

See "Interparietal Bone."

= occipital foramen = *foramen magnum* (Anderson, 1879:428; Owen, 1866a:34; Schulte, 1917:365)

– occipitomastoid suture (*sutura occipitomastoidea*)

The occipitomastoid suture lies between the occipital and the mastoid process of the temporal (Schaller, 1992:76.7; Evans and Christensen, 1979:123; Feneis, 1994:54.5; Gray, 1918:183). In some mammals (horse, dog) it is a continuation of the occipitosquamous suture; in others (humans), of the **lambdoid suture**. This suture is visible in the posterior and lateral views of the skulls. Vesalius (1543:23) referred to the occipitomastoid suture as *charactibus*.

In delphinids, including *Tursiops*, isolation of the parts of the temporal (**tympanic bulla** and **periotic bone** (**petrosal**)) has removed them from contact with the exterior surface of the skull, and the occipitomastoid suture, as such, does not occur. In cetaceans whose **posterior process of the tympanic bulla** is visible on the external surface of the skull (e.g., ziphiids), there may also exist an occipitomastoid suture.

See discussion under **mastoid portion of the squamosal, mastoid process of the petrosal**, and **posterior process of the tympanic bulla.**

= oval condyle = occipital condyle (Flower, 1885:211)

= paracondylar process (*processus paracondylaris*) = paroccipital process

Paracondylar process or paracondyloid process is frequently used for noncetacean mammals (see e.g., Evans and Christensen, 1979: fig. 4.9; Wible, 2003:166; Wible et al., 2005:110, 111), but the terminology is rare in cetacean literature (e.g., Ridewood, 1922:216, noted as a synonym for **paroccipital process**; Eales, 1950:5), where paroccipital process is used widely. See also McDowell's (1958:126) comment on synonymy of paroccipital and **jugular process.**

Kernan (1918) used paracondyloid process (p. 358) in *Ziphius* as equivalent to the paroccipital process (p. 357).

– paramastoid process (*processus paramastoideus*)

The paramastoid process is an obtuse projection of the ventral surface of the **jugular process**, at the insertion of the *rectus capitis lateralis* muscle (Whitney, 1889–1910:[vol. 6]4746). It is variable in humans (Gray, 1918:131). This definition indicates that the paramastoid process is the same as the **paroccipital process** (q.v.) of cetacean use.

There seems to be no distinct insertion of the *rectus capitis lateralis* muscle in odontocetes, but Geisler et al. (2005:18) described a depressed possible insertion in the archaeocete *Carolinacetus*.

*** paroccipital concavity** (Figures 2, 9a,b)

The paroccipital concavity ("concavity of the **paroccipital process**," Fraser and Purves, 1960:9) is the anteroventral surface of the paroccipital process that is filled with a branch of the **posterior sinus**. The paroccipital concavity is unique to cetaceans.

= **paroccipital notch** = jugular notch (Rommel, 1990:37)

= **paroccipital pneumatic sinus** (*sinus pneumaticus paroccipitalis*) (van der Klaauw, 1931:37, 263) = posterior sinus

* **paroccipital process** (Figures 2, 5, 9b,c)

The paroccipital process in cetaceans is known by various names in some other mammals. According to Mangal et al. (2004:335), in humans, "owing to the proximity of diverse osseous landmarks, the PCP [**paracondylar process**] has also been variously termed as the paraoccipital [sic], parajugular, jugular, juxtamastoid, or **paramastoid process**." For example, in some terrestrial mammals, the **jugular process** is identified as a rounded process lateral to the **occipital condyles** on the exoccipital bones. It lies just lateral to the **ventral condyloid fossa** (Evans and Christensen, 1979:122). In humans this forms the attachment for the *rectus capitis lateralis* muscle and the lateral atlantoccipital ligament (Gray, 1918:131, 181).

In his description of the intact skull of the dog, ventral view, Miller labeled the process at the posterolateral angle of the skull as the jugular process (Evans and Christensen, 1979:152, figs. 4–39) and discussed it on page 153. In his description of the **occipital bones**, Miller labeled the same process the paracondylar process (Evans and Christensen, 1979:121, figs. 4–9) and discussed this process on page 122 as the jugular process. Further, Wible and Gaudin (2004:138) discussed the term "paroccipital process" as applied to features of the **petrosal** (**periotic bone**) and the adjacent exoccipital; they noted that the so-called paroccipital process of the exoccipital is more appropriately referred to as the jugular process (base) and paracondylar process (tip); see also Wible et al. (2005:110, 111).

In odontocetes the paroccipital process lies lateral to the posterior end of the **basioccipital crest** and the **hypoglossal canal**. It lies posterior or posteromedial to the **postglenoid process** of the squamosal bone. The paroccipital process articulates via a synchondrosis with the lateral end of the stylohyal bone. Paroccipital process in this sense has had a long and unambiguous history of use in cetacean anatomy (see Fraser and Purves, 1960:9, 15, 35, 37–47, 49–63, 65–68, 72, 73, 77, 108).

Kernan (1918) used paracondyloid process (p. 358) as equivalent to the paroccipital process (p. 357) and Owen (1866a:26, 30, 34, 35, 36, 40) referred to the paroccipital process as just the paroccipital (no process).

– **posterior condyloid foramina**

The posterior condyloid foramina applies to the two areas in *Platanista* of the **occipital shield** where bone may be developmentally absent (Anderson, 1879:502). This condition occurs in the exoccipital in *Platanista*. It is reminiscent of the situation in monodontids where the foramina occur at the juncture of the exoccipitals and **supraoccipitals**.

= **posterior lacerate foramen**

MacPhee (1981:60) noted that the posterior **lacerate foramen** is distinct from the **jugular foramen** in some mammals, in which case it transmits nerves IX, X and XI.

In *Tursiops* and other odontocetes, the **condylar foramen** may become constricted in older specimens by bony outgrowths, producing sulci or endocranial foramina for nerves and vessels. Heavy ossification may produce a more-anteriorly placed posterior lacerate foramen for nerves IX, X, and XI that is separate from a distinct more-posterior jugular foramen for the jugular vein. We recommend that "posterior lacerate foramen" be used only when the bony path for nerves IX, X, and XI is separate from the jugular foramen.

See **cranial hiatus** and Table 4.

= **posterior pterygoid sinus** (Luo, 1998:285) = posterior sinus

– **posterior sinus**

The posterior sinus is one of the **accessory air sinuses** connected with the **tympanic cavity** in cetaceans. The sinus arises through the **elliptical foramen** and spreads out over the anteroventral part of the **paroccipital concavity** occupying the paroccipital fossa (Fraser and Purves, 1960:8–10, 62, 63, 65–68, 70–72, 74).

In *Tursiops* the posterior sinus, sensu stricto, has also been termed the **paroccipital pneumatic sinus** (*sinus pneumaticus paroccipitalis* of van der Klaauw, 1931:37, 263), and the **posterior pterygoid sinus** (Luo, 1998:285). The posterior sinus, sensu stricto, is not to be confused with the posterolateral sinus, which is a posterolateral extension of the **peribullary sinus**. This lies dorsal to the **paroccipital process** and posterior to the **tympanic bulla**, and often occupies a marked **posterolateral sinus fossa** in the anterior face of the paroccipital process.

* **posterior sinus crest [new term]** (Figure 9b,d)

The posterior sinus crest in *Tursiops* and other odontocetes lies at the anterodorsal margin of the **posterior sinus fossa** in the anterior portion of the **paroccipital process**.

* **posterolateral sinus crest [new term]** (Figure 9a,d)

The posterolateral sinus crest is unique to cetaceans. The crest lies on the anterior surface of the **paroccipital process** just ventral to the level of the **jugular notch** and immediately dorsal to the **paroccipital concavity**. The crest is formed by the posterolateral sinus, which is a posterolateral extension of the **peribullary sinus**.

* **posterolateral sinus fossa [new term]** (Figure 9a,d)

The posterolateral sinus fossa is formed by the posterolateral extension of the **peribullary sinus**. The posterolateral sinus fossa lies on the **paroccipital concavity** and extends along the ventral surface of the **paroccipital process** (shown by Fraser and Purves, 1960:8, 25:fig. 8, 70, who did not differentiate it from the **posterior sinus fossa**), where lies in the posterolateral sinus fossa. The posterolateral extension of the peribullary sinus is distinct from the **posterior sinus** (q.v.), which is identified by its origin via the **elliptical foramen**. The posterolateral sinus fossa is terminated anterodorsally by the **posterolateral sinus crest**.

= **precondyloid foramen** (Anderson, 1879:502, 504, 510) = cranial hiatus

= **precondyloid notch** = hypoglossal notch (Anderson, 1879:502)

TABLE 4. Terms applied to the region of the mammalian skull that includes the cranial hiatus sensu lato, namely, foramina or openings associated with the periotic and/or tympanic bulla and medially adjacent bones. The authors cited are not necessarily the first users of the terms. References to synonyms for *foramen ovale* and jugular foramen are not included. See discussion under **cranial hiatus** and **posterior lacerate foramen**.

Term	Reference(s)	Comments
Basicochlear fissure	MacPhee, 1981:48, Wible and Gaudin, 2004	Wide gap between basioccipital and petrosal in some mammals.
Basicapsular fenestra	MacPhee, 1981:48, Geisler and Sanders, 2003:87, Wahlert, 2000	Basicochlear fissure (see above), according to MacPhee. Cranial hiatus, according to Geisler and Sanders, 2003. Open basioccipital-petrosal suture according to Wahlert, 2000.
Piriform fenestra	MacPhee, 1981:59; Wible and Gaudin, 2004:162; Wible et al., 2005:109; Wahlert, 2000:8	Large gap occasionally in adult mammals, anterior to petrosal and/or bulla, usually between petrosal and/or bulla and sphenoid (basisphenoid, alisphenoid), and squamosal. Middle lacerate foramen of some authors.
Lacerate foramen	Gabbert, 2004:185, 186, 189	Confluent piriform fenestra, basicochlear fissure, and jugular foramen. See sphenotympanic fissure.
Sphenotympanic fissure	Gabbert, 2004:185	Composite foramen ventral to piriform fenestra in Toxodontia, probably for the mandibular branch of the trigeminal nerve, nerves of the pterygoid canal, and any derivative of the internal carotid artery.
Anterior lacerate foramen	Sisson, 1910:57	Median lacerate foramen, = *incisura carotica*, *incisura ovalis*, and *incisura spinosum* of Sisson; = Sisson's anterior part of the *foramen lacerum basis cranii*.
Foramen lacerum basis cranii	Sisson, 1910:57	= *Foramen lacerum et jugulare* in sense of Sisson, = *foramen lacerum anterius* + *foramen lacerum posterius* in sense of Sisson.
Posterior lacerate foramen	MacPhee, 1981:60	As distinguished from jugular foramen when the latter is distinct. See text on lacerate foramina in general, and on posterior lacerate foramen.
Jugular foramen	MacPhee, 1981:60	As distinguished from posterior lacerate foramen when the latter is separate. See text on jugular foramen.
Cranial hiatus	Fraser and Purves, 1960	See text on cranial hiatus.
Tympano-periotic hiatus	Fraser and Purves, 1960:133	Synonym for cranial hiatus.
Petro-occipital fissure [petrooccipital]	Gray, 1918:193	Groove between petrosal and basioccipital, anterior to jugular foramen, associated with groove for inferior petrosal sinus.
Incisura basiparoccipitalis	McFarland et al., 1979:21, 38	"A notch in the ventral surface of the skull . . . angled somewhat dorsad and outwards to the perioticum . . ." associated with passage of the internal carotid artery.
Tympano-occipital fissure	Evans and Christensen, 1979:135; Fordyce, 2002	Contact of the tympanic part of the temporal bone with the basioccipital.
Otocranial vacuity, otocranial cavity	Owen, 1866a:30, 40	Synonym for cranial hiatus.

= **secondary internal auditory canal** = cranial hiatus (Schulte, 1917:374)

= **secondary internal auditory meatus** = cranial hiatus (Schulte, 1917:374)

* **sulcus for intracranial extensions of the spinal meningeal arteries** (Figure 9a)

The intracranial extensions of the spinal meningeal arteries are a development of cetaceans in response to their increased dependence on the vasculature of the spinal column to supply the brain (McFarland et al., 1979). The sulcus for the intracranial extensions of the spinal meningeal arteries enters the cranial cavity along the dorsolateral aspect of the ***foramen magnum***. The sulcus for the intracranial extensions of the spinal meningeal arteries then courses anteriorly across the **concavity for lobes of the**

cerebellum, crossing the ***tentorium*** at its midpoint. The sulcus for the intracranial extensions of the spinal meningeal arteries then turns ventrally across the parietal and the **alisphenoid** and breaks up into an internal ophthalmic *rete mirabile* in the region of the hypophysis (pituitary body).

McFarland et al. (1979) presented admirable illustrations of the course of the intracranial extensions of the spinal meningeal arteries (IESMA). We have used primarily their figure 42 (p. 63) in discussing the course of the arteries. They represented the arteries in their schematic illustration (p. 17: fig. 2) and give angiograms showing the course of those arteries in figures 27 and 28 (1979:48, 49).

* **sulcus for the sigmoid sinus** (*sulcus sinus sigmoidei*) (Figure 9a)

The sulcus for the sigmoid sinus is a continuation of the **sulcus for the transverse sinus**. The sulcus for the sigmoid sinus runs from the posterior end of the periotic, medial to the petro-occipital synchondrosis, and terminates at the **jugular foramen** (Evans and Christensen, 1979:793, 794).

In *Tursiops* the sulcus for the sigmoid sinus lies just dorsal to the jugular foramen. The sulcus extends dorsally where it joins the sulcus for the **transverse sinus**. The sulcus is better developed in young animals.

* **tentorial crest** (*crista tentoric*) (Figures 9a,d, 31a)

The tentorial crest is on the medial (cranial) surface of the squamous part of the temporal. It serves as an attachment for the *tentorium cerebelli* (Schaller, 1992:24.35; not in Feneis, 1994).

The squamosal (squamous part of the temporal) does not participate in the formation of the cranial cavity in delphinids. The attachment of the *tentorium cerebelli* has moved onto the exoccipital bones.

– **tentorial process** (*processus tentoricus*)

The tentorial process is the shelf-like body of the ***tentorium*** (q.v.) (Evans and Christensen, 1979:124, figs. 4–12; Schaller, 1992:16.34, 18.2, 26.4; not in Feneis, 1994).

Owen (1866a:40) used and illustrated the term “tentorial process” in *Kogia sima*. All cetaceans have a tentorial process, although they differ in the degree to which it is developed.

* ***tentorium*** (tentorial ossification) (*tentorium cerebelli osseum*) (Figure 9a,d)

The *tentorium* is formed by a leaf of bone that projects anteromedially from the dorsal part of the posterior border of the parietal and the **internal occipital protuberance** (Evans and Christensen, 1979:124, figs. 4–12; Schaller, 1992:10.10). The *tentorium* separates the cerebellum from the cerebrum. The *tentorium* is formed by the **tentorial process** (*processus tentoricus*) (Schaller, 1992:10.10, 16.34, 18.2, 26.4).

The anterolateral margin of the tentorial ossification in odontocetes ends on the most medial aspect of the **internal surface of the parietal**. The primary portion of the *tentorium* is on the exoccipital bone (Schulte, 1917:376, 379).

– **ventral condyloid foramen**

Wible and Gaudin (2004:166) stated that some armadillos may have small ventral condyloid foramina posterolateral to each **hypoglossal foramen**.

Tursiops lacks ventral condyloid foramina.

* **ventral condyloid fossa** (*fossa condylaris ventralis*) (Figures 5, 9c,e)

The ventral condyloid fossa lies between the **jugular process** and the **occipital condyles** on the exoccipital bone. The fossa provides room for movement of the atlas (Evans and Christensen, 1979:122).

The ventral condyloid fossa is present but indistinct in cetaceans. It is well developed in some fossil species.

FRONTAL BONE

Os Frontale

FIGURES 1, 2–5, 6A,C,D, 10, 31A, 32

The frontal bones are paired midline ossifications that form the anterior wall of the cranium. They contribute to the orbital elements of the face (Schulte, 1917:369–371, 373, 376, 379–381, 384, 386, 389–394, 398, 400–402). Vesalius (1543:21, 23, 25) referred to the frontal bones as the *frontis os*.

The frontal bones are anterior to the interparietals; posteroventral to the nasals; ventral to the maxillae; posterior to the lacrimals; and lateral to the alisphenoids and orbitosphenoids.

= **anterior process** (Ting et al., 2002:7) = narial process of the frontals

– **anterolateral part of the frontal sinus** (*sinus frontals rostralis lateralis*)

The anterolateral part of the frontal sinus is developed in suids and bovids (Sisson, 1910:125, 145; Schaller, 1992:180.15). It is not developed in humans (Feneis, 1994:138).

The anterolateral part of the frontal sinus is not developed in cetaceans due to the complete lack of the paranasal sinus system (Fraser and Purves, 1960:5, 75).

– **aperture to the frontal sinus** = nasofrontal opening

Paranasal sinuses are not developed in cetaceans (Fraser and Purves, 1960:5, 75) but occur in some fossils (Edinger, 1955).

= **ascending process of the frontal bone** = maxillary surface of the frontal

– **caudal frontal sinus** (*sinus frontalis caudalis*) = posterior portion of the frontal sinus

Paranasal sinuses are not developed in extant cetaceans (Fraser and Purves, 1960:5, 75).

* **cerebral juga** (Figures 10b,e, 31a)

The cerebral juga consist of all the bony internal elevations formed by the sulci of the brain. The elevation formed by the sulci of the cerebellum is sometimes distinguished as **cerebellar juga** (Evans and Christensen, 1979:157).

The cerebral juga are the same in cetaceans as they are in other mammals.

* **cerebronasal plate of the frontal bone** (Anderson, 1879:510, 511) (Figure 10a)

The cerebronasal plate of the frontal bone or the **vertical plate** consists of the medial and dorsal parts of the frontal, comprising the **maxillary surface of the frontal**, **frontal eminence**, and those parts of the **external surface of the frontal** that project back to the nasal and interparietal margin. The cerebronasal plate is the frontal bone minus the temporoorbital plate.

This concept was described in *Platanista* but is equally applicable to delphinids.

– **cornual process** (*processus cornulis*)

The cornual process is the process that is developed on the frontal bones for the horn in horned ungulates. As such, it does not occur in cetaceans.

? **coronal suture** (*sutura coronalis*)

The coronal suture is the suture formed by the frontal and parietal bones in humans (Vesalius, 1543:21, 23, 25; Gray, 1918:178; Feneis, 1994:54.2) and most mammals (Evans and Christensen, 1979:125; Schaller, 1992:76.2).

In odontocetes the parietal is excluded from the dorsal midline by the interparietal ossification, which is not normally recognized in other mammals. We have interpreted the suture formed by the parietals / interparietal and the frontals in odontocetes as the coronal suture.

– **crown of the cornual process** (*corona processus cornualis*)

The crown of the cornual process (literally the "horny" process) is developed only in horned ungulates. It consists of an enlargement on the base of the horn on the frontal bone, distal to the **neck of the cornual process** (Schaller, 1992:28.20).

= **digital impressions** = cerebral juga, cerebellar juga

The digital impressions are formed on the internal surface of the cranial bones by the sulci and gyri of the brain (Evans and Christensen, 1979:157).

The digital impressions are the same in *Tursiops* and other cetaceans as they are in other mammals.

See **cerebral juga** and **cerebellar juga**.

* **ethmoidal foramen** (*foramen ethmoidale*) (Figure 10b,c,e)

The ethmoidal foramina are two small openings about 1 cm anterior to the **optic canal**. In dogs the smaller opening is in the frontosphenoidal suture. The larger opening, located posterodorsal to the smaller, passes obliquely through the **orbital part of the frontal** bone (Evans and Christensen, 1979:125; Schaller, 1992:14.26). In horses the ethmoid takes part in forming the ethmoidal foramina (Schaller, 1992:30.2). These two foramina carry the ethmoidal vessels and ethmoidal nerve (Evans and Christensen, 1979:137).

The ethmoidal foramina exist in *Tursiops* (the right one is patent in USNM 571695). They are most apparent on the internal surface of the cranium where they lie on the frontal about 2 cm anterolateral to the optic canal. The ethmoidal foramina exit the cranial cavity on the **ventral orbital crest** near the lateral extent of the optic canal.

– **ethmoidal incisure** (*incisura ethmoidalis*) = ethmoidal notch (Gray, 1918:137)

The ethmoid incisure is a smooth concave part of the edge of the internal table of the frontal bone, that lies dorsal and lateral to the **cribriform plate** of the ethmoid (Gray, 1918: fig. 135; Evans and Christensen, 1979:126).

The ethmoid incisure is not developed in cetaceans due to the modifications to the frontal and ethmoid bones connected with the lack of development of the olfactory sense.

* **ethmoidal margin of the frontal bone** (*margo ethmoidalis*) (Figure 10a,b,d,e)

The ethmoidal margin (articular surface for the ethmoid) consists of the margin of the frontal bone that is bounded or articulates with the ethmoid. The ethmoidal margin is entirely internal to the skull (Evans and Christensen, 1979:125).

The articular surface for the ethmoid bone in odontocetes lies on the posterior or cranial wall of the narial passage. In neonatal *Tursiops* the ethmoid ossification has not expanded dorsally to contact the frontals and thus a wide area of cartilage is still present.

= **ethmoidal notch** = frontal fontanelle = ethmoidal incisure (Gray, 1918:137)

= **external angular process** = zygomatic process of the frontal

See **postorbital process of the frontal bone**.

– **external frontal crest** (*crista frontalis externa*) (Evans and Christensen, 1979:125)

The external frontal crest is a continuation of the **external sagittal crest** onto the frontal bone (Schaller, 1992:16.30, 18.3, 26.6; not in Feneis, 1994).

The external frontal crest is not developed in *Tursiops* and other delphinids due to the lack of an external sagittal crest. The development of the nasal ridge on the frontals in *Platanista* is unrelated.

* **external surface of the frontal bone** (*facies externa*) (Figure 10a,c)

The external surface of the frontal bone is the smooth convex surface in which the **frontal eminences** and superciliary arch lie (Gray, 1918:135).

The external surface of the frontal bones in *Tursiops* and other odontocetes is that portion of the **frontal squama** that is not overlain by the maxilla. It is bounded by the maxilla anteromedially, the **nuchal crest** of the interparietal posteriorly, the nasals medially, and the **orbit** laterally.

– ***foramen cecum*** [*foramen cæcum*]

The *foramen cecum* is formed by the divergence of the crests that unite to form the **frontal crest.** It lies at the anteroventral end of the **internal surface of the frontal** bone where it articulates with the ethmoid. This foramen is variable in size and frequently impervious. When it is patent it transmits a vein from the nose to the **sagittal sinus** (Gray, 1918:137).

The frontal crest is not developed in *Tursiops* or any other odontocetes.

– **foramen for the frontal diploic vein**

In the dog (Evans and Christensen, 1979:796) the frontal diploic vein drains from the diploe between the roof of the cranium and the caudal part of the frontal sinus, leaving the skull by the small frontal foramen (q.v.). A foramen for the frontal diploic vein occurs in other mammals (Schaller 1992:362.19). Wible (2003:171, on *Monodelphis*) listed frontal foramen and supraorbital foramen as synonyms.

Comparable features may be present in some Cetacea; see discussion under **frontal foramen** and **supraorbital foramen of the frontal bone**.

– foramina in frontal, dorsal surface

In some armadillos (Wible and Gaudin, 2004:155), conspicuous scattered foramina may open on the dorsal surface of the frontal bone. Wible and Gaudin identified these foramina of the dorsal surface of the frontal bone as transmitting branches of the external ethmoidal artery and vein.

The dorsal surface of the frontal bone in *Tursiops* is restricted in area compared to other mammals. The bone surface may be quite finely porous, with occasional small foramina, but *Tursiops* lacks conspicuous foramina on the dorsal surface of the frontal bone as seen in armadillos.

The multiple foramina that open on the dorsal surface of some archaic mysticetes and archaeocetes may represent foramina of the dorsal surface of the frontal bone sensu Wible and Gaudin (2004:155).

– foramina in frontal, ventral surface

In the yellow armadillo (Wible and Gaudin, 2004:155) multiple foramina may open on the ventral surface of the frontal bone to transmit temporal rami from the **orbitotemporal canal** to the temporalis muscle.

Tursiops lacks a consistent pattern of foramina on the ventral (temporal) surface of the frontal bone, between the **infratemporal crest** and the orbitotemporal or **temporal crest**.

– fossa for the lacrimal gland (*fossa glandulae lacrimals*)

The fossa for the lacrimal gland is located at the juncture of the palatine / lacrimal / **frontal sutures** (Evans and Christensen, 1979:126).

The fossa for the lacrimal gland is not present in cetaceans due to the absence of the gland.

– fossa for the postorbital lobe of the pterygoid sinus

See “Sphenoid Bone.”

* **fossa for the preorbital lobe of the pterygoid sinus** (Figure 10b)

The **pterygoid sinus** system is peculiar to cetaceans. The **preorbital lobe of the pterygoid sinus** is a lateral diverticulum of the pterygoid sinus that arises just anterior to the **optic canal** and **orbital fissure** (Beauregard, 1894; Fraser and Purves, 1960:8, 25:fig. 8, 70, pl. 44). The preorbital lobe of the pterygoid sinus sometimes makes a shallow triangular depression in the frontal bone that lies between the **ventral orbital crest** and the **supraorbital margin of the frontal**. This has been referred to as the preorbital smoothed area or recess (Fraser and Purves, 1960:51, 53, 54, 59, 61), preorbital extension of the smoothed area (1960:57), or the preorbital depression (1960:56).

– *frons*

Frons is Latin for the forehead (Dox et al., 1979:174) and in humans it is the anterior surface of the frontal bones lying between the **orbits**, the **temporal lines**, and the **vertex**.

Due to the changes in morphology of the facial region as a result of telescoping, cetaceans do not express a *frons*.

= frontal crest (*crista frontalis*)

See **external frontal crest, internal frontal crest**.

* **frontal eminence** (*tuber frontale*) (Figure 10a,c,d)

The frontal eminence in humans is a low rounded structure that occurs just dorsal to the **supraorbital margin of the frontal**. It is the first portion of the frontal bones to ossify and represents a manifestation of the bulge that is produced by the anterior part of the frontal lobes of the cerebrum (Gray, 1918:135; Feneis, 1994:18.4). In domestic animals the term is used for a flat eminence on the **external surface of the frontal** bone (Schaller, 1992:26.27). Sisson and Grossman (1953:135, 136) used the vernacular term “frontal eminence” in a slightly different context to mean the highest point of the frontals in oxen, and used the Latin phrase *torus frontalis* in connection with frontal eminence. In the sense of Sisson and Grossman, the frontal eminence is comparable to the **vertex**.

The frontal eminence in odontocetes is covered by the **ascending process of the maxilla** but is noticeable as a slight external bulging of the maxilla and premaxilla just lateral to the **external bony nares**.

– frontal fontanelle

The frontal fontanelle is an unossified membranous interval that occurs in early ontogeny at the junction of the frontal and parietal sutures on the midline of the young animal.

Because of modification in the arrangement of the cranial bones (telescoping) in Cetacea, the parietals no longer occur in the midline and the frontal fontanelle is not developed.

– frontal foramen (*foramen frontale*)

In humans the frontal foramen (or **frontal notch**) lies on the supraorbital margin (**external surface of the frontal** bone) medial to the **supraorbital foramen** (or notch) (Evans and Christensen, 1979:152, 913–915; Schaller, 1992:26.30; Feneis, 1994:18.9; not in Gray, 1918). It is formed by the arching over of the frontal incisure and transmits the supratrochlear artery and the medial branch of the supraorbital nerve. The frontal foramen is of sporadic occurrence in mammals and is treated incompletely in the references given. We suspect there is some confusion with the supraorbital foramen.

Frontal foramen is used in different senses for other mammals. See **foramen for the frontal diploic vein; foramina in frontal, dorsal surface**; and **foramina in frontal, ventral surface**.

There is no indication of development of a frontal foramen in delphinids in the sense of a foramen or notch on the **supraorbital margin of the frontal.**

Fordyce (1994:155) identified “frontal foramen” in a different sense, namely a foramen on the ventral surface of the frontal bone, some distance lateral to the ethmoid foramina in the fossil platanistoid *Waipatia*. Since Fordyce’s frontal foramen is well within the orbital surface of the skull, it is doubtful that it is homologous with the frontal foramen that we have defined, but is more likely a **foramen for the frontal diploic vein** (q.v.) or **foramen in frontal, ventral surface** (q.v.).

– frontal notch (*incisura frontalis*)

See **frontal foramen**.

– frontal sinus (*sinus frontalis*)

The frontal sinus is a paranasal sinus (air cavity) located between the inner and outer tables of the anterior end of the frontal bone (Schaller, 1992:28.24, 180.11). It varies more in size than any other cavity of the skull. It may extend into the dorsal parts of the maxilla and parietal bones (Evans and Christensen, 1979:159) and be known as the *sinus frontalis rostralis* (Schaller, 1992:180.12), *sinus frontalis medialis* (ibid., 180.16), *sinus frontalis lateralis* (ibid., 180.17), ***sinus frontalis caudalis*** (ibid., 180.18), *sinus frontalis intermedius* (ibid., 180.14) *sinus frontalis rostralis lateralis* (ibid., 180.15), or the *sinus frontalis rostralis medialis* (ibid., 180.13). In most mammals the frontal sinus opens into the nasal cavity via the **nasofrontal opening** (*apertura sinus frontalis*). Vesalius (1543:51; Vesalius et al., 1998:131) referred to the frontal sinus as the *cavitas inter duas frontis os*.

The frontal sinus is lacking in delphinids owing to the lack of development of the entire paranasal sinus system (Fraser and Purves, 1960:5, 75). The situation of the paranasal sinus system in nondelphinid cetaceans is not well known. The paranasal sinus system, including frontal and **maxillary sinus** is developed in at least some archaeocetes (Kellogg, 1928:199; Uhen, 2004).

= frontal squama (*squama frontalis*) = maxillary surface of the frontal

In humans (Gray, 1918:135) the frontal squama is the vertical portion corresponding to the region of the forehead. This part of the frontal bone is so modified in *Tursiops* and other odontocetes that the term "**maxillary surface of the frontal**" (q.v.) seems more appropriate.

* **frontal suture** (*sutura interfrontalis*) (Figure 4)

The frontal suture joins the contralateral frontal bones (Evans and Christensen, 1979:126). **Metopic suture** (q.v.), interfrontal suture, and anterior portion of the **sagittal suture** are alternatives.

All cetaceans have a frontal suture (e.g., Owen, 1866a:27, 36, 37) at the sagittal margin of each frontal. The suture may fuse to become indistinct.

* **frontomaxillary suture** (*sutura frontomaxillaris*) (Figure 1)

The frontomaxillary suture is formed between the frontal bone and maxilla (Gray, 1918:189; Evans and Chistensen, 1979:125, 126, 141; Schaller, 1992:76.22; Feneis, 1994:54.16;). Vesalius (1543:23) referred to the frontomaxillary suture as merely the *sutura*.

All Neoceti, as a result of their cranial telescoping, change the sutural relationship of the frontal bone and maxilla from a dentate to a squamous suture, which does not fuse.

– frontozygomatic suture (*sutura frontozygomatica*)

The frontozygomatic suture is formed between the frontal and the zygomatic (jugal) in some mammals, such as horses (Schaller, 1992:76.24) and humans (Feneis, 1994:54.18). In humans this suture has also been known as the zygomaticofrontal suture (Gray, 1918:182). Vesalius (1543:22) mentioned it merely as the *sutura*.

The boundary of the lacrimal and jugal and their relationship with the frontal is not resolved in odontocetes (see discussion of lacrimojugal under "Lacrimal Bone"). It is unlikely that the frontal contacts the jugal in *Tursiops*.

– *glabella*

The *glabella* is a low smooth midline elevation that joins the **superciliary arches** (Gray, 1918:135).

The *glabella* does not occur in cetaceans due to the modifications of telescoping and the overriding of the frontal bone by the maxilla.

– groove for angularis oculi vein

The angular vein (*vena angularis*) is formed by the junction of the frontal vein and supraorbital vein. It courses ventrally through the medial angle of the **orbit**. It may produce a groove in the medial part of the **supraorbital margin of the frontal** bone near where the attachment of the *m. orbicularis oculi* occurs (Gray, 1918:136, 644; Evans and Christensen, 1979:125, 126).

The groove for the angularis oculi vein is not known to occur in cetaceans.

– infratemporal crest

See "Sphenoid Bone."

* **infratemporal fossa**

See discussion under **infratemporal fossa** in "Maxilla."

– interfrontal crest (Owen, 1866a:34)

Owen used the interfrontal crest, without defining it, in a table of the cranial measurements of *Kogia*. As far as we can tell he used the interfrontal crest to refer to the unusual modification of the **vertex** of *Kogia*.

– internal frontal crest (*crista frontalis intera*) (Evans and Christensen, 1979:126)

The internal frontal crest is formed by the uniting of the crest that defines the sagittal sulcus into the **internal sagittal crest**. The internal frontal crest occurs in the anterior part of the **internal surface of the frontal** bone (Gray, 1918:136; White and Folkens, 1991:58). The internal frontal crest consists of the ventral portion of the **septum of the frontal sinus** (Evans and Christensen, 1979:126).

The internal frontal crest is not developed in *Tursiops*. The sagittal sulcus extends only as far anteriorly as the interparietal. The internal frontal crest is well developed in *Platanista* where the **frontal suture** is relatively well developed (Anderson, 1879:507).

* **internal surface of the frontal** (*facies interna*) (Figure 10b,e)

The internal surface of the frontal bone forms a part of the braincase and the nasal cavity (Evans and Christensen, 1979:126).

The internal surface of the frontal bone in odontocetes forms a part of the braincase and the nasal cavity, as it does in most mammals.

* **interparietal margin of the frontal bone** (Figure 10a–c,e)

The interparietal margin of the frontal bone is that portion of the frontal bone that abuts the interparietal bone.

In delphinids the interparietal margin consists of the posteromedial edge of the frontal bone. It is bordered laterally by the parietal margin of the frontal bone and anteromedially by the frontal margin of the frontal bone.

See **parietal margin of the frontal bone**.

= intraorbital fossa (Owen, 1866a:36)

This is a lapsus calami for **antorbital fossa**.

– lacrimal fossa
See "Lacrimal Bone."

– lateral part of the frontal sinus (*sinus frontalis lateralis*)
The lateral part of the frontal sinus (q.v.) in many mammals occupies the whole of the **supraorbital process of the frontal** bone.

The frontal sinus is absent in cetaceans due to the absence of the **paranasal sinuses** (Fraser and Purves, 1960:5, 75).

*** maxillary surface of the frontal** (Figure 1a,c,d)
The maxillary surface of the frontal bone or **frontal squama** is the surface that articulates with the maxilla. This term does not appear to have been used in noncetacean mammals, instead "frontal squama" is the name given to the portion of the frontal bone that is bounded posteriorly by the **orbitotemporal crest**, laterally by the **supraorbital margin of the frontal** bone, and dorsally by the **frontonasal suture**. It is largely subcutaneous in life and forms the forehead in humans (Gray, 1918:131; Evans and Christensen, 1979:126; Schaller, 1992:26.25; Feneis, 1994:18.2).

Anderson (1879:525) used the maxillary surface of the frontal bone to refer to the surface of the frontal bone that is overlain by the **ascending process of the maxilla**. Kernan (1918:359) used the term "ascending process of the frontal" to mean that part of the frontal bone that underlies the ascending process of the maxilla. The **ascending process of the frontal bone** is therefore equivalent to the maxillary surface.

The maxillary surface in *Tursiops* and other odontocetes is largely overlain by the ascending process of the maxilla, although the frontal is often exposed to dorsal view lateral, posterolateral, and posterior to the ascending process of the maxilla.

– metopic suture
The metopic suture is the suture between the two frontals (Gray, 1918:135). Not to be confused with metoptic (e.g., **metoptic process**, q.v.).

Frontal suture (q.v.) is a more widely used alternative.

– narial process of the frontals (Kellogg, 1936:21, 106, 179)
Kellogg (1936:21, 106, 179) referred to a narrow wedge-like narial process of the frontals that separates the posterior of the nasals in Archaeoceti, and Fordyce (2002:199) noted an equivalent in the archaic odontocete *Simocetus*. In other mammals the narial process has been termed the **anterior process** of the frontal (e.g., Ting et al., 2002:7).

Tursiops has a variably developed narial process, contributed mainly or wholly by the left frontal.

*** nasal margin of the frontal bone** (*margo nasalis*) (Figure 10a,d)
The nasal margin of the frontal bones is that part of the bones that is bounded by and articulates with the nasals. It lies at the anteroventral border of the frontal bone.

The relationship of the nasals to the frontals has changed in odontocetes and the nasal margin now occupies the posterodorsal border of the frontal bone. Topographically it is posterodorsal but phylogenetically it is anterodorsal (anteromedial).

– nasal part of the frontal bone (*pars nasals*)
The nasal part of the frontal bone is the rostral extension of the frontal bone that faces the nasal cavity (Evans and Christensen, 1979:126; Schaller, 1992:28.8; Feneis, 1994: 18.12).

The frontal bone does not extend onto the rostrum in any cetaceans nor does it face the nasal cavity.

*** nasal ridge of the frontals** (Anderson, 1879:525, 527) (Figure 4)
In *Platanista* the posteromedial part of the frontals forms the nasal ridge of the frontals (Anderson, 1879:525, 527). The nasal ridge is a transverse elevation that lies immediately posterior to the nasal bones and forms the posterior border of the nasal passage and the anterior portion of the **vertex**. Anderson also referred to this as the nasal crest (Anderson, 1879:525).

The nasal ridge of the frontal in *Tursiops* and other delphinids is a low eminence on the frontal bone just posterior to the nasals.

The nasal ridge of the frontal (Carte and Macalister, 1868:212) in the Mysticeti *Balaenoptera acutorostrata* is probably not homologous.

– nasal spine of the frontal
In humans the frontal bone develops a process that projects ventrally beneath the nasal bones and **frontal process of the maxilla** that terminates in a spine (Gray, 1918:136; Feneis, 1994:18.13).

The relationship of the frontal bones to the nasal bones in *Tursiops* and other odontocetes is much simpler and a frontal or nasal spine is not developed. Bilateral nasal spines occur in minke whale, *Balaenoptera acutorostrata*.

– nasofrontal opening = aperture to the frontal sinus
The nasofrontal opening is an opening in the partition between the two tables of the frontal bones that allow communication between the frontal sinuses and the nasal cavity (Evans and Christensen, 1979:159).

The **paranasal sinuses** are not developed in *Tursiops* and other odontocetes, and there is no nasofrontal opening.

– neck of the cornual process (*collum processus cornualis*)
The neck of the cornual process (literally the "horny" process) is developed only in horned ungulates. It consists of the base of the horn on the frontal bone (Schaller, 1992:28.20).

*** orbit** (*orbit*) (Figures 3, 32)
The orbit is a conical cavity that contains the eyeball and associated structures (Evans and Christensen, 1979:1093). The orbit in most mammals is readily apparent in the skull owing to its bony limitations, particularly in mammals with a closed orbit (i.e., with a postorbital bar; Heesy, 2005). Owen (1866a:28) and Schulte (1917:373) referred to the orbit as the orbital fossa. Vesalius (1543:23) referred to the orbit as *sedis oculorum*.

The bony orbit in cetaceans is very open (Schulte, 1917:381, 384, 390, 391). The external margins are formed by the frontal, lacrimal, and jugal.

See also **orbital part of the frontal**.

= orbital palate of the frontal (Schulte, 1917:381) = orbital plate of the frontal
Orbital palate appears to be a misspelling.

*** orbital part of the frontal** (*pars orbitalis*) (Figure 10b)
The orbital part of the frontal bone is a segment of a cone with the apex located at the **optic canal** and the base forming the

medial border of the supraorbital margin (Schaller, 1992:28.10). Evans and Christensen (1979:125) actually referred to this as the infraorbital margin, which is an obvious lapsus calami.

The orbital part of the frontal bone in delphinids consists of the region bounded anteriorly by the **antorbital fossa** (**infratemporal fossa** of Davis, 1964:48), posteriorly by the **temporal fossa**, medially by the optic canal and **orbital fissure**, and laterally by the supraorbital margin. The orbital part has also been referred to as the infundibulum for the optic and oculomotor nerves (Fraser and Purves, 1960:66) or the **optic infundibulum** (Fraser and Purves, 1960:30, 61, 68–70, 72, 73, 100, 102).

See also **orbital surface of the frontal**.

= **orbital plate of the frontal** (Owen, 1866a:28; Schulte, 1917:378, 380–382, 384, 391, 401) = orbital part (Gray, 1918:137)

= **orbital process of the frontal** (Owen, 1866a:42; Anderson, 1879:497, 525; Schulte, 1917:391; Fraser and Purves, 1960:37, 38, 42, 47, 58, 66) = supraorbital process of the frontal

= **orbital roof** (Schulte, 1917:381, 390) = supraorbital process of the frontal

– **orbital surface of the frontal** (*facies orbitalis*)

The orbital surface of the frontal bone is the portion of the frontal facing the **orbit** (Feneis, 1994:18.22; Schaller, 1992:28.11); Gray (1918) and Evans and Christensen (1979) did not use this term).

In delphinids the orbital surface of the frontal is the same as the orbital part. We have chosen to illustrate and use the **orbital part of the frontal** instead of the orbital surface.

= **orbital wing of the frontal bone** = supraorbital process of the frontal (Anderson, 1879:525; Miller, 1923:8)

= **orbitofrontal plate** (Anderson, 1879:512) = orbital part

– **orbitotemporal canal**

The orbitotemporal canal opens in the frontal, or sometimes the **orbitosphenoid**, in various mammals, to transmit a branch of the stapedial artery into the **orbit** (Wible and Gaudin, 2004:162).

In *Tursiops* the internal carotid artery is reduced (see section on arterial circulation and basicranial foramina in "Multielement Complexes"), the **stapedial foramen** is nonpatent, and there appears to be no significant stapedial circulation. There is no evidence of an orbitotemporal canal in *Tursiops*.

* **orbitotemporal crest** (*crista orbitotemporalis*) (Figure 10a–c,e)

The orbitotemporal crest is the anterior portion of the **temporal crest** directly posterior to the **zygomatic process** (postorbital process) of the frontal bone (Evans and Christensen, 1979:125, 126; Schaller 1992:28.1). It should not be confused with the temporal crest (q.v.) or suprameatal crest on the **zygomatic process of the squamosal**. Davis (1964:48, fig. 17) referred to it as the *crista orbitalis superior* (superior orbital crest).

The orbitotemporal crest in odontocetes lies on the posterior margin of the **postorbital process of the frontal bone**. This has also been referred to as the temporal crest (Fordyce, 1994: fig. 5a.) and the **supratemporal crest** (Schulte, 1917:392).

– **orbitotemporal fossa**

The orbitotemporal fossa is the confluent **orbit** and **temporal fossa** in those mammals that lack a complete postorbital bar (Wible and Gaudin, 2004:175; Heesy, 2005:367).

In *Tursiops* and many other Cetacea, the postorbital process closely approaches the **zygomatic process of the squamosal** so that the orbitotemporal fossa, although present in the strict sense, is effectively eliminated.

– **paranasal sinuses** (*sinus paranasales*)

The paranasal sinuses consist of the **frontal sinuses**, **maxillary sinuses**, ethmoidal sinuses, and **sphenoidal sinuses** (Feneis, 1994:136.14).

The paranasal sinus system is not developed in *Tursiops* or other extant cetaceans (Fraser and Purves, 1960:5, 75). The situation of the paranasal sinus system in nondelphinid cetaceans is not well known. The paranasal sinus system developed in at least some archaeocetes (Kellogg, 1928:199; Uhen, 2004:54).

* **parietal margin of the frontal bone** (*margo parietalis*) (Figure 10b,c,e)

The parietal margin of the frontal bone is that margin of the bone that is bounded by and articulates with the parietal. The parietal margins of the frontal bone lie at the posterior margin of the frontals. In many cases this is actually the interparietal margin.

The parietal margin of the frontal bone is extensive in odontocetes, forming at least half of the posterior border of the frontal bone.

– **pit for reception of the *zygoma***

The pit for reception of the *zygoma* lies on the lateral surface of the **postorbital process of the frontal bone** in *Platanista* (Anderson, 1879:510). Here, the apex of the **zygomatic process of the squamosal** approaches the frontal to within a few millimeters, although there does not appear to be an actual suture.

The pit for reception of the *zygoma* does not occur in delphinids.

= **posterior ethmoidal foramen**

See **ethmoidal foramen**.

= **posteroventral face** = temporal surface (Fraser and Purves, 1960:57)

– **postfrontal**

The postfrontal is a membrane bone found with extreme rarity in human skulls between the frontal and the jugal. This element may represent a remnant of the reptilian postfrontal (de Beer, 1937:368).

The postfrontal has not been reported in cetaceans.

* **postorbital angle** (Figure 10c)

The postorbital angle is the point of maximum inflection of the postorbital process (Kellogg, 1936:21). The term has been used in archaeocetes and other fossil cetaceans.

– postorbital diverticulum [new term]

Fraser and Purves (1960:108) described a feature of the postorbital lobe that they observed in *Cephalorhynchus* sp. (They referred to *C. heavisidei* and *C. commersoni* (1960:53) and said they were similar enough to be considered together.) They observed (1960:108):

> In the genus *Cephalorhynchus* the chief advance in development is in the pre- and post-orbital lobes which are moderately approximated to each other. In addition, the post-orbital lobe has a narrow diverticulum which passes dorso-posteriorly under the post-orbital process of the frontal.

We have chosen to use the name "postorbital diverticulum" for this feature.

– postorbital lobe of the pterygoid sinus (Fraser and Purves, 1960:56, 57, 59, 61, 68, 69, 76, 100, 102, 107, 108)

The postorbital lobe of the pterygoid sinus lies in the **orbit**, posterior to the **postorbital ridge**. The postorbital lobe originates from the **pterygoid sinus**, posteroventral to the **optic foramen** but anterior to the ***foramen ovale***. There is a **postorbital diverticulum** in *Cephalorhynchus* (Fraser and Purves, 1960:108).

*** postorbital process of the frontal bone** (Whitney, 1889–1910: [vol. 6]4644) = zygomatic process (Schaller, 1992:28.2) (Figure 10a–e)

The **zygomatic process of the frontal** bone extends posteriorly to meet with the jugal (or **zygomatic bone**) and form the zygomatic arch (Schaller, 1992:28.2, 34.3; Feneis, 1994:18.13). It is not to be confused with the **zygomatic process of the squamosal** (Schaller, 1992.26), which forms the connection of the squamosal to the zygomatic arch.

Due to the possibility of confusion with the zygomatic process of the squamosal, and because of a long history of use of "postorbital" for Cetacea, we prefer to use the term "postorbital process" for this feature of the frontal bone, as have Schulte (1917:365, 370, 373, 381, 382, 392, 393, 401), and Fraser and Purves (1960:13, 47, 54, 60, 61, 64, 67–70, 72, 108), and many others. Owen (1866a:36) referred to this process as the "**postfrontal**" or "postorbital process."

The postorbital process of the frontal bone in odontocetes is an angular process that extends posteriorly from the supraorbital process. It defines the posterior limit of the **orbit** and the anterior limit of the **temporal fossa**, and thus divides the **orbitotemporal fossa**.

= postorbital ridge = infratemporal crest (Fordyce, 1994:155)

See "Sphenoid Bone."

– prefrontal bone

The prefrontal bone is a membrane bone that occurs extremely rarely in humans. It lies between the lacrimal and the frontal. Such a bone is more common in other mammals and may represent a remnant of the reptilian prefrontal bone, which in Mammalia would normally be crowded out by the frontal (de Beer, 1937:368).

Owen (1866a:27, 30, 37, 38) used the term "prefrontal" but in reference to the external exposure of the **mesethmoid** in both *Orcaella brevirostris* and *Kogia sima*.

– preorbital lobe of the pterygoid sinus (Fraser and Purves, 1960:1,67–69, 73, 76, 100, 107)

The preorbital lobe of the pterygoid sinus lies in the **orbit** around the **ventral infraorbital foramen**, anterior to the preorbital ridge. The preorbital lobe originates from the **pterygoid sinus** anteroventral to the **optic foramen**. The preorbital lobe has also been called the pre-orbital extensions of the pterygoid sinus (Fraser and Purves, 1960:67).

*** preorbital process of the frontal** (Kellogg, 1936:21) (Figures 3, 10a–d)

The preorbital process of the frontal bones is not known in humans and other noncetacean mammals. The preorbital process is present in archaeocetes (Kellogg, 1936:21), in other fossil cetaceans (*Australodelphis*, Fordyce et al., 2002; *Simocetus*, Fordyce, 2002), and in all recent cetaceans (e.g., *Kogia*, Schulte, 1917:391, 392, 401).

The preorbital process of the frontal bone in cetaceans is a thickening of the **orbital process of the frontal** that forms the anterior border of the **orbit**. It articulates with the lacrimal and sometimes the maxilla.

Diagram 2 shows the complex terminology for structures near the preorbital process and antorbital notch.

See **antorbital notch** under "Maxilla."

*** sagittal margin of the frontal bone** (*margo sagittalis*) (Figure 10a,b,d,e)

The sagittal margin of the frontal bone is that margin of the frontal bone that participates in the **sagittal suture**, that is, the medial margin of the frontal bone.

The sagittal margin of the frontal bone is reduced in odontocetes. It consists of the medial margin of the frontal bone that underlies the nasal bones and a small portion of the frontal that extends anterior and posterior to the nasal bones.

– sagittal sinus (*sinus sagittalis*)

The sagittal sinus drains the dorsal surface of the cranial cavity. It begins at the confluence of the rhinal veins and continues posteriorly in the attached edge of the *falx cerebri*. It terminates posteriorly in the **transverse sinus** (Evans and Christensen, 1979:791).

In cetaceans this sinus lies along the interparietal and **occipital bones** and may extend onto the frontal bones. Anderson (1879:501) referred to the sagittal sinus as the longitudinal sinus.

– septal processes of the frontal bone (*processus septalis*)

The septal processes of the frontal bone form the dorsal part of the **nasal septum** in some mammals (Schaller, 1992:28.27, 30:17; not in Evans and Christensen, 1979).

The frontal bone does not contribute to the nasal septum in delphinids.

– septum of the frontal sinus (*septum sinuum frontalium*)

The septum of the frontal sinus is a vertical median partition that separates the right and left frontal sinuses (Evans and Christensen, 1979:126).

This feature is not developed in cetaceans because of the lack of **paranasal sinuses** (Fraser and Purves, 1960:5, 75).

– sinciput

The sinciput is the upper anterior part of the head from the forehead to the crown (Dox et al., 1979:434; Whitney, 1889–1910:[vol. 7]5643). It has also been spelled synciput and has also been used as equivalent to the craniometric point bregma. Eustachius and Lancisius (1714:111) referred to it as *syncipite*.

Due to changes caused by telescoping of the cetacean skull, the sinciput is not expressed.

– superciliary arches (*arcus superciliaris*)

The superciliary arches are a pair of rounded elevations that lie between the **frontal eminences** and the **supraorbital margin of the frontal** bones (Gray, 1918:135). They contribute to the "brow ridges."

The superciliary arches do not occur in cetaceans due to the modifications of telescoping and the overriding of the frontal bone by the maxilla.

= superorbital ridge (Owen, 1866a:27) = supraorbital margin of the frontal

– supraorbital canal (*canalis supraorbitlis*)

The supraorbital canal lies in the **supraorbital process of the frontal** bone and carries the supraorbital nerve and the supraorbital vessels (supraorbital artery and supraorbital vein) (Schaller, 1992:26.32); it is particularly developed in artiodactyls. Thewissen et al. (2001: fig. 3) identified a supraorbital canal in the archaeocete *Pakicetus*.

– supraorbital foramen of the frontal bone (*foramen supraorbital*)

The supraorbital foramen of the frontal bone is a small foramen in the middle of the **supraorbital margin of the frontal** that houses the supraorbital artery, supraorbital vein, and the lateral branch of the supraorbital nerve (Sisson, 1910:53, 55, 66, 119, 125; Gray, 1918:136; Evans and Christensen, 1979:12, 913–915; Schaller, 1992:26.30; Feneis, 1994:18.9). The margin of the supraorbital foramen is sometimes incomplete, in which case it is known as the **supraorbital notch**. There has been a tendency to confuse this foramen with the more medial frontal foramen. Vesalius (1543:48; Vesalius et al., 1998:131) referred to the supraorbital foramen as the *foramen ad medium supercillii incisum*.

The supraorbital foramen does not occur in odontocetes. The supraorbital nerve is small and is reflected around the **supraorbital process of the frontal** bone producing a supraorbital notch in some odontocetes. We have noted it in specimens of *Orcinus orca*, *Kogia breviceps* (Schulte, 1917:369, 392, 401), *K. sima*, and *Physeter catodon*. A supraorbital notch is not present in *Tursiops*.

Multiple foramina may open on the dorsal surface of some archaic mysticetes and archaeocetes; these may not be supraorbital foramina, but rather may represent foramina of the dorsal surface of the frontal (q.v.) sensu Wible and Gaudin (2004:155).

– supraorbital groove = supraorbital notch

* **supraorbital margin of the frontal** (*margo supraorbitalis*) = orbital margin (Figure 10a–c)

The supraorbital margin of the frontal bone lies at the anteroventral end of the frontal and forms the dorsal border of the **orbit** (Gray, 1918:136). It is also known as the **orbital margin**.

The supraorbital margin of the frontal bone occurs on the lateral aspect of the frontal in Cetacea. Owen (1866a:27, 36) called the supraorbital margin the **superorbital ridge**.

= supraorbital notch (*incisura supraorbitalis*)

We have found the supraorbital notch in *Orcinus*, *Kogia* and *Physeter* but not in *Tursiops*.

See **supraorbital foramen of the frontal bone, groove for angularis oculi vein**.

= supraorbital plates (Flower, 1885:212) = supraorbital process of the frontal

* **supraorbital process of the frontal** (Figure 10a–d)

The **zygomatic process, supraorbital process, or postorbital process of the frontal** bone is formed where the **supraorbital margin of the frontal** meets the **temporal line** (Whitney, 1889–1910:[vol. 6]4644; Evans and Christensen, 1979:114).

We prefer to restrict the term "supraorbital process" to that portion of the **orbital part of the frontal** bone that is directly dorsal to the **orbits**. It is bounded anteriorly by the **preorbital process of the frontal** and posteriorly by the postorbital process of the frontal bone. Due to the possibility of confusion with the **zygomatic process of the squamosal**, we prefer not to use the term "zygomatic process." Owen referred to the supraorbital process as the **orbital roof** (1866a:36) or **orbital process of the frontal** (1866a:42). He also referred to the supraorbital process as the superorbital process (1866a:37)—a lapsus calami. See Schulte (1917:369) and Fraser and Purves (1960:5, 48, 102).

– supraorbital sulcus (*sulcus supraorbitalis*)

The supraorbital sulcus is a groove leading out of the **supraorbital foramen** in some ungulates in which the supraorbital foramen is placed well dorsal and medial to the **orbit** (Schaller, 1992:26.33, 30.15).

A supraorbital sulcus is not developed in delphinids.

= supraorbital wing (Miller, 1923:4) = supraorbital process of the frontal

= supratemporal crest (Schulte, 1917:392) = orbitotemporal crest

See **supratemporal crest** under "Maxilla."

= temporal line (*linea temporalis*)

See "Parietal Bone."

* **temporal plate of the frontal** (Anderson, 1879:509) (Figure 10b)

The temporal plate of the frontal is the ventral part of the frontal that forms the anterior part of the **temporal fossa**.

* **temporal surface of the frontal** (*facies temporalis*) (Figure 10b,c)

The temporal surface of the frontal bone is that part that is posterior to the orbital part (*pars orbitalis*), lying in the anterior portion of the **temporal fossa** (Evans and Christensen, 1979:126).

The temporal surface is small in odontocetes. The surface is bounded anteriorly by the **orbitotemporal crest** and posteriorly by the frontoparietal suture.

* **temporoorbital plate of the frontal** (Anderson, 1879:510) (Figure 10c)

The temporoorbital plate of the frontal bone comprises the **orbital process of the frontal** (preorbital process, supraorbital process, and postorbital process) and the temporal surface and temporal plate. The temporoorbital plate consists of the frontal bone minus the cerebronasal plate.

– **trochlear pit** (*fovea trochlearis*)

The trochlear pit is situated on the medial portion of the **orbital plate of the frontal** and forms a site of attachment for the cartilaginous pulley of the *m. superior oblique* (Gray, 1918:137). It is sometimes replaced by the **trochlear spine**.

The trochlear pit is not developed in Cetacea.

– **trochlear spine** (*spina trochlearis*)

The trochlear spine is situated on the medial portion of the **orbital plate of the frontal** and forms an attachment for the cartilaginous pulley (trochlea) of the *m. superior oblique* (Gray, 1918:137). It is sometimes replaced by the **trochlear pit**.

The trochlear spine is not developed in Cetacea.

* **ventral orbital crest** (*crista orbitalis ventalis*) (Figure 10b,d)

The ventral orbital crest forms the anteroventral boundary of the **orbit** (Schaller, 1992:2.15) and separates the orbit from the **antorbital fossa**. The ventral orbital crest runs from the **optic canal** to the dorsal border of the **maxillary foramen** (**ventral infraorbital foramen**). Davis (1964:48) referred to this crest as the inferior orbital ridge (*crista orbitalis inferior*).

In delphinids the ventral orbital crest is an anteriorly placed feature that runs from the anterior margin of the optic canal anterolaterally to end in the **preorbital process of the frontal** and the **orbital crest** of the lacrimal bone.

* **vertex** (Figure 3)

The vertex of the skull is the highest portion or the crown (Schaller, 1992:10.20; Feneis, 1994:28.26; not in Gray, 1918; not in Evans and Christensen, 1979). Dox et al. (1979:517) illustrated the vertex as the entire **sagittal suture** of the parietal. Vesalius (1543:21, 22) referred to the vertex as the *verticis ossi* or merely the *verticis*.

In odontocetes the term “vertex” has generally been used to apply to the dorsal protuberance on the skull that consists variously of the frontals, interparietal, nasals, premaxillae, and maxillae (Schulte, 1917:362, 370–373, 375, 376, 380, 382, 385, 387, 388, 391, 392; Moore, 1963; Fordyce et al., 2002:45). Fordyce et al. (2002) noted that the vertex is not homologous among odontocetes, and their use would make synvertex of Moore (1968:255) a synonym. Flower’s (1867:89) earlier term “postnarial prominence of the frontal bones” appears to be a forgotten synonym.

= **vertical plate** (Anderson, 1879:510) = cerebronasal plate of the frontal

= **zygomatic fossa of the frontal bone** = infratemporal fossa

= **zygomatic process of the frontal** (*processus zygomaticus*) = postorbital process of the frontal bone

The **zygomatic process, supraorbital process, or postorbital process of the frontal** bone is formed where the **supraorbital margin of the frontal** meets the **temporal line** of the frontal bone (Whitney, 1889–1910:[vol. 6]4644; Evans and Christensen, 1979:114; Schaller, 1992:28.2; Feneis, 1994:18.16).

The zygomatic process of the frontal bone is a thickening and lateral extension of the posterior part of the **orbital process of the frontal**. It defines the posterior limits of the **orbit** and the anterior limits of the **temporal fossa**. It is also known as the **external angular process** (Whitney, 1889–1910:[vol. 6]4644).

In odontocetes the zygomatic process of the frontal bone is an angular process that extends posteriorly from the supraorbital process. It defines the posterior limit of the orbit and the anterior limit of the temporal fossa.

Due to the possibility of confusion with the **zygomatic process of the squamosal**, we prefer to use the term “**postorbital process of the frontal**” for this feature.

HYOID APPARATUS

Apparatus Hyoideus, Os Hyoideum

The hyoid apparatus in mammals consists of a series of ossifications that are remnants of the gill arches of primitive vertebrates. The hyoid arch is the next gill arch posterior to the mandible. The hyoid arch is principally involved with supporting the muscles that aid in swallowing. In addition it serves as support for the larynx and, in cetaceans, is a link in the chain of ventral muscles that function in locomotion.

The hyoid apparatus consists of a single ventral midline element, the basihyoid, which has two paired posteriorly projecting elements, the thyrohyoids (Gray, 1918:177; Evans and Christensen, 1979:148–150; Schaller, 1992:38.38; Feneis, 1994:28.16;). Eustachius and Lancisius (1714:96, 97, 114) referred to the hyoid apparatus as the *hyoides os*. These three ossifications fuse in older animals. Dorsal to the basihyoid lies a pair of stylohyoids. These have an anterior cartilaginous articulation with the basihyoid and a posterior cartilaginous articulation with the paroccipital process. Three more elements are present in primitive vertebrates: the ceratohyoid, epihyoid, and tympanohyoid.

In *Tursiops* and other cetaceans the ceratohyoid and the epihyoid are not ossified and are represented in the cartilaginous articulation between the basihyoid and the stylohyoid. The tympanohyoid is a vestigial element that is fused to the posteroventral surface of the periotic.

The suffixes -hyoid and -hyal are used interchangeably in the literature.

See **tympanohyoid** under “Hyoid Apparatus” and **tympanohyal** under “Periotic Bone.”

* **basihyoid** (*basihyoidum, corpus*) (Figure 11a–c,e,f)

The basihyoid is the midline element that connects the right and left portion of the hyoid apparatus (Evans and Christensen, 1979:148; Schaller, 1992:39; Feneis, 1994:28). It articulates with the paired **thyrohyoid** elements posteriorly and the **cera-**

tohyoid anteriorly. The basihyoid and the thyrohyoid form the most ventral part of the hyoid apparatus.

In *Tursiops* and other odontocetes the basihyoid and thyrohyoid ossify as separate elements connected by a cartilaginous joint (Flower, 1885:216; Rommel, 1990:38). This joint fuses about the time that the individual becomes sexually mature.

* **ceratohyoid** (*ceratohyoidum, cornu minus*) (Figure 11c)

In most mammals the ceratohyoid is a separate bony element that articulates with the anterior portion of the **basihyoid** distally and the paired **epihyoids** proximally (Evans and Christensen, 1979:148; Schaller, 1992:39). In humans the ceratohyoid forms the lesser cornua, which connects via the **stylohyoid** ligament with the **styloid process** of the petrous part of the temporal (periotic). The stylohyoid ligament sometimes contains a cartilage in its midportion that is homologous with the epihyoid element of other mammals.

In *Tursiops* and other odontocetes the ceratohyoid and epihyoid are reduced to a cartilage that lies between the basihyoid and the stylohyoid elements. Synovial-like joints exist between the cartilage and the basihyoid and stylohyoid elements in at least some individuals (Flower, 1885:217; Rommel, 1990:38).

* **epihyoid** (*epihyoideum*) (Figure 11c)

The epihyoid element forms an ossification between the **ceratohyoid** distally and the **stylohyoid** proximally. In humans the epihyoid is sometimes represented by a cartilage that may ossify in the midportion of the stylohyoid ligament (Gray, 1918:393).

The epihyoid element may be represented by the variable cartilages and ossifications that occur between the stylohyoid and the **basihyoid** in odontocetes (Flower, 1885:217).

– lingual process (*processus lingualis*) **of the basihyoid**

The lingual process projects anteriorly from the midportion of the **basihyoid** in some mammals (horse, ox, pig: Sisson, 1910:65, 122, 144; Schaller, 1992:39) and is absent in others (dog: Sisson, 1910:159; Evans and Christensen, 1979:148). The root of the tongue is attached to the lingual process (Sisson, 1910:65).

The lingual process of the basihyoid is absent in *Tursiops* and other cetaceans.

* **stylohyoid** (*stylohyoideum*) (Figure 11a–f)

The stylohyoid or stylohyal lies between the **epihyoid** distally and the **tympanohyoid** cartilage proximally (Sisson, 1910:65; Evans and Christensen, 1979:148; Schaller, 1992:39). In humans the stylohyoid (stylohyal) element occurs as the distal ossification of the **styloid process** of the temporal bone (Gray, 1918:145).

In *Tursiops* and other cetaceans the stylohyoid is a long rod-shaped bone that forms the attachment of the hyoid apparatus to the **paroccipital process** on the skull (Fraser and Purves, 1960:7). Unlike in many other mammals, in cetaceans it is not involved in a styloid process associated directly with the **tympanic bulla** or periotic.

See **tympanohyoid** under "Hyoid Apparatus" and **tympanohyal** under "Periotic Bone."

– stylohyoid angle (*angulus stylohyoideus*)

The stylohyoid angle is situated on the posteroventral portion of the **stylohyoid** in some mammals (horse, ox: Sisson, 1910:65, 122). The stylohyoideus muscle attaches to the angle (Sisson, 1910:223). It is absent in humans (Gray, 1918:178).

The stylohyoid angle is absent in cetaceans.

* **thyrohyoid** (*thyrohyoideum; cornu majus*) (Figure 11a–c,e,f)

The thyrohyoid or thyrohyal is a paired ossification that is attached to the posterolateral aspect of the **basihyoid**. In some mammals (horse: Sisson, 1910:445), the thyrohyoid muscle, which runs to the thyroid cartilage of the larynx, is attached; in others (dog: Evans and Christensen, 1979:148) the thyrohyoid element articulates directly with the thyroid cartilage. In humans the connection between the thyrohyoid bone and the thyroid cartilage is by means of both the lateral hyothyroid ligament and the thyrohyoideus muscle (Gray, 1918:178). Thyreohyoid is a rare lapsus calami.

Odontocetes are born with a paired thyrohyoid ossification that becomes fused to the basihyoid later in life (Flower, 1885:216; Fraser and Purves, 1960:7). The thyrohyoid muscle is present in delphinids (Lawrence and Schevill, 1965:18, 53, figs. 5, 14).

* **tympanohyoid** (*tympanohyoideum*) (Figure 25k,m,o,t,u)

The tympanohyoid cartilage is the most proximal of the hyoid elements. It runs between the **stylohyoid** and the **petrosal** (Sisson, 1910:64, figs. 27, 33; Evans and Christensen, 1979:148; Schaller, 1992:39). In humans the tympanohyoid (or **tympanohyal**) forms the proximal portion of the **styloid process** of the temporal bone (Gray, 1918:145).

In *Tursiops* and other delphinids the base of the tympanohyoid (tympanohyal) is fused to the posteroventral side of the periotic (Figure 25k,m,o,t,u) as discussed further under **tympanohyal** of "Periotic Bone." This leaves the hyoid chain broken between the tympanohyoid and the proximal end of the stylohyoid element, which attaches to the **paroccipital process**. In the dog (Evans and Christensen, 1979:284, 286) the jugulohyoideus muscle runs from the tympanohyoid cartilage to the **jugular process** (paroccipital process). There may have been a muscular or ligamentous connection between the tympanohyoid and the paroccipital process in the ancestral cetacean that has disappeared. That may explain the migration of the stylohyoid to the paroccipital process in delphinids. Lawrence and Schevill (1965:19, 20) also commented on the changes in the delphinid hyoid anatomy in terms of the change in relative position of the larynx and skull.

See discussion of **tympanohyal** under "Periotic Bone" of the "Tympanoperiotic Complex."

INTERPARIETAL BONE

Os Interparietale

FIGURES 3, 5, **6A,C,E**, 12A,C,E, 24A–D, 31A

The interparietal ossification is commonly fused to the supraoccipital bone in mammals. For example, in the dog the interparietal ossification fuses to the supraoccipital on day 45 of gestation and is rarely present as an independent bone (Evans and Christensen, 1979:45).

Flower, in speaking of odontocetes (1885:211), mentioned "the immense supraoccipital (SO), with which an interparietal

(IP) is ankylosed." Schulte (1917:376, 382, 390, 392) described the interparietal in *Kogia*. In odontocetes the interparietal can be seen in newborn or fetal specimens as a relatively large ossification lying anterior to the supraoccipital, medial to the parietals, and posterior to the frontals. Soon after birth it fuses with the supraoccipital and loses its identity as a discrete element. The interparietal has been noted in adult mysticetes, such as *Balaenoptera omurai* (Wada et al., 2003: fig. 1). It is likely that the interparietal is more common in Cetacea than previously noted, and has been overlooked because of fusion with adjacent elements.

The interparietal fuses to the supraoccipital in delphinids just before birth. The interparietal in *Tursiops* forms the dorsal midline element of the cranium. It is bordered anteriorly by the frontal. In mature animals the ascending process of the maxilla overlaps the interparietal. Laterally it abuts the parietal and posteriorly the supraoccipital.

Because some landmarks on the occipital region of the skull in *Tursiops* have not been defined, and dissection is needed to help such definitions, we are not entirely certain about the homologies of some features with those of other mammals.

* **dorsal sagittal sinus sulcus** (*sulcus sinus sagittalis dorsalis*) (Figure 12b)

The dorsal sagittal sinus sulcus is formed in the bones along which the **sagittal sinus** flows.

In most mammals this sulcus lies along the **sagittal suture** of the parietals, but in cetaceans it lies along the median portion of the **supraoccipital** bone, the interparietal bone, and may extend a bit onto the frontal bone.

* **external occipital protuberance** (*protuberantia occipitalis externa*) (Figures 5, 12a,c,d)

The external **occipital protuberance** is the median, triangular projection forming the most posterodorsal part of the skull (Sisson, 1910:50; Evans and Christensen, 1979:122; Schaller, 1992:16.26). The *ligamentum nuchae* is attached to it in horses.

In *Tursiops* and other odontocetes, the external occipital protuberance is limited to the median portion of the **nuchal crest**. This shift in position is the result of the anterior shift of the insertion of the dorsal axial muscles with telescoping.

– **external sagittal crest** (*crista sagittalis externa*)

See this term under "Supraoccipital Bone."

= **falciform crest** = internal sagittal crest (Evans and Christensen, 1979:157)

– **highest nuchal line**

See **highest nuchal line** under "Supraoccipital Bone."

– **inferior nuchal line**

See **inferior nuchal line** under "Supraoccipital Bone."

* **internal sagittal crest** (*crista sagittalis interna*) (Figure 12b)

The internal **sagittal crest**, because it is a feature of the dorsal midline of the skull, occurs on the **supraoccipital** bone and interparietal bone in odontocetes, not the parietal as in other mammals. In both odontocetes and other mammals the internal sagittal crest extends anteriorly from the **internal occipital protuberance** and forms the site of attachment of the *falx cerebri* (Evans and Christensen, 1979:157).

In odontocetes the internal sagittal crest is a short crest on the cranial surface of the interparietal and **supraoccipital** bones. The internal sagittal crest is bifurcated in delphinids by the **sagittal sinus**.

– **interparietal process** (*processus interparietalis*)

In noncetacean mammals a process that projects between the parietals represents the interparietal ossification and is called the interparietal process. The interparietal process commonly fuses with the **supraoccipital** (Evans and Christensen, 1979:121).

In *Tursiops* and other odontocetes the interparietal ossification has extended anteriorly to exclude the parietals from the dorsal surface of the cranial cavity.

= **lambdoid crest** = nuchal crest

– **lambdoid suture** (Schulte, 1917:370, 375)

The lambdoid suture in humans is the suture between the parietals and **occipital bone**, so named because it has the shape, when viewed occipitally, of a capital Greek lambda (λ, or inverted Y) (Whitney, 1889–1910:[vol. 4]3334). Vesalius (1543) referred to the lambdoid suture as *sutura λ exprimens* (ibid., 23), *sutura λ imitantis* (ibid., 23, 25), *sutura λ literam* (ibid., 25), *sutura λ referentis* (ibid., 21), *sutura λ simili* (ibid., 21, 23), or λ *graecorum mainsculae literae assimilatur* (ibid., 21). It is abundantly evident that Vesalius likened the shape of the lambdoid suture to the Greek letter lambda (λ).

Because of the development of the interparietal and exclusion of the parietals from the midline in Cetacea, the lambdoid suture does not exist. Anderson (1879:428, 501) mistakenly called the **temporal crest** the lambdoidal ridge.

* **nuchal crest** (*crista nuchae*) (Figures 1, 5, 12a,c,d)

The nuchal crest forms the dividing line between the posterior portion of the skull (occipital region) and the dorsal (anterior) portion. It is normally part of the **supraoccipital** bone (Evans and Christensen, 1979:121; Schaller, 1992:16.28). The nuchal crest has also been known as the **occipital crest** or the **lambdoid crest** (Flower, 1885:135; Wible and Gaudin, 2004:127). In the archaeocete *Dorudon*, Uhen (2004:61) identified the contact between squamosal and exoccipital as forming the lateral part of the nuchal crest.

In *Tursiops* and other odontocetes the nuchal crest extends from the midline, where it forms on the interparietal bone laterally where it terminates on the parietal bone adjacent to and nearly perpendicular to the prominent **temporal crest**. The frontal bone abuts the nuchal crest laterally, but as far as we can tell forms only a supporting structure for the crest. The nuchal crest shifts anteriorly as the cranial vault develops in ontogeny.

Fraser and Purves (1960:8, 89) referred to the nuchal crest as the occipital crest, but Uhen (2004:159) commented that modern cetaceans lack a nuchal crest in the sense of the structure present in archaeocetes.

= **nuchal line** (*linea nuchae*)

See **highest nuchal line, inferior nuchal line, superior nuchal line.**

= nuchal tubercle
See this term under "Supraoccipital Bone."

= occipital crest = nuchal crest

* **occipital fontanelle** (Figure 12a,e)
The occipital fontanelle is a developmental feature that normally occurs in the fetus at the junction of the parietal and occipital centers of ossification (Gray, 1918:196).

In *Tursiops* and other odontocetes the dorsal midline of the skull is occupied by the interparietal. There is evidence of a developmental structure (foramen) in the center of the parieto-interparietal suture (USNM 571643) that may represent the occipital fontanelle.

– parietal foramen (*foramen parietale*)
The parietal foramen is a variable feature in humans, located at the posterior sagittal surface of the parietal bone (Gray, 1918:178). It transmits a vein that communicates with the **sagittal sinus** and sometimes a small branch of the occipital artery (Feneis, 1994:16.39).

We can find no trace of the parietal foramen in the interparietal, **supraoccipital**, or temporal exposure of parietal in *Tursiops* or other delphinids. There are variable paired or unpaired foramina on the parietal in some archaeocetes that may have been identified as postparietal foramina (q.v. under Parietal). Gingerich et al. (2005: fig. 4) showed the parietal foramen opening at the junction of the parietal, squamosal, and occipital in the archaeocete *Makaracetus*.

* **parietal margin of the interparietal bone** (*margo parietalis*) (Figure 12a,c,e)
The parietal margin of the interparietal bone in noncetacean mammals represents those parts of the interparietal and supraoccipital ossifications that border the parietal. It consists of the posterior and lateral margins of the interparietal and the anterior margin of the **supraoccipital** (Evans and Christensen, 1979:121).

Delphinids and most odontocetes have modified the relationships of the parietal through telescoping. The interparietal is relatively large and has extended anteriorly and developed a new anterior margin with the frontal. The parietal margin of the interparietal bone has become the posterolateral border of the interparietal.

– preinterparietals
The preinterparietals are ossifications that occur rarely in humans and other mammals. They are regarded as either Wormian ossicles or separate centers of ossification that are variously related to the more complex condition in reptiles (de Beer, 1937:444).

Preinterparietal ossifications have not been reported in cetaceans.

– sagittal crest
See this term under "Supraoccipital Bone."

* **sagittal sinus** (*sinus sagittalis*) (Figure 12b)
The sagittal sinus drains the dorsal surface of the cranial cavity. It begins at the confluence of the rhinal veins and continues posteriorly in the attached edge of the *falx cerebri*. It terminates posteriorly in the **transverse sinus** (Evans and Christensen, 1979:791).

In cetaceans the sagittal sinus lies along the interparietal and **occipital bones** and may extend onto the frontal bones.

See **dorsal sagittal sinus sulcus**.

– ***septum sinuum frontalium*** (septum of the frontal sinus)
See **septum of the frontal sinus** under "Frontal Bone."

– ***sinus frontalis caudalis*** (caudal frontal sinus)
See **caudal frontal sinus** under "Frontal Bone."

– sulcus for the transverse sinus
See **sulcus for the transverse sinus** under "Parietal Bone."

– superior nuchal line (*linea nuchae superior*)
The superior nuchal line is formed by the insertion of the *m. trapezius* and *m. sternocleidomastoideus* in humans (Gray, 1918:129).

These muscles are normally absent in cetaceans. However, Schulte (1916) reported *trapezius* in a fetus of *Balaenoptera borealis*. Yamada et al. (1998) have tracked down the innervation of what was called the anterior portion of the rhomboideus and have demonstrated accessory nerve input, hence it is *trapezius*. It is possible that the superior nuchal line may be identifiable in cetaceans as the line on the interparietal bone dorsal to the insertion of the *m. semispinalis capitis*.

– temporal line (*linea temporalis*)
See term under "Parietal Bone."

– tentorial process (*processus tentoricus*)
See term under "Exoccipital Bone."

– transverse sinus
See **groove for transverse sinus** under "Supraoccipital Bone."

JUGAL BONE

Malar, Os Zygomaticum

FIGURES 3–5, 13, 14, 32

The jugal in most mammals forms part of the zygomatic arch that bridges the ventral portion of the temporal fossa. Vesalius (1543:22, 23) referred to it as the *os iugale* or first bone of the upper jaw (*os maxillae superioris ossium primum*). Eustachius and Lancisius (1714:111) referred to the jugal as the *os jugale* in one section but *os zygoma* or *zygoma os* in another (ibid., 95, 105). Schulte (1917:398, 399, 401) referred to the zygomatic arch as the suborbital arch or suborbital bar of the malar. The jugal contacts the maxilla and/or the lacrimal anterodorsally and is sutured to the squamosal posteriorly. The jugal has also been called the malar (cheek bone) (Owen, 1866a:27, 28, 36, 38, 39, 41; Schulte, 1917:369–371, 373, 380, 383, 389–391, 393, 398, 401) and the zygomatic bone (Gray, 1918:164; Evans and Christensen, 1979:142; Schaller, 1992:36; Feneis, 1994:26.1). We prefer to limit use of the term "zygomatic" because of possible confusion with other structures (zygomatic process, zygomatic recess, zygomatic nerve, etc.).

Danois (1910:161, figs. iii, iv) described a fibrous infraorbital arcade that runs between the area of the antorbital notch and the exoccipital as the jugal. This structure turned out to be the facial nerve (Schulte, 1917:390). The infraorbital arcade is synonymous with the zygomatic arch (Schulte, 1917:401).

In *Tursiops* and most odontocetes other than Ziphiidae, the jugal is fused with the lacrimal to form a conspicuous lacrimojugal element anterior to the orbit, as detailed under lacrimal. That part of the element anterior to the lacrimojugal cleft presumably is jugal, but the only certainly identified jugal is the slender rod (styliform part) that forms the ventral border of the orbit (Fraser and Purves, 1960:26,51). With such provisos, the jugal in *Tursiops* articulates with the maxilla dorsally and medially, with the lacrimal posterodorsally, and with the squamosal posteroventrally.

= anterior process of the jugal = maxillary process of the jugal = antorbital process (Lavrov and Emry, 1998:753; Muirhead and Wroe, 1998; Ting et al., 2002:29)

Tursiops and other delphinids do not have a distinct anterior process of the jugal in the sense of the **maxillary process of the jugal** (q.v.) seen in humans.

The term "anterior process of the jugal" was recently used, without definition, for fossil dolphins. Kazar (2005:59) mentioned that "the anterior process of the jugal is ankylosed to the lacrimal," and Lambert (2005:658, text-fig. 3) used anterior process of the jugal for what is here termed the "**antorbital process**" (q.v.).

See also **infraorbital border of the jugal**.

= antorbital portion (Owen, 1866a:28) = lacrimal

The antorbital portion, as defined by Owen (1866a:28, pl. 9, figs. 1, 3(26′)) for the delphinid *Orcaella brevirostris*, consists of the fused lacrimal and jugal, or lacrimojugal of our use (see introduction to "Lacrimal Bone"), except for the **styliform part** of the jugal. Owen (1866a:34) also referred to it as the antorbital process of the malar.

Antorbital portion in the sense of Owen is not used for *Tursiops*, but see **antorbital process of the lacrimal**.

= ascending process of the jugal (Naples, 1982: fig. 3, ascending process of jugal, in the sloth *Bradypus*) = frontal process of the jugal

= dorsal process of the jugal = frontal process of the jugal

– frontal process of the jugal (*processus frontalis*)

The frontal process of the jugal bone unites with the **zygomatic process** (postorbital process of our use) of the frontal bone in humans and other mammals (Feneis, 1994:26.6; Schaller, 1992:36.31). In mammals without a postorbital bar, the frontal process is an origin for the postorbital ligament (Wible, 2003:146). Synonyms include ascending process (e.g., Naples, 1982: fig. 3), dorsal process, postorbital process (e.g., Geisler, 2001:43), and zygomatic process (Huxley, 1865:54; Frick and Taylor, 1971:10).

The jugal has lost direct connection with the frontal in delphinids, and the frontal process is not identifiable. However, an indistinct frontal process may be present in archaeocetes, separating the jugal into orbital (anterior) and temporal (posterior) portions.

*** infraorbital border of the jugal** (*margo infraorbitalis*) (Figure 13c)

The infraorbital border of the jugal bone forms the ventral margin of the **orbit** in most mammals. It is relatively thick and beveled medially.

The jugal in *Tursiops* and other delphinids has been reduced. The bone still forms the ventral margin of the orbit posteriorly, but the anterior portion of the jugal has shifted medially to where it still lies along the ventral surface of the orbital contents, but it no longer forms the ventral or anterior margin of the orbit.

See also **anterior process of the jugal**.

*** lacrimal border of the jugal [new term]** (Figure 13a)

The lacrimal border of the jugal bone in delphinids consists of the contact between the jugal and the lacrimal. In *Tursiops* and most odontocetes other than ziphiids, this contact is fused before birth. Owen (1866a:39) referred to the lacrimal border as the "outer facet."

– lateral surface of the jugal (*facies lateralis*)

The lateral surface of the jugal bone in most mammals is convex longitudinally and transversely. This surface usually lies immediately beneath the skin (Evans and Christensen, 1979:142).

In *Tursiops* and other odontocetes the concept of defining surfaces is not applicable. In odontocetes the anterior end of the jugal lies close to (medial in the case of *Tursiops*) the **antorbital notch** and thus the anterior part of the bone lies under the superficial muscles and connective tissue associated with the antorbital notch. In mysticetes there is a definable lateral surface and the bone lies in the normal mammalian situation.

= malar = jugal bone

= malar foramen = zygomaticofacial foramen (Hrdlička, 1902; Simons, 2001)

– marginal tubercle (*tuberculum marginale*)

The marginal tubercle is a prominence usually present on the posterior margin of the **frontal process of the jugal** in humans (Feneis, 1994:26.7; not mentioned in Gray, 1918). The marginal tubercle serves as one of the points of origin of the temporalis muscle.

The jugal has lost direct connection with the postorbital part of the frontal in delphinids and the frontal process is not developed. The temporal muscle originates entirely from the **temporal fossa**.

– masseteric border of the jugal = masseteric margin

The masseteric border of the jugal bone forms the ventral portion of the bone and serves as origin for the strongly developed *m. masseter*.

The masseter is reduced in delphinids to a thin sheet of muscle, highly invested with fat, that originates on the **zygomatic process of the squamosal**, not the jugal bone (Fraser and Purves, 1960:19, 23, 76, 84).

* **maxillary border of the jugal** (Figure 13b)

The maxillary border or surface of the jugal is that portion of the jugal that articulates with the maxilla. In the dog it normally forms an unusually stable articulation with the **zygomatic process of the maxilla** (Evans and Christensen, 1979:143).

The homology of structures in *Tursiops* with those of other mammals is not clear. We cannot judge how the maxillary border of the jugal relates to the **maxillary process of the jugal** (q.v.) in *Tursiops* or to Owen's (1866a:39) antero-internal facet in *Kogia sima*.

* **maxillary process of the jugal [new term]** (Figure 13a,d,e)

The maxillary process of the jugal in humans articulates with the maxilla below the **orbit** (Gray, 1918: fig. 165); it carries the infraorbital border. In an alternative use, the term **"maxillary process" (of the zygomatic arch)** has also been applied to the posterolateral extension of the maxilla that bounds the **temporal fossa** in monotremes and the extinct Multituberculata (see comment by Wible and Rougier, 2000:83). The names **anterior process of the jugal** (Lavrov and Emry, 1998:753, for the Eocene mammal *Hyaenodon*) or anterior process of the zygomatic (e.g., marsupials: Muirhead and Wroe, 1998; basal gliroids: Ting et al., 2002:29) appear to be synonyms for maxillary process of the jugal in the sense of Gray (1918).

Tursiops and other delphinids do not have a distinct maxillary process of the jugal in the sense of other mammals (although see comment under **antorbital process of the lacrimal**). Accordingly, "maxillary process of the jugal" is used here in a new sense for *Tursiops*: the rounded anteromedial portion of the fused lacrimojugal, anterior to the **lacrimojugal cleft** (and thus presumably formed by jugal) that is lodged in the **zygomatic recess** of the maxilla. The homology with parts of the jugal as seen in other mammals is not clear.

– **orbital eminence** (*eminentia orbitalis*)

The orbital eminence is a small tubercle just within the lateral margin of the **orbit** in humans (Feneis, 1994:26.6a). It serves for attachment of the lateral palpebral ligament.

The bony orbit has been modified in cetaceans and the jugal is markedly reduced. The palpebral ligaments have been absorbed into the dense connective tissue around the lateral and dorsal surface of the orbit.

– **orbital process of the jugal**

The orbital process of the jugal in humans is a thick strong plate projecting posteriorly from the **orbit**. Its anteromedial or orbital surface (q.v.) forms part of the floor and lateral wall of the orbit (Gray, 1918:165).

Anderson (1879: pl. 40, fig. 15) labeled the styloform (sic) process the **orbital process** in *Platanista*. He did not discuss the term in the text, where he refers to the styloform process as styloform posterior half.

See **styliform portion**.

– **orbital surface of the jugal** (*facies orbitalis*)

The orbital surface or border of the jugal bone in most mammals is concave longitudinally and transversely. This surface lies adjacent to the **orbit** (Evans and Christensen, 1979:143) and forms the ventral (inferior) border of the orbit in humans (Gray, 1918).

In *Tursiops* and other odontocetes, where the only readily identifiable part of the jugal is reduced to a narrow rod, the concept of defining surfaces is not applicable. However, Owen (1866a:39) used "orbital surface" in describing *Kogia sima*. In mysticetes there is a definable lateral surface and the bones lie in the normal mammalian situation. In archaeocete whales the orbital surface of the jugal is that part of the jugal anterior to the **frontal process of the jugal**.

= **postorbital process of the jugal** = frontal process of the jugal (Geisler, 2001:43)

* **rostral border of the jugal** (Figure 13a,b)

In *Tursiops* the rostral border is the anterior border of the jugal (or lacrimojugal) between the **antorbital process** of the jugal and the **maxillary process of the jugal**. The rostral border may be exposed to dorsal view within the **antorbital notch**.

– **squamosal articulation** (Owen, 1866a:28)

The squamosal articulation in odontocetes is an extremely small, simple planar suture between the jugal and the squamosal bone. This suture is almost never fused with age. Owen (1866a:28) described the squamosal articulation in *Orcaella*.

See **temporal border of the jugal**.

* **styliform part** (Figure 13b)

The bulk of the jugal, posterior to the **maxillary process of the jugal**, is known as the styloform part (sic; styliform part) (Flower, 1868:319; Anderson, 1879:524). Owen (1866a:39) referred to this as the "slender zygomatic style." Schulte (1917:398, 399, 401) referred to the styliform part as the suborbital bar of the malar or the **zygomatic process of the malar** (Schulte, 1917:390, 391).

= **styliform portion** (Owen, 1866a:28) = styliform part

* **temporal border of the jugal** (Figure 13a,c)

The temporal border of the jugal bone (Hrdlička, 1902:274) is that part posterior to the **frontal process of the jugal** that forms the lateral boundary to the **temporal fossa** and posteriorly forms a simple suture with the **squamous part of the temporal bone** (squamosal).

Tursiops and other delphinids lack a frontal process, and the temporal border of the jugal is lost in association with the proximity of the **postorbital process of the frontal bone** with the tip of the **zygomatic process of the squamosal**.

– **temporal process of the jugal** (*processus temporalis*)

The temporal process of the jugal is an elongation of the jugal bone that lies on the posteroventral margin of the jugal (Evans and Christensen, 1979:143). It increases the area of the jugalotemporal suture.

The temporal process is not developed in delphinids.

– **temporal surface of the jugal** (*facies temporalis*)

The temporal surface of the jugal bone is that portion of the bone that lies adjacent to the **temporal fossa** in most mammals. In delphinids the jugal bone is not adjacent to the temporal fossa.

= zygomatic bone = jugal bone

– zygomatic fossa of the jugal

Meng and Wyss (2001:41) noted the presence of a zygomatic fossa for the *m. masseter lateralis* on the lateral surface of the thin, deep zygomatic arch of lagomorphs. The zygomatic fossa of the jugal should not be confused with the **zygomatic fossa of the frontal bone** in the sense of the **infratemporal fossa** (q.v.).

The jugal in *Tursiops* and other odontocetes lacks a zygomatic fossa on the lateral face of the jugal.

– zygomaticofacial foramen (*foramen zygomaticofaciale*)

The zygomaticofacial foramen or **malar foramen** opens on the **lateral surface of the jugal** bone in humans (Feneis, 1994:26.9). It transmits the zygomaticofacial nerve.

The zygomaticofacial nerve is a branch of the maxillary division of the trigeminal nerve. It supplies sensory innervation to the lateral portion of the lower eyelid and surrounding skin in dogs (Evans and Christensen, 1979:916). The ventral area of the **orbit** is relatively open in Cetacea, there is no obvious foramen in the jugal of *Tursiops*, and the zygomaticofacial nerve can reach its destination without penetrating bone.

– zygomaticoorbital foramen (*foramen zygomaticoorbitale*)

The zygomaticoorbital foramen lies on the orbital surface of the temporal bone in humans (Feneis, 1994:26.8). It transmits the zygomatic nerve.

The zygomatic nerve is a branch of the maxillary division of the trigeminal nerve (Evans and Christensen, 1979:914). The zygomatic nerve branches from the maxillary nerve shortly after the maxillary nerve exits the **foramen rotundum**. The zygomatic nerve divides into two rami, the zygomaticofacial nerve and the zygomaticotemporal nerve.

The ventral area of the orbit is relatively open in Cetacea and the zygomatic nerve does not penetrate bone.

– zygomaticotemporal foramen (*foramen zygomaticotemporale*)

The zygomaticotemporal foramen lies on the **temporal surface of the jugal** in humans (Feneis, 1994:26.10). It transmits the zygomaticotemporal nerve.

The zygomaticotemporal nerve supplies sensory innervation to the upper eyelid and surrounding skin (Evans and Christensen, 1979:914–916). The **orbit** is relatively open in cetaceans and the zygomaticotemporal nerve reaches its destination without penetrating bone.

= zygomatic process of the jugal

See **zygomatic process of the malar**.

= zygomatic process of the malar = zygomatic process of the jugal = frontal process of the jugal

Frick and Taylor (1971:10) referred to the zygomatic process of the malar in the camel *Michenia*; Owen, cited in Huxley (1865:54), referred to the zygomatic process of the malar in the sloth *Glyptodon*.

Owen (1866a:39) referred to the zygomatic process of the malar in *Kogia sima*, presumably in reference to the robust, short, descending jugal.

LACRIMAL BONE

Os Lacrimale

FIGURES 3, 4, 6B, 13A,C–E, **14**, 32

The lacrimal (also spelled lachrymal) is normally a small bone in mammals, wedged between the ascending process of the palatine, the maxilla, and the frontal. The lacrimal lies in the medial or anterior portion of the orbit and conveys the lacrimal duct from the orbit to the nasal cavity (Owen, 1866a:39; Flower, 1885:128). In *Tursiops* and odontocetes other than Ziphiidae, the lacrimal is fused with the jugal to form a conspicuous lacrimojugal (q.v.) anterior to the orbit. Early fusion (in fetus or neonate) in *Tursiops* eliminates the lacrimojugal suture. Further, with change in orientation of the orbit, loss of the lacrimal sac and associated bony features, and development of the antorbital notch, the bones differ markedly in shape and position from other mammals. Thus, homologies of parts of the lacrimal and jugal are not clear.

In *Tursiops* the distal slender rod of the jugal (styliform part) is readily identifiable; comparison with Ziphiidae suggests that the anterior and anteromedial parts of the lacrimojugal probably also represent the jugal. The medially placed lacrimojugal cleft may be homologous with part of the lacrimojugal suture; the relationship of the cleft to the lacrimal foramen, fossa, and sulcus of other mammals is uncertain. The posterior part of the lacrimojugal is presumed to consist of lacrimal. The lacrimal is notably enlarged in *Kogia* (Schulte, 1917:369, 380, 389–391, 398, 401).

In *Tursiops* the lacrimal is a thin, broad, wedge-shaped bone lying ventral to the antorbital process of the maxilla, anterior to the preorbital process of the frontal bone, and posterior to the anterior end of the jugal. Cetaceans are considered to lack the lacrimal gland and lacrimal duct (Slijper, 1962:229), and it appears that the lacrimal is imperforate.

= anterior lacrimal crest = anterior lacrimal crest of the maxilla

– anterior lacrimal process (*processus lacrimalis rostralis*)

The anterior lacrimal process is a small process on the **facial surface of the lacrimal** bone in horses and pigs (Schaller, 1992:30.27).

The anterior lacrimal process is not developed in cetaceans.

= antorbital notch

See "Maxilla."

= antorbital pit of the lacrimal = external lacrimal fossa (Geisler, 2001:43)

Not to be confused with **antorbital fossa**.

= antorbital process

See "Maxilla."

= antorbital process of the lacrimal

See **anterior process of the jugal**.

* **antorbital process of the lacrimal [new context]** (Figure 14a,b)

In *Tursiops* and other delphinids the anterolateral part of the lacrimal or lacrimojugal may project anteriorly, beyond the level of the **antorbital notch**. The projection, which is conspicuous ventrally and may be visible dorsally, is the antorbital process; the term is modified from that of Owen (1866a:28). "Antorbital" is preferred because of the close association with the antorbital region in general (see Diagram 2, associated with "antorbital notch" entry under "Maxilla"). "Antorbital process" should not be confused with the more-posteriorly placed **preorbital process of the lacrimal**, which is the **ventral process** of presumed lacrimal adjacent to the **preorbital process of the frontal**.

The term "**anterior process of the jugal**" was recently used, without definition, for fossil dolphins (see Kazar, 2005:59; Lambert, 2005:658, text-fig. 3), apparently in the sense of antorbital process as used here. The feature illustrated by Lambert (2005: text-fig. 3) could be jugal or lacrimal. To reduce uncertainty, we use the term "**antorbital process of the lacrimal**" (q.v.).

See also **infraorbital border of the jugal**.

– antorbital vacuity (Brooke, 1879:884)

The antorbital vacuity (Brooke, 1879:884) forms at the junction of the lacrimal, frontal, nasal, and maxilla so that the lacrimal is excluded from contact with the nasals. This forms an open space at the junction of (between) the lacrimal, frontal, nasal, and maxilla and occurs independently in a number of artiodactyls (Janis and Scott, 1987:22). Geisler and Uhen (2003: S23) referred to the antorbital vacuity as the antorbital pit.

Cetaceans do not develop an antorbital vacuity.

– aperture for the lacrimal sinus (*apertura sinus lacrimalis*)

The aperture for the lacrimal sinus is the opening from the nasal cavity into the **lacrimal sinus** in artiodactyls (Sisson, 1910:126; Schaller, 1992:32.2).

The lacrimal sinus is a paranasal sinus and is not developed in cetaceans (Fraser and Purves, 1960:5, 75).

* ***dacryon*** (Dox et al., 1979:119) (Figures 3, 4, 14a,c)

The *dacryon* in humans is the craniometric point where the lacrimal, frontal, and maxillary meet, at the angle of the ocular orbit (Dox et al., 1979:119).

The cetacean **orbit** has been modified extensively from terrestrial mammals and humans. In *Tursiops* and other delphinids, the *dacryon* is on the **facial surface of the lacrimal** where it meets the frontal and maxilla.

– external lacrimal fossa (*fossa lacrimalis externa*)

The external lacrimal fossa lies on the anterior portion of the **facial surface of the lacrimal** bone in artiodactyls, including deer (Janis and Scott, 1987:23), and pigs and sheep (Schaller, 1992:30.28). **Antorbital pit of the lacrimal** (Geisler, 2001:43) is a synonym. The external lacrimal fossa should not be confused with the **lacrimal fossa** (q.v.), that is, the **fossa for the lacrimal sac**.

The external lacrimal fossa is not developed in *Tursiops* or other cetaceans.

– facial surface of the lacrimal

The facial surface of the lacrimal is that portion of the lacrimal bone exposed outside of the orbit on the face, separated from the orbital part by the **orbital crest** of the lacrimal bone. The facial surface is variable in size in mammals, being negligible in the dog but large in *Odocoileus* and other artiodactyls. The facial surface is also apparent in Archaeoceti (see Uhen, 2004) and the archaic odontocete *Simocetus* (Fordyce, 2002).

Major changes in shape and position of the lacrimal and jugal in *Tursiops* and most other odontocetes means that the facial surface and associated features cannot be identified clearly.

See **lateral surface of the lacrimojugal bone**.

– fossa for the lacrimal sac (*fossa sacci lacrimalis*)

The fossa for the lacrimal sac lies at the middle of the dorsal surface of the **orbital surface of the lacrimal** bone, at the orbital opening of the **lacrimal canal**.

The fossa for the lacrimal sac in cetaceans is missing due to the absence of the lacrimal gland.

– fossa for the ventral oblique muscle (*fossa m. obliqui ventralis*)

A groove for the origin of the ventral oblique muscle (*m. obliqui ventralis*) frequently exists on the palate adjacent to the suture between the palatine, lacrimal, and maxillary bones in dogs, pigs, and cattle (Evans and Christensen, 1979:287; Schaller, 1992:30.33).

Tursiops appears not to have a fossa for the origin of the ventral oblique muscle. The bony origins of extrinsic eyeball muscles in odontocetes are poorly known.

– frontal process of the lacrimal (*processus frontalis*)

The frontal process of the lacrimal bone is a narrow strip of the **orbital margin** of the lacrimal bone that projects dorsally on the orbital surface in carnivores (Evans and Christensen, 1979:145; Schaller, 1992:30.25). In such cases, the frontal process is more or less equivalent to the **orbital crest** of the lacrimal bone. The lacrimal is enlarged in *Odocoileus* and other artiodactyls, so that there is a large facial surface rather than a frontal process.

A frontal process of the lacrimal bone does not appear to be distinct in *Tursiops*.

– infratrochlear notch (*incisura infratrochlearis*)

The infratrochlear notch lies in the anterior margin of the lacrimal bone where it passes the infratrochlear nerve in cattle (Schaller, 1992:30.24). The infratrochlear nerve is a branch of the ophthalmic division of the trigeminal nerve serving the anterior surface of the upper eyelid.

In cetaceans the **orbit** is open and the infratrochlear nerve reaches the eyelid without notching bones.

– lacrimal bulla (*bulla lacrimalis*)

The lacrimal bulla is a large thin-walled protuberance into the **orbit** in ruminants (Sisson, 1910:121; Schaller, 1992:30.34). It contains an extension of the **maxillary sinus**.

Paranasal sinuses are not developed in cetaceans (Fraser and Purves, 1960:5, 75), and the maxillary sinus is absent in *Tursiops*.

– lacrimal canal (*canalis lacrimalis*)

The lacrimal canal begins in the **fossa for the lacrimal sac**, runs ventrolaterally through the lacrimal bone and exits in the nasal cavity at the anteroventral apex of the lacrimal bone. It carries the lacrimal duct.

The lacrimal canal is absent in *Tursiops* and other Cetacea, and the lacrimal glands and ducts have not been described. However, a lacrimal canal, with associated channels in the lacrimal, has been reported in Archaeoceti (Kellogg, 1936: fig. 31c; Uhen, 2004:56, fig. 26).

– lacrimal fenestra (Wible and Gaudin, 2004:125)

Wible and Gaudin (2004:158) noted this variably developed depression (sometimes a foramen) for the origin of an extraocular muscle, the *musculus obliquus*. The feature occurs in some armadillos, and in the dog (Evans and Christensen, 1979:1111, figs. 20–26); it may be at the junction of the lacrimal, frontal, and maxilla (Wible and Gaudin, 2004) or in the lacrimal immediately dorsal to the **infraorbital foramen** (Novacek, 1986).

Tursiops appears not to have a lacrimal fenestra for the origin of the oblique muscle. The bony origins of extrinsic eyeball muscles in odontocetes are poorly known.

– lacrimal foramen (*foramen lacrimale*)

The lacrimal foramen is the opening for the lacrimal duct in the lacrimal bone (Schaller, 1992:30.30). The foramen may be paired, as in *Odocoileus* and other cervids (e.g., Janis and Scott, 1987, as the **lacrimal orifice**).

The lacrimal gland and its accessories are not developed in Cetacea (Owen, 1866a:30), and *Tursiops* appears to lack a lacrimal foramen.

– lacrimal fossa

In humans (Gray, 1918:137, 164) the lacrimal fossa is developed in the lacrimal, maxilla, and sometimes the frontal. The **lacrimal sulcus** contributes posteriorly. It contains part of the lacrimal sac (Gray, 1918: fig. 159, **fossa for the lacrimal sac**) and nasolacrimal duct.

The lacrimal fossa is absent in *Tursiops* and other delphinids.

See also **lacrimal sulcus**.

– lacrimal hamulus (*hamulus lacrimalis*)

The lacrimal hamulus in humans is a small, hook-like projection at the ventral end of the **posterior lacrimal crest** at the entrance to the **nasolacrimal canal** (Gray, 1918:164; Feneis, 1994:20.24).

The lacrimal hamulus and posterior lacrimal crest are not developed in odontocetes.

= lacrimal orifice = lacrimal foramen (Janis and Scott, 1987:24)

– lacrimal pit (Brooke, 1879:884)

Brooke (1879:884) defined a lacrimal pit or **lacrimal fossa** as a depression in the facial plate of the lacrimal that served as a diagnostic character of some cervids. The relationship of this lacrimal pit to the **preorbital fossa** (q.v.) of some other artiodactyls (e.g., pig: Sisson, 1910:140) needs to be clarified.

Cetaceans do not develop a lacrimal pit.

– lacrimal sinus (*sinus lacrimalis*)

The lacrimal sinus is a paranasal sinus developed in artiodactyls (Schaller, 1992:32.1; Sisson, 1910:126). It lies in the lacrimal bone and opens through the **aperture for the lacrimal sinus** into the nasal cavity.

Paranasal sinuses are not developed in cetaceans (Fraser and Purves, 1960:5, 75), and the lacrimal sinus is absent in *Tursiops*.

– lacrimal sulcus (*sulcus lacrimalis*)

The lacrimal sulcus is a **longitudinal groove** on the lacrimal, which, together with a groove on the medial or **nasal surface of the maxilla**, forms the **lacrimal fossa** in humans (Gray, 1918:159f; Feneis, 1994:22.19). It lodges the lacrimal sac and the nasolacrimal duct (Gray, 1918:189; Feneis, 1994:334.21).

The lacrimal sulcus is lacking in *Tursiops* and other delphinids; the **lacrimojugal cleft** is not clearly homologous with the lacrimal sulcus.

See this term also under "Maxilla."

– lacrimojugal bone

In *Tursiops* as in many other Odontoceti (e.g., *Kogia*; Schulte, 1917:400), the jugal becomes fused to the lacrimal sufficiently early in development that it is not possible to differentiate the two ossifications. The bone in this situation has been referred to as the "lachrymo-malar" (Schulte, 1917:400). We prefer "lacrimojugal."

See also **lateral surface of the lacrimojugal bone** and introduction to "Lacrimal Bone."

*** lacrimojugal cleft [new term]** (Figure 14b,d,e)

In *Tursiops* the medial face of the fused lacrimal and jugal has a reentrant, conspicuous in ventral view, which is here termed the lacrimojugal cleft. It is possible that the cleft is homologous with part of the lacrimojugal suture. Whether it is a vestige of structures associated with the **lacrimal sulcus** is uncertain. In *Tursiops* the cleft is occupied by the **lacrimojugal crest** of the maxilla. In one skull, USNM 550403, three grooves (associated with two ridges) are directed medially into the right lacrimojugal cleft. It is not known what soft tissues are associated with the grooves and ridges.

*** lacrimomaxillary fossa [new term]** (Figures 2, 14b)

In *Tursiops* the ventral surface of the lacrimal and associated maxilla may develop a prominent lacrimomaxillary fossa between the medial and posteromedial processes of the lacrimal and the region of the **ventral infraorbital foramen**. The soft tissue relationships are uncertain for the lacrimomaxillary fossa. This fossa may be the structure that Owen (1866a:28) termed the **malomaxillary fossa** in *Orcaella*, but his description was not clear enough to be sure, and he did not identify the feature on an illustration.

= lateral part of the frontal sinus

See "Frontal Bone."

*** lateral surface of the lacrimojugal bone** (Figure 14a–e)

In *Tursiops* and other cetaceans major changes in shape and position of the lacrimal and jugal mean that the facial surface and **orbital crest** as seen in other mammals are not readily identifiable. Alternative names are thus needed for lateral parts of the lacrimojugal.

The lateral surface of lacrimal (or **lacrimojugal bone**) is defined as the elongate to sometimes triangular face exposed to lateral view, lying ventral and/or anteroventral to the **preorbital**

process of the frontal and the anterolateral portion of the maxilla. In *Tursiops* the lateral face carries the preorbital process (posteroventrally), the **ventrolateral crest of the lacrimojugal** (ventrally), and the **maxillofrontal crest** (dorsally).

= **malomaxillary fossa** (Owen, 1866a:28) = lacrimomaxillary fossa

Owen, in his description of the skull of *Orcaella*, described the "rough malomaxillary fossa" as lying external to the **antorbital fossa** (**pterygopalatine fossa**). He labeled the malomaxillary fossa as (e) and the antorbital fossa as (d) in the text (1866a:28) but did not include (d) and (e) in the illustrations (Owen, 1866a: pl. 9). We have interpreted this as the **lacrimomaxillary fossa** (q.v.). Because the malomaxillary fossa is not clearly identified, and the name appears not to have been used in later literature, it is not applied to *Tursiops* here. The new term "lacrimomaxillary fossa" may be equivalent.

= **maxillary process**

See **maxillary process of the jugal**.

* **maxillofrontal crest** [**new term**] (Figure 14a,e)

The maxillofrontal crest on the lacrimal in odontocetes consists of the portion of the lacrimal bone that projects dorsally into the cleft formed between the **ascending process of the maxilla** and the **preorbital process of the frontal**.

* **medial process of the lacrimal** [**new term**] (Figure 14a,b,d,e)

The medial process of the lacrimal bone is here defined as the medially projecting process that lies posterior to the **lacrimojugal cleft**. Its shape in *Tursiops* is extremely variable, particularly in ontogeny. In delphinids, it is affected by resorption associated with development of the fossa for the **anterior sinus**; in *Tursiops* specimen USNM 550403, the ventral surfaces of both left and right medial processes are smoothed and more or less continuous anteromedially with the smooth surface of the antorbital sinus fossa.

– **nasal surface of the lacrimal bone** (*facies nasalis*)

The nasal surface of the lacrimal bone forms a small portion of the nasal cavity.

The lacrimal bone is excluded from the nasal cavity in cetaceans.

– **nasolacrimal canal** (*canalis nasolacrimalis*)

The nasolacrimal canal lies in the lateral wall of the nasal cavity and contains the nasolacrimal duct (Schaller, 1992:14.9; Feneis, 1994:32.7). The nasolacrimal canal begins in the lacrimal, runs ventrally into the maxilla, issuing forth ventral to the **nasoturbinate crest** in the dog. The nasolacrimal canal is also known as the **lacrimal canal** (Gray, 1918:164; Evans and Christensen, 1979:141,144). Vesalius (1543:48; Vesalius et al., 1998:131) referred to the nasolacrimal canal as the *foramen . . . quod ex magno internove oculi angulo in narium cavitatem recta deorsum pertinet*.

The nasolacrimal canal is not developed in modern cetaceans.

* **orbital crest** (Figure 14a–e)

The orbital crest forms the lacrimal bone's contribution to the **orbital margin** (Evans and Christensen, 1979:144). In the dog the orbital crest and **frontal process of the lacrimal** are the same. The structure is also termed **orbital rim** and orbital margin of the lacrimal (e.g., in artiodactyls; Janis and Scott, 1987:23, 24).

In *Tursiops* and other delphinids the lacrimal and jugal are so modified that the orbital crest in the sense of artiodactyls is not identifiable.

See **lateral surface of the lacrimojugal bone**, **preorbital process of the lacrimal**, and **ventrolateral crest of the lacrimojugal**.

= **orbital margin** = orbital crest (Janis and Scott, 1987:23, 24)

= **orbital rim** = orbital crest (Janis and Scott, 1987:23, 24)

* **orbital surface of the lacrimal** (*facies orbitalis*) (Figure 14a–e)

The orbital surface of the lacrimal bone is the surface that is exposed in the **orbit**. It is concave and bears the opening of the **lacrimal canal** and the **fossa for the lacrimal sac**.

In *Tursiops* and other odontocetes the only portion of the lacrimal bone that is on the orbital surface is the small **orbital crest**.

– **outer facet of the malar**

Owen (1866a:39) referred to a structure he called the outer facet of the malar. This may be related to the **lateral surface of the lacrimojugal bone**, **preorbital process of the lacrimal**, **ventrolateral crest of the lacrimojugal**, or the **orbital crest** of the lacrimal bone.

– **posterior lacrimal crest** (*crista lacrimalis posterior*)

The posterior lacrimal crest in humans is a vertical ridge that divides the **orbital surface of the lacrimal** into two parts (Feneis, 1994:20.22). It forms the posterior border of the entrance to the **nasolacrimal canal**.

The nasolacrimal canal and posterior lacrimal crest are not developed in *Tursiops* and other cetaceans.

See also **anterior lacrimal crest**.

– **posterior lacrimal process** (*processus lacrimalis caudalis*)

The posterior lacrimal process lies on the supraorbital margin of the lacrimal bone in ruminants and horses (Schaller, 1992:30.26). It forms the dorsal border to the **infratrochlear notch**.

The **orbit** has become simplified in cetaceans and the infratrochlear notch and posterior lacrimal process are absent.

* **posteromedial process of the lacrimal** [**new term**] (Figure 14a–e)

The posteromedial process of the lacrimal in *Tursiops* is the lobe-like posterior projection of the medial surface of the lacrimal, as seen in ventral view, that lies just anterior to the frontal. It is conspicuous in juveniles but may be partly obscured by maxilla in adults.

* **preorbital process of the lacrimal** [**new term**] (Figures 3, 14c)

The preorbital process of the lacrimal in adult *Tursiops* is the ventral projection of the facial surface (or lateral border) of the lacrimal, pronounced in lateral view that arises at the posterior end of the lacrimal just anterior to the **orbit**. It is associated closely with the **preorbital process of the frontal**. A preorbital ridge may develop medial to the preorbital process.

* **preorbital ridge of the lacrimal [new term]** (Figure 2)

The preorbital ridge of the lacrimal in adult *Tursiops* is a variably distinct ventral elevation on the lacrimal that arises at the apex of the preorbital process and extends medially or posteromedially.

* **rostral border of the lacrimal** (Schulte, 1917:390) (Figure 14a,b,d)

The rostral border of the lacrimal is the anterior border. The rostral border is just medial to the facial surface.

* **ventrolateral crest of the lacrimojugal [new term]** (Figures 2, 14b–d)

In *Tursiops* major changes in shape and position of the lacrimal and jugal mean that the facial surface and **orbital crest** as seen in other mammals are not readily identifiable. Alternative names are thus needed for lateral parts of the lacrimojugal.

In *Tursiops* the ventrolateral crest is the prominent inflection between the lateral surface and the ventral surface of the lacrimal or lacrimojugal. Posteriorly, the ventrolateral crest passes into the **preorbital process of the lacrimal**.

MANDIBLE

Mandibula

FIGURE 15

The mandible, or lower jaw (Schaller, 1992:38.1; Evans and Christensen, 1979:146; Feneis, 1994:26.11; Gray, 1918:172), is usually joined to the skull by a synovial joint, the temporomandibular joint. This joint is one of the characteristics of mammals in that it lies between the mandible and the squamosal and not between the articular and the quadrate as it does in reptiles. Embryologically the mandible in Cetacea arises from the dentary; the articular and the quadrate have been incorporated into the middle ear as the malleus and the incus, respectively (Romer, 1955:520). Vesalius (1543:43) referred to the mandible as *maxilla inferiori* (lower jaw).

In odontocetes the temporomandibular joint has lost its synovial cavity (Perrin, 1871:807; Pivorunas, 1977:299) and become an extended fibrous joint or syndesmosis (sensu Evans and Christensen, 1979:225). In delphinids the mandible has become long and narrow and the coronoid process has been reduced. The mandibular foramen has become extremely large and filled with relatively clear adipose tissue (intra-mandibular fat body). Schulte (1917:376) described the mandible in *Kogia*.

The term "mandible" is used as both singular and plural in the literature. "Mandibles" is often used for the plural (e.g., Wible and Gaudin, 2004:146), whereas "hemi-mandible" is rarely used for the single right or left element in the mammalian literature. Symphysis is the feature that necessarily involves both mandibles, whereas the symphyseal surface may be viewed on a single mandible.

* **acoustic window** (Norris, 1968:298, 308–312) (Figure 15c)

Norris (1968:298, 308–312) defined the acoustic window as an area in the external lamina of the mandible, directly lateral to the **mandibular foramen**, that was markedly thin. Norris hypothesized that this area had thinned to form an "acoustic window" for the reception of sound. This area of the mandible is central to the "**pan bone**" of sperm whalers (Whitney, 1889–1910:[vol. 5]4253).

* **alveolar border of the mandible** (*arcus alveolaris*) (Figure 15c)

The alveolar border of the mandible in the dog is the dorsal border that bears the **dental alveoli** (Evans and Christensen, 1979:146). The term is applicable to *Tursiops* and other delphinids.

= **alveolar foramina of the mandible** (Kellogg, 1968: figs. 40, 48) = gingival foramina

* **alveolar groove of the mandible** (*sulcus alveolaris*) = alveolar gutter (Figure 15a)

The **alveolar groove** of the mandible is the groove on the dorsal surface of the mandible that contains the **dental alveoli**. This feature appears early in embryonic life, before the embryonic teeth have formed, and controls the sites at which teeth are formed. It also is known as the **dental groove** (Whitney, 1889–1910:[vol. 11]548). Alveolar grooves are found in adults of some species of odontocetes and baleen whales (Owen, 1866a:38; Schulte, 1917:375–377, 389), and in the fossil delphinid *Australodelphis* (see Fordyce et al., 2002). The term "dental sulcus" was used by Schulte (1917:376) to refer to confluent or indistinctly separate dental alveoli in *Kogia*, in other words, the alveolar groove.

= **alveolar gutter**

See **alveolar groove of the mandible**.

– **alveolar juga** (*juga alveolaria*)

Alveolar juga are smooth elevations caused by roots of teeth that are expressed on the **external surfaces of the maxilla** and mandible.

Alveolar juga are not present in delphinids and are not developed in most odontocetes. In some ziphiids that have relatively well-developed teeth (e.g., *Mesoplodon densirostris*), there is a structure that could be homologous with the alveolar juga. The alveolar juga are present in some fossil cetaceans, for example *Waipatia*.

* **alveolar margin of the mandible** (*margo alveolaris*) (Figure 15c)

The alveolar margin of the mandible is the border of the process alveolaris (Schaller, 1992:38.7).

Odontocetes have a normal **alveolar margin**.

= **alveolar portion** (*pars alveolaris*) = alveolar process of the mandible

* **alveolar process of the mandible** (*processus alveolaris*) (Figure 15c)

The alveolar process of the mandible is the part of the mandible that bears the **dental alveoli**. The alveolar process of the mandible is also known as the **alveolar portion** (Schulte, 1917:376). We have chosen to use the term "alveolar process of the mandible" to parallel the terminology use for the maxilla (i.e., **alveolar process of the maxilla**).

= **alveolar sulcus** (Schulte, 1917:375–377) = alveolar groove of the mandible

= alveolar walls = interalveolar septa

= alveolus (Owen, 1866a:29) = dental alveoli

* **angle of the mandible** (*angulus mandibulae*) (Figure 15b,c,e)

The angle of the mandible is the posteroventral portion of the bone. It bears the angular process (Evans and Christensen, 1979:148). ***Gonion*** (q.v.) is equivalent.

The angle is present in *Tursiops* and other odontocetes (Owen, 1866a:41; Fraser and Purves, 1960:6, 16).

Angle of the mandible and angular process have been used interchangeably. The former appears more common in human anatomy; the latter is more common in comparative anatomy and vertebrate paleontology.

* **angular process of the mandible** (*processus angularis*) (Figure 15c,e)

The angular process of the mandible is the area of insertion of the medial pterygoid muscle (*m. pterygoideus medialis*) medially and the masseter muscle (*m. masseter*) laterally (Evans and Christensen, 1979:148, 294; Schaller, 1992:102.22; Feneis, 1994:80.17). The medial pterygoid muscle is also known as the internal pterygoid muscle (*m. pterygoideus internus*) (Gray, 1918:387; Fraser and Purves, 1960:12).

The *m. pterygoideus medialis* is weakly developed in *Tursiops* and other delphinids. The angular process is the ventrolateral surface of the posterior portion of the mandible and the medial edge of the mandible that lies ventral to the **mandibular fossa** (Fraser and Purves, 1960:1, 6, 12, 13, 14, 18, 22, 23, 26).

See also **angle of the mandible**.

* **base of the mandible** (*basis mandibulae*) (Figure 15c)

The base of the mandible is the lower portion of the **body of the mandible** minus the **alveolar portion** (Feneis, 1994:26.13).

* **body of the mandible** (*corpus mandibulae*) = mandibular body (Figure 15c)

In the dog the mandible consists of paired horizontal bodies, one right and one left, that bear the teeth. The vertical parts or ramuses (rami) form most of the area for muscular attachment (Evans and Christensen, 1979:146). Owen (1866a:41) referred to the body of the mandible as the horizontal ramus or the mandibular ramus (1866a:42).

In *Tursiops* we have defined the body of the mandible as ending at the level of the last tooth.

* **buccal surface of the mandible** (*facies buccalis*) (Figure 15a)

The buccal surface of the mandible is that part of the lateral surface that faces the cheeks in the dog (Evans and Christensen, 1979:147). It is posterior to the labial surface. In some mammals with extremely mobile lips and cheeks, the distinction between the buccal and labial surface is not well defined and the terms buccal, facial, and labial are sometimes confused.

In odontocetes, with relatively rigid lips and cheeks, the distinction between buccal and labial is obvious in live or freshly dead animals. The border between the two surfaces lies slightly anterior to the posterior teeth, at the level of the angle of the mouth. The position of the border between buccal and labial surfaces is not distinct on the isolated mandible.

* **condylar articular surface** (Flower, 1885) (Figure 15c)

The condylar articular surface in *Tursiops*, as in other mammals, is that surface of the **mandibular condyle** that is in direct articulation with the **mandibular fossa** of the squamosal bone.

= condylar plate = pan bone (in *Platanista,* Anderson, 1879:528)

– condylar process of the mandible

In the yellow armadillo (Wible and Gaudin, 2004:146) the condylar process carries but is distinct from the **mandibular condyle**, and forms an attachment for the lateral pterygoid muscle. In the laboratory mouse the condylar process is that part of the mandible that projects posteriorly, distinct from the adjacent coronoid and angular processes (Hall, 2003: fig. 4). The condylar process is also known as the **mandibular neck.**

Tursiops lacks a distinct condylar process in the sense of other mammals. Murie (1873:284; see Fraser and Purves, 1960:8) mentioned the association of pterygoid muscles with the “articulating condylar process of the mandible” in *Globicephala*. In the medial face of the mandible of *Tursiops* (USNM 550403), the region of the **mandibular notch** between the **mandibular condyle** and the **coronoid process** is thickened and rough, possibly reflecting muscle insertion.

The condylar process of the mandible is not to be confused with the **condyloid process** (mandibular condyle).

= condyloid articular process (Anderson, 1879:365) = mandibular condyle

* **condyloid crest** (Figure 15a,c)

The condyloid crest is a low crest that extends anteriorly on the **buccal surface of the mandible** from the **condyloid process** (Evans and Christensen, 1979:148).

In *Tursiops* and other odontocetes the low condyloid crest disappears just below the **coronoid crest**.

= condyloid process = mandibular condyle

Not to be confused with condylar process (**mandibular neck**).

* **coronoid crest** (Figure 15a,c,e)

The coronoid crest lies on the anterior surface of the **coronoid process** in the dog (Evans and Christensen, 1979:148).

In *Tursiops* the coronoid crest lies between the coronoid process and the tooth row. It is a low, wide crest in newborns that forms a distinct narrow ridge as the animal matures.

* **coronoid process** (*processus coronoideus*) (Figure 15a,c,e)

The coronoid process in the dog is the most dorsal part of the mandible, located between the teeth and the **mandibular condyle** (Evans and Christensen, 1979:148). It serves for attachment of the tendon of insertion of the *m. temporalis* (Evans and Christensen, 1979:148).

In *Tursiops* and other delphinids the coronoid process is relatively low and situated immediately anterior and dorsal to the mandibular **condyloid process** (condyle) (Owen, 1866a:29, 41; Fraser and Purves, 1960:6, 22).

* **dental alveoli** (*alveoli dentales*) (Figure 15a)

The dental alveoli are receptacles in the mandible and maxilla for the tooth roots.

= **dental canal** (Anderson, 1879:528) = mandibular canal

= **dental foramen** (Anderson, 1879:528; Flower, 1885:216; Schulte, 1917:376) = mandibular foramen

– **digastric fossa** (*fossa digastrica*)

The digastric fossa is a small depression at the ventromedial portion of the **body of the mandible** near the symphysis. It is the attachment site for the anterior belly of the digastric (Feneis, 1994:26.20; not in Evans and Christensen, 1979; not in Schaller, 1992). The anterior attachment of the digastric in delphinids is extremely fatty and difficult to define (Lawrence and Schevill, 1965:12) and there is no digastric fossa.

= **external mandibular angle** = angle of the mandible (*angulus mandibulae*)

– **facial vessel notch** (*incisura vasorum facialium*)

The facial vessel notch is a wide, low depression on the ventral surface of the mandible just anterior to the angular process (Schaller, 1992:38.9). The facial artery and vein pass over the notch.

In *Tursiops* and other delphinids the facial vessels pass around the lower jaw without apparently affecting it. There does not seem to be a facial vessel notch.

= **gingival foramina** (Cope, 1895:141) = alveolar foramina of the mandible

Kellogg (1968: figs. 40, 48) identified the gingival or **alveolar foramina of the mandible** dorsally on the medial face of the mandible in fossil mysticetes. The gingival foramina are the medial openings of the terminal branches of the **mandibular canal**. The lateral openings are the **mental foramina**. We prefer to use "gingival foramen" because alveolar foramen is likely to be confused with alveolar foramina of the maxilla, which are internal to the alveoli.

Although the nerves and vessels from the mandibular canal reach the medial surface of the mandible, they do not coalesce into discrete foramina in *Tursiops*.

* ***gnathion*** (Figure 15a)

Gnathion is the lowest point of the midline of the **mandibular symphysis** (Dox et al., 1979:187).

Tursiops has a normal *gnathion*.

= ***gonion*** = angle of the mandible

The *gonion* in humans is the most posterior, inferior, and lateral point of the **external mandibular angle** (Dox et al., 1979:187).

Tursiops has a normal *gonion*; it is equivalent to the **angle of the mandible**.

= ***gonys*** (Dall, 1874:298 in Scammon, 1874) = symphysis

Gonys is the term applied to the keel or lower outline of the bill (in birds) as far as the mandibular rami are united (Whitney, 1889–1910:[vol. 3]2572). We have seen it used in only one instance (Dall, 1874:298 in Scammon, 1874), where it pertained to the symphysis of the jaw in *Orcinus*.

* **groove for remains of Meckel's cartilage** (Figure 15)

Meckel's cartilage is the remains of the primitive cartilaginous jaw that the mandible forms around (Flower, 1885:147, 221, fig. 67). Depending on the ontogenetic development of the species, the remains of this cartilage form a groove at one or both ends of the ventral portion of the mandible.

In delphinids this groove is present on the medial side of the anteroventral portion of both sides of the mandible. Eales (1950:9) documented it quite well in the narwhal (*Monodon monoceros*).

– **incisive portion of the mandibular body** (*pars incisiva*)

The *pars incisiva* of the **mandibular body** bears the incisor teeth (Evans and Christensen, 1979:146).

Tursiops and other odontocetes are homodont, the lower incisors are not identifiable, and the incisive portion is not applicable. However, the *pars incisiva* should be identifiable in heterodont extinct Cetacea.

= **inferior dental canal** (Flower, 1885:211 fig.) = mandibular canal

= **inferior dental foramen** (Schulte, 1917:376) = mandibular foramen

– **interalveolar margin** (*margo interalveolaris*)

In the dog the dorsal border of the mandible between the canine and first premolar is larger than the others and is known as the interalveolar margin (Evans and Christensen, 1979:147). The term may be applied to any mammal in which there are **diastemata** between the teeth, such as moose (see Clifford and Witmer, 2004:346, fig. 6). The interalveolar margin is also known as the diastematic ridge.

Tursiops and other delphinids have closely spaced teeth, and the interalveolar margin is not developed. An interalveolar margin may be present in heterodont extinct Cetacea.

* **interalveolar septa** (*septa interalveolaria*) (Figure 15a)

Interalveolar septa are the bony partitions between adjacent teeth (Evans and Christensen, 1979:140; Schaller, 1992:34.14). The term "interalveolar septa" is also used to refer to spaces on the **alveolar border of the mandible** between the adjacent premolar teeth (Evans and Christensen, 1979:147).

Interalveolar septa are variably developed in *Tursiops*. The septa are characteristic of all odontocetes except those with reduced dentition.

= **internal alveolar plate** (Anderson, 1879:528)

See **symphysial plate**.

– **interradicular septa** (*septa interradicularia*)

Interradicular septa are the bony partitions between the roots of an individual tooth (Evans and Christensen, 1979:140).

Tursiops and other odontocetes have simple teeth with only one root, so this term does not apply. Interradicular septa are present in heterodont extinct Cetacea.

* **labial surface of the mandible** (*facies labialis*) (Figure 15a,c)

The labial surface of the mandible faces the lips (Evans and Christensen, 1979:147). In some mammals with extremely mobile lips and cheeks, the distinction between the buccal and labial surface is not well defined and the terms buccal, facial, and labial are sometimes confused.

In odontocetes, with relatively rigid lips and cheeks, the distinction between buccal and labial is obvious in live or freshly dead animals. The border between the two surfaces lies slightly anterior to the posterior teeth, at the level of the angle of the mouth. In *Tursiops* the position of the border between buccal and labial surfaces is not distinct on the isolated mandible.

* **lingual surface of the mandible** (*facies lingualis*) (Figure 15a)

The lingual surface of the mandible faces the tongue (Evans and Christensen, 1979:147).

– *lingula mandibulae*

The *lingula mandibulae* is a sharp bony spine that projects posteriorly from the anterior margin of the **mandibular foramen**. It gives attachment to the sphenomandibular ligament in humans (Gray, 1918:173).

Tursiops and other delphinids do not appear to develop a *lingula mandibulae*.

= mandibular body = body of the mandible

* **mandibular canal** (*canalis mandibulae*) (Figure 15b,e)

The mandibular canal is a continuation of the **mandibular foramen** anteriorly. The mandibular canal runs the full length of the **mandibular body** and contains the mandibular nerve (or inferior maxillary nerve (Schulte, 1917:374) and vessels (Evans and Christensen, 1979:148; Schaller, 1992:38.30).

The mandibular canal, which is present in *Tursiops* and other odontocetes, has been called the **dental canal** (Owen, 1866a:41; Anderson, 1879:528; Schulte, 1917:376, bottom).

* **mandibular condyle** = condyloid process = articular process (*processus condylaris*)) (Figure 15a–c,e)

The mandibular condyle in the dog is a transversely elongate process that forms the mandibular portion of the **temporomandibular joint** (Evans and Christensen, 1979:148) as in humans (Gray, 1918:174; Feneis, 1994:28.12) and other mammals (Schaller, 1992:38.34). Vesalius (1543:22) referred to the mandibular condyle as the *capitulum inferioris maxillae* (head of the lower jaw).

In *Tursiops* and other delphinids the mandibular condyle is located in the middle of the posterior margin of the mandible (Owen, 1866a:41, 42). The mandibular condyle is also known as the **condylar process of the mandible** (Fraser and Purves, 1960:6) or the articular condyle (Schulte, 1917:366).

* **mandibular foramen** (*foramen mandibulae*) (Figure 15b,d,e)

The mandibular foramen in the dog lies on the medial (lingual) surface of the mandible at the junction of the ramus and body (Gray, 1918:173; Schaller, 1992:38.29; Feneis, 1994:28.6). Vesalius (1543:22) referred to the mandibular foramen as merely the *sinus*. The mandibular foramen houses the mandibular nerve and mandibular vessels (Evans and Christensen, 1979:148).

In *Tursiops* and other odontocetes, the mandibular foramen is greatly enlarged, houses the intra-mandibular fat body, and is generally termed the **mandibular fossa** (q.v.). The mandibular foramen in odontocetes has also been called the **dental foramen** (Anderson, 1879; Flower, 1885:216; Schulte, 1917:376), the **inferior dental foramen** (Schulte, 1917:376), the **mandibular hiatus** (Boenninghaus, 1904:46, Fraser and Purves, 1960:13) or the proximal infundibular cavity (Murie, 1873; Fraser and Purves, 1960:6).

* **mandibular fossa of the mandible** (Figure 15d)

The mandibular fossa of the mandible (not of the squamosal) is the enlarged (high, long, and voluminous) **mandibular foramen** as seen in *Tursiops*, *Phocoena*, and other odontocetes. The mandibular fossa houses the intramandibular fat body (intra-mandibular fatty body of Fraser and Purves, 1960:10, 13, 24, 26, 27, 29, 32, 133, 140), which is homologous with the marrow of the mandible) (Boenninghaus, 1904:46, fig. K; Fraser and Purves, 1960:27). The fossa occupies about one-third of the **lingual surface of the mandible**, extending from the **mandibular condyle** nearly to the most posterior tooth. The mandibular fossa is bounded laterally by the **pan bone**. This use of mandibular fossa has wide and consistent application in odontocetes and sometimes other Cetacea; see, for example, Norris (1968:310), Perrin (1975: fig. 2, item 40, for a recommended measurement in dolphins), Fordyce (1994:162), Wang et al. (2000:149), and Geisler et al. (2005:24). Geisler and Sanders (2003:71 "small mandibular fossa") appeared to use mandibular fossa in some mysticetes as equivalent to mandibular foramen.

The term "**mandibular fossa** of the squamosal" as used in humans and other mammals (e.g., Gray, 1918:139, fig. 137) is rarely used in the cetacean literature, and there seems little chance of confusing the feature of the squamosal bone with that of the mandible.

= mandibular head (*caput mandibulae*) = mandibular condyle

= mandibular hiatus (*hiatus mandibularis*) = mandibular fossa

Fraser and Purves (1960:13, in *Phocoena phocoena*, citing Boenninghaus, 1904:46) appeared to use this term to mean the mandibular fossa (q.v.). See also Rommel (1990:37).

– mandibular neck (*collum mandibulae*)

In humans the mandibular **neck** connects the **mandibular condyle** to the mandibular ramus (Gray, 1918:172).

There is no distinct mandibular neck in *Tursiops*, the mandibular condyle being closely attached to the ramus.

* **mandibular notch** (*incisura mandibulae*) (Figure 15c,e)

The mandibular notch in the dog is located between the **mandibular condyle** and the **coronoid process** (Evans and Christensen, 1979:148).

The mandibular notch is present in *Tursiops*.

– mandibular space

The mandibular space is the area between the two articulated bodies of the mandibles (Evans and Christensen, 1979:147). *Tursiops* and other delphinids have a mandibular space.

– mandibular sulcus

In the yellow armadillo, the **lingual surface of the mandible** carries faint, narrow, longitudinal sulci, each sometimes carrying one or more tiny foramina that have been called mandibular sulci (Wible and Gaudin, 2004:159).

Tursiops lacks a consistent pattern of mandibular sulci, but the term could be applied to variably developed fine grooves in the mid-length to posterior of the lingual face of some mandibles. The occupants of these sulci are currently unknown.

– **mandibular symphysis** (*symphysis mandibulae*)

The bodies of the mandible in the dog and other mammals are united at the mandibular symphysis, a strong fibrous articulation that frequently fuses with age (Evans and Christensen, 1979:146; Feneis, 1994:26.14; not in Schaller, 1992). Strictly, the term "symphysis" should apply only to the two associated or fused mandibles. The symphysis is fused in adults of many but not all odontocetes but never fuses in mysticetes. Schulte (1917:365, 366, 376, 401) described the symphysis in *Kogia* and Anderson (1879:496, 528) described it in *Platanista*.

– **mandibular torus** (*torus mandibularis*)

Mandibular tori are variable ossifications that occur as thickenings of the ventral surface of the mandible (Whitney, 1889–1910:[vol. 8]6396).

– **masseteric fossa** (*fossa masseterica*)

The masseteric fossa is the area of insertion of the *m. masseter*. The masseteric fossa in the dog lies on the dorsolateral surface of the ramus and is limited by the **coronoid crest** anteriorly / dorsally and the **condyloid crest** posteriorly / ventrally (Evans and Christensen, 1979:148).

The masseter is a relatively small, diffuse, and fat-laden muscle in delphinids. The insertion of the masseter has extended ventrally to the angular process in delphinids, and the masseteric fossa generally lacks distinct boundaries (Fraser and Purves, 1960:19, 23, 76, 84).

* **masseteric line** (Figure 15b,c,e)

The masseteric line in the dog lies on the lateral surface of the mandible and extends forward from the angular process. It marks the ventral limit of insertion of the *m. masseter* (Evans and Christensen, 1979:147).

Because of the diffuse nature of the masseter muscle in *Tursiops* and other delphinids, its insertion generally does not produce a definable masseteric line. In one specimen of *Tursiops* (USNM 550403), however, the ventral border of the angular process carries a small laterally produced flange that might be the masseteric line.

– **masseteric tuberosity** (*tuberositas masseterica*)

The masseteric tuberosity is located on the lateral surface of the **angle of the mandible** in humans (Feneis, 1994:26.4). It is formed by the tendon of insertion of the *m. masseter* (Gray, 1918:172f). It is hence a specialization of the **masseteric line**.

A masseteric tuberosity is not present in *Tursiops*.

* **mental foramina** (*foramina mentalia*) (Figure 15c)

The mental foramina are located on the anterior portion of the **labial surface of the mandible** in the dog (Evans and Christensen, 1979:147). They are commonly multiple and contain branches of the mental nerve (trigeminal; mandibular).

The mental foramina are well developed toward the anterior of the mandible in *Tursiops* and other delphinids. In Cetacea the mental foramina are extremely variable in number and position.

– **mental protuberance** (*protuberantia mentalis*)

The mental protuberance or mental point in humans is a triangular eminence at the anteroventral portion of the **mandibular body** (chin) (Gray, 1918:172; Feneis, 1994:26.15). This is exceedingly variable in development in humans and appears to be sexually dimorphic. No functional element is associated with it. The term seems to have little use other than in humans; "***pogonion***" is used in other species.

– **mental spine** (*spina mentalis*) (Figure 15b)

The mental spines are small spinous processes on the internal surface of the ventral portion of the symphysis. They serve as origins for the *m. genioglossus* and *m. geniohyoideus* (Gray, 1918:172).

We can find no trace of a mental spine in delphinids.

– **mental tubercle** (*tuberculum mentale*)

The mental tubercles are small raised areas on either side of the **mental protuberance**.

Mental tubercles are lacking in cetaceans.

– **molar portion** (*pars molaris*)

The *pars molaris* of the **mandibular body** bears the molar teeth in the dog (Evans and Christensen, 1979:146).

Tursiops and other odontocetes are homodont, the molars are not identifiable, and the mandibles do not have a *pars molaris*. Because of the uncertainty of homologies in the cheekteeth of heterodont extinct Cetacea, the *pars molaris* is likely to be identifiable only in archaeocetes.

– **mylohyoid crest**

Miller (Evans and Christensen, 1979:147) illustrated a low crest on the **lingual surface of the mandible** that he labeled the mylohyoid crest. He did not mention it in the text and there was no mention of it in the other anatomical works we used. We treat this as a lapsus calami, probably for the **mylohyoid line**.

* **mylohyoid groove** (*sulcus mylohyoideus*) (Figure 15d)

The mylohyoid groove runs anteroventrally from the ventral margin of the **mandibular foramen**. It contains the mylohyoid vessels and mylohyoid nerve (Schaller, 1992:38.31; Feneis, 1994:28.9). Wible and Gaudin (2004:165) identified a weak sulcus for the mylohyoid nerve on the mandibular ramus below the mandibular foramen in some armadillos.

In some dolphins there is a well-marked groove on the ventromedial aspect of the posterior portion of the mandible near the mandibular foramen. This groove is evident where the posterior border of the mandibular foramen lies close to the bottom of the mandible. This might be the mylohyoid groove in *Tursiops*; dissection is needed for confirmation.

* **mylohyoid line** (*linea mylohyoidea*) (Figure 15d)

The mylohyoid line in the dog is a smooth longitudinal ridge located in the posterior section of the **lingual surface of the mandible** for the attachment of the *m. mylohyoideus* (Evans and Christensen, 1979:147; Schaller, 1992:38.17; Feneis, 1994:26.22).

The mylohyoid line starts near the dorsal lingual aspect of the mandible just anterior to the **mandibular foramen** (USNM

571952). Anteriorly it drops ventrally, reaching the middle of the **body of the mandible** and disappearing just posterior to the symphyseal region.

= **neck** = mandibular neck = condylar process

– **oblique line** (*linea obliqua*)

The oblique line is a line on the lateral surface of the mandible that runs from the **mental tubercles** to the anterior border of the ramus. It serves as the attachment for the *m. quadratus labii inferioris* and *m. triangularis* (Gray, 1918:172).

Tursiops and other odontocetes have lost the facial muscles associated with the lips on the lower jaw and the oblique line is not identifiable.

= **pan bone** = acoustic window

The term "pan" has been applied to the human skull, the patella, and the socket of the hip or shoulder joint and, as pan bone, to "the broad posterior end of the lower jawbone of a marine mammal" (Benbow et al., 2002).

In *Tursiops* and other odontocetes, pan bone refers to the thin lateral wall of the mandible over the **mandibular foramen**, especially in sperm whales (Brown, 1884:293; Whitney, 1889–1910:[vol. 5]4253). Schulte (1917:366, 401) coined the term "*pars papyracea*" for this structure. Anderson referred to it as the **condylar plate** (1879:528).

= **papyraceous portion** (*pars papyracea*) = pan bone (in *Kogia*, Schulte, 1917:366, 376, 401)

* ***pogonion*** (Figure 15a,b)

The *pogonion* in the dog is the most anterior part of the mandible, at the symphysis, located between the roots of the most anterior teeth (Evans and Christensen, 1979:118). In humans the *pogonion* is the foremost point of the chin in the midline, for which feature, however, the term "**mental protuberance**" is often used.

The *pogonion* is identifiable in *Tursiops* and other odontocetes.

= **postalveolar tubercle** = coronoid crest

Schulte (1917:377) used postalveolar tubercle in *Kogia* to refer to a process on the dorsal profile of the mandible between the last **alveolus** and the **coronoid process**. As seen in lateral view, "the postalveolar tubercle separates two well marked concavities in the outline." Schulte thus appeared to refer to the **coronoid crest**.

– **precoronoid crest**

The precoronoid crest is a distinct elevation between the **coronoid process** and the posterior of the vestigial **alveolar groove** in the fossil delphinid *Australodelphis* (see Fordyce et al., 2002: fig. 3a). The precoronoid crest represents a dorsal bulge in the **coronoid crest**.

A precoronoid crest is present in *Tursiops*; dissection is needed to establish its function.

– **preorbital fossa** (Sisson, 1910:140)

The preorbital fossa is illustrated by Sisson (1910:140) in the domestic pig, but he did not discuss it—we found no reference to it in the surrounding pages nor in the index. The preorbital fossa lies on the **external surface of the maxilla**, jugal, and lacrimal. The preorbital fossa may house the *m. levator labii superioris proprius* (*levator rostri*) (Sisson, 1910:311). A topographically similar depression exists in the skull of the dromedary where it lies near the juncture of the cranium with the rostrum and occupies the dorsal portion of the maxilla, nasal, and frontal (Smuts et al., 1987:2, fig. 1.2; 4, fig. 1.4). The depression contains the posterior dilation of the lateral nasal diverticulum (Smuts et al., 1987:106, fig. 4.5).

Although the facial muscles in odontocetes are diverse and extensive (Mead, 1975), they do not develop a homologue to the preorbital fossa.

* **pterygoid fovea** (*fovea pterygoidea*) (Figure 15d)

The pterygoid fovea is a pit associated with the **mandibular neck** for the insertion of the lateral pterygoid muscle; in humans it lies on the anterior portion of the **neck** of the mandible (Feneis, 1994:28:15), whereas in horse and pig it lies more ventrally, close to the condyle (Schaller, 1992:38:37).

There is a small rounded eminence on the lingual side of the mandible of *Tursiops*, just below the **coronoid process** and anterior to the **mandibular notch**, that we have interpreted as the pterygoid fovea. The insertion for the lateral pterygoid muscle is not detailed in the literature for *Tursiops*, and there is not a clear pterygoid fovea. Murie (1873:284; see Fraser and Purves, 1960:8) mentioned the association of pterygoid muscles with the "articulating **condylar process of the mandible**" in *Globicephala*. In the medial face of the mandible of *Tursiops* (USNM 550403), the region of the mandibular notch between the condyle and the coronoid process is thickened and rough, possibly marking a muscle insertion.

– **pterygoid tuberosity** (*tuberositas pterygoidea*)

The pterygoid tuberosity is located on the medial surface of the **angle of the mandible** in humans. It is formed by the tendon of insertion of the medial pterygoid muscle (*m. pterygoideus medialis*) (Feneis, 1994:28.5) (= *m. pterygoideus internalis*; Gray, 1918:172f). This is not to be confused with the pterygoid tubercle of the pterygoid bone on the skull base.

The insertion of the medial pterygoid muscle is a diffuse tendon and no pterygoid tuberosity is developed in *Tursiops* or other delphinids. For *Phocoena*, Boenninghaus (1904: fig. K) showed the medial pterygoid muscle inserting into what Fraser and Purves (1960:13) identified as the medial periosteal wall of the intramandibular fat body. We cannot identify an obvious pterygoid tuberosity associated with the angular process in *Tursiops*.

* **ramus of the mandible** (*ramus mandibulae*) (Figure 15c)

The ramus of the mandible is the vertical non-tooth-bearing portion of the bone (Schaller, 1992:38.23; Feneis, 1994:28.1). The ramus is vertical in the dog but not necessarily in other taxa (Evans and Christensen, 1979:148). Davis (1964) regarded the ramus as the portion of the mandible posterior to the teeth; thus, it has both horizontal and vertical components. Such use appears to be common. Owen (1866a:41) divided the mandible into the tooth-bearing horizontal ramus and the ascending ramus.

The mandible in odontocetes is not divided into vertical and horizontal parts, in contrast to many other mammals. Owen

(1853:444; 1866a:41) referred to the mandibular parts as the ascending ramus, which is comparable to the ramus of Evans and Christensen (1979:148), and the horizontal or descending ramus, which is comparable to the **body of the mandible**. This was based mainly on his human experience.

Fraser and Purves (1960:24, 26) used "ramus" to mean the entire mandible. We take the expanded definition of Davis (1964) and treat the ramus in *Tursiops* as that portion of the mandible that is posterior to the **dental alveoli**. In species where the dentition is reduced, such as beaked whales, the mandibular ramus extends from the **mandibular condyle** to the anterior end of the **coronoid crest**.

= sockets = dental alveoli

– sternomandibular tuberosity (*tuberositas m. sternomandibularis*)

The sternomandibular tuberosity is a feature on the posterior margin of the mandible of the horse (Schaller, 1992:38.26). It is dorsal to the angular process. The sternomandibular tuberosity is formed by the insertion of the sternomandibular muscle. This muscle is homologous with the sternal portion of the *m. sternocleidomastoideus* in humans (Sisson, 1910:225); it is also known as the *m. sternocephalicus*.

The muscular connection between the sternum and the skull in cetaceans has become limited to attachments through the hyoid. The sternohyoid muscle forms the distal link and various combination of the occipitohyoid muscle, *m. hyomandibularis*, and omohyoid muscle form the proximal link (Schulte, 1916:416, 417, pls. 46–48; Schulte and Smith, 1918:36–41; Lawrence and Schevill, 1965:17). There is no sternomandibularis or any other muscle that inserts on the middle portion of the **mandibular condyle**.

– sublingual fovea (*fovea sublingualis*)

The sublingual fovea is the small pit that the sublingual salivary gland occupies in humans (Feneis, 1994:26.24). It is located dorsal to the **mylohyoid line** and ventral to the root of the canine tooth. It is also known as the fossa for the sublingual gland (Gray, 1918:173) or the sublingual depression (Gray, 1918:1136).

Salivary glands are rudimentary or absent in Cetacea (Slijper, 1962:285), hence the sublingual gland is likely to be absent in *Tursiops* and other delphinids.

– submandibular fovea (*fovea submandibularis*)

The submandibular fovea is the depression that the submandibular salivary gland occupies in humans (Feneis, 1994:26.25). It is located ventral to the **mylohyoid line** in the posterior half of the **body of the mandible**. It is also known as the fossa for the submaxillary gland (Gray, 1918:173) or the submaxillary depression (Gray, 1918:1136). Gray called the gland in question the "submaxillary gland" because of its relationship with the submaxillary triangle (Gray, 1918:1135).

Salivary glands are rudimentary or absent in Cetacea (Slijper, 1962:285); hence, the submandibular (submaxillary) gland is likely to be absent in *Tursiops* and other delphinids.

*** symphyseal surface** (Figure 15d)

The symphyseal surface in the dog is the most anterior portion of the **lingual surface of the mandible** that bears the **mandibular symphysis** (Evans and Christensen, 1979:147). More strictly, the symphyseal surface is the feature that can be seen on either the left or right mandible, whereas the symphysis is apparently only in two associated or fused mandibles.

The symphyseal surface is generally quite distinct in *Tursiops* as an irregularly planar surface, unfused, and less than twice as long as deep. There is a long, narrow, shallow groove in the symphyseal surface of USNM 504560, similar to that described in mysticetes: "at the symphyseal end there was a distinct fissure, the remains of the channel for the distal extremity of the Meckelian cartilage" (Carte and Macalister, 1868:212). Owen (1866a:41) referred to the symphyseal part of the mandible.

= symphysial plate (Anderson, 1879:528)

Anderson, in his description of *Platanista* (1879:528), used symphysial plate (or **internal alveolar plate**) in referring to the **symphyseal surface** of the mandible. He did not differentiate the symphysial plate from the symphyseal surface.

*** ventral margin of the mandible** (*margo ventralis*) (Figure 15d)

The ventral margin of the mandible consists of the entire ventral border of the mandible from the symphysis to the angular process.

MAXILLA

Os Maxilla

FIGURES 1, 3, 4, 6C,D, **16**, 32

The maxilla is the principal tooth-bearing element of the upper jaw, forming the site for development of the canines, premolars, and molars (Gray, 1918:157; Evans and Christensen, 1979:140; Schaller, 1992:32.6; Feneis, 1994:22.2). Vesalius (1543:23) referred to the maxilla as the *superiori maxillae*, fourth bone of the upper jaw (*quartum maxillae superioris os*) (ibid., 22, 23), largest bone of the upper jaw (*maximo superioris maxillae ossi*) (ibid., 22, 23), or just the *maxilla* (ibid., 25). Eustachius and Lancisius (1714:113) referred to the maxilla as the *maxilla*. The maxilla is developed from the dorsal portion of the primitive cartilaginous jaw apparatus. The maxilla is intimately related the nasal passage; it forms the bulk of the floor (the palate) and the lateral walls, including some of the paranasal sinuses. In most terrestrial mammals the maxilla articulates with the jugal, forming the zygomatic arch. In delphinids and other Cetacea, the jugal has moved its anterior articulation to the lacrimal. The principal changes to the maxilla involve the increase in relative size, posterior movement of the external bony nares, and development of the extensive ascending process.

The maxilla forms a significant portion of the rostrum. The maxilla was also known as the maxillary bone or just the maxillary (Owen, 1866a:27). Wible and Gaudin (2004:122) found it convenient to recognize five components to the mammalian maxilla: the facial, palatine, zygomatic and orbital processes, and the contribution of the maxilla to the lateral wall of the nasal cavity.

See also Schulte's references to the maxilla (1917:362, 369–375, 377, 378, 380, 381, 383, 385–389, 391, 393, 394, 398–400, 402) in *Kogia*.

– *aditus nasomaxillaris* (nasomaxillary opening)

The *aditus nasomaxillaris* in the dog forms the communication between the nasal passage and the **maxillary sinus** (Evans and Christensen, 1979:159).

Paranasal sinuses are not developed in cetaceans (Fraser and Purves, 1960:5, 75) and the *aditus nasomaxillaris* is absent in *Tursiops*.

– alveolar canal (*canalis alveolaris*)

The alveolar canals in the dog lead from the **infraorbital canal** in the maxilla to the individual roots of the incisors, canines, and premolar teeth, in both the mandible and the maxilla (Evans and Christensen, 1979:140; Schaller, 1992:32.14, 38.5).

In *Tursiops* the alveolar canals lead from the infraorbital canal or the **mandibular canal** to the roots of the teeth.

*** alveolar foramina** (*foramina alveolaria*) (Figure 16c)

Alveolar foramina in the dog are the openings of the **alveolar canal**s at the apex of each **dental alveolus**. They contain the alveolar nerves and alveolar vessels (Evans and Christensen, 1979:141). In the neonatal specimen of *Tursiops* illustrated (Figure 16c), the alveolar canal is open in the region of the anterior teeth, forming an **alveolar sulcus**. It is only in the posterior alveoli that the alveolar canals are closed and the alveolar foramina have formed. This situation occurs on both the upper and the lower dentitions.

= alveolar groove (*sulcus alveolaris*)

See **alveolar groove of the mandible** under "Mandible."

= alveolar juga (*juga alveolaria*)

See this term under "Mandible."

*** alveolar margin of the maxilla** (*margo alveolaris*) (Figure 16c)

The alveolar margin of the maxilla is the border of the *processus alveolaris* (Schaller, 1992:34.11).

Odontocetes have a normal **alveolar margin**.

= alveolar portion of the maxilla (*pars alveolaris*) = alveolar process

*** alveolar process of the maxilla** (*processus alveolaris*) (Evans and Christensen, 1979:140; Schaller, 1992:34.10) (Figure 16c)

The alveolar process of the maxilla in the dog is the ventrolateral surface, which forms the thickest and most cancellous portion of the bone. It houses the **dental alveoli** (Evans and Christensen, 1979:140).

The alveolar process is present in *Tursiops* and other odontocetes that bear teeth in the maxilla. The alveolar process is also known as the **alveolar portion of the maxilla** in humans (Feneis, 1994:26.26).

– anterior lacrimal crest of the maxilla (*crista lacrimalis anterior*)

The anterior lacrimal crest of the maxilla forms the anterior border of the **fossa for the lacrimal sac** and associated **lacrimal foramen** in humans (Gray, 1918:164). The **anterior lacrimal crest** is absent in *Odocoileus* and other artiodactyls in which one or two lacrimal foramina open within the lacrimal.

Tursiops has a **lacrimojugal crest** (q.v.) of the maxilla that is associated with the lacrimal and jugal but is not, however, clearly homologous with the anterior lacrimal crest in humans.

– anterior maxillary sinus (*sinus maxillaris rostralis*)

The anterior **maxillary sinus** is the anterior part of the sinus that lies in the maxilla in equids (Sisson and Grossman, 1953:80; Schaller, 1992:32.29, 180.2).

Paranasal sinuses are not developed in cetaceans (Fraser and Purves, 1960:5, 75), and the anterior maxillary sinus is absent in *Tursiops*.

– anterior sinus (Fraser and Purves, 1960:62) = anterior lobe

Fraser and Purves (1960) used different definitions for anterior sinus and **anterior sac** (q.v.), names that, from perusal of their text, refer to the same structure. Here, "anterior sinus" is preferred.

According to Fraser and Purves (1960:62), Beauregard (1894) used the term "pterygoid sac" [or sinus] only for "that part of the air sinus system which occupies the pterygoid hamuli, the remainder of the system anterior to the **tympanic cavity** being designated the anterior sinus." Under discussion of *Pontoporia*, Fraser and Purves (1960:63) redefined the anterior sinus (q.v.) as comprising those parts of the **pterygoid sinus** system (sensu lato) that extend farther forward than the most anterior limits of the pterygoid. Fraser and Purves gave the examples of the anterior sinus in *Inia* (1960:64; a sinus that penetrates the bony rostrum), *Grampus* (ibid., 69; a sinus on the **ventral surface of the hard palate** of the maxilla), *Tursiops* (ibid., 70; a sinus on the ventral surface of the maxilla), and *Delphinus* (ibid., 72; a long sinus on the ventral surface of the maxilla).

*** anterior sinus fossa** (Figure 2)

The anterior sinus fossa lies on the ventral portion of the base of the rostrum anterior to the **ventral infraorbital foramen** (Fraser and Purves, 1960:8, 25, fig. 8, 70, 72). The **anterior sinus** arises from the **preorbital lobe of the pterygoid sinus**, and the boundary of the posterior extent of the anterior sinus fossa is indeterminant. The fossa can be seen in preparations of adult *Tursiops* as a smooth area around the ventral infraorbital foramen, involving maxilla and sometimes the **medial process of the lacrimal**. The fossa may extend anteriorly to about the level of the last **dental alveolus**. Medially the fossa may develop onto the palatine, being limited by the origin of the pterygoid muscles ventrally. The border of the anterior sinus / pterygoid muscles can be followed as a crest across the **perpendicular lamina of the palatine**.

*** anterior surface of the maxilla** (*facies anterior*) = facial surface (Figure 16a)

The anterior surface of the maxilla is on the **external surface of the maxilla** and faces anteriorly and laterally (Feneis, 1994:22.8).

The anterior surface of the maxilla in *Tursiops* and other Cetacea forms the laterodorsal surface of the rostrum.

= antorbital angle = antorbital process

= antorbital foramen = dorsal infraorbital foramen = ventral infraorbital foramen (Diagram 1; Table 6)

Antorbital foramen has had a long occasional use for the anterior or dorsal opening of the **infraorbital foramen** or **infraorbital canal** in mammals; see e.g., Owen (1859:312) for the marsupial *Thylacoleo*.

Use in Cetacea varies; Kellogg (1928:38) commented about the antorbital foramen in "zeuglodonts" (archaeocetes): "The premaxillary has an ascending process which does not reach the frontal, but terminates behind the antorbital foramen (above upper premolar 2 or 3)." (See also Gingerich et al., 2005: fig. 4, in the archaeocete *Makaracetus*). Fraser and Purves (1960:137, and pl. 9ff.) identified the antorbital foramen only in illustrations, as the structure identified in *Tursiops* as the **ventral infraorbital foramen**.

* **antorbital fossa** (Figures 2, 6f, 30, 32)

Novacek (1986:30) identified the antorbital fossa in the extinct *Leptictis* as a depression on the lateral surface of the maxilla and associated with the **infraorbital foramen** (anterior opening of the **infraorbital canal**), serving as an origin for various snout muscles. Antorbital pit and antorbital depression (Wible et al., 2004:41, for *Zalambdolestes*) appear to be synonyms.

In Cetacea, *Tursiops*, and other odontocetes, the **facial fossa** similarly serves as the origin for facial muscles. It is likely that the facial fossa and antorbital fossa are homoplastic, having evolved independently in odontocetes and other mammals. We recommend that "antorbital fossa" not be used in this sense for Odontoceti.

In Cetacea, Owen (1866a:28) described the "rough **malomaxillary fossa**" as lying external to the "antorbital fossa" in the skull of *Orcaella*. He labeled the malomaxillary fossa as (e) and the antorbital fossa as (d) in the text (1866a:28) but did not include (d) and (e) in his figures (Owen, 1866a: pl. 9). Later, antorbital fossa was used for the enlarged vacuity around the **ventral infraorbital foramen** in *Mesoplodon densirostris* (see Besharse, 1971:308) and in species of *Stenella* (see Perrin, 1975:91, fig. 39). Confusingly, Fraser and Purves (1960:137) used the term "**antorbital foramen**" (q.v.) in this part of the skull.

The antorbital fossa is recognized here in *Tursiops* and other delphinids as the dorsally excavated region anterior to the preorbital ridge, variably involving the ventral infraorbital foramen, preorbital recess, and **anterior sinus fossa**. Fraser and Purves (1960:51) mentioned some taxonomic variation in this feature (e.g., for *Orcinus*: "pre-orbital smoothed area"). The feature is quite variable in form across the Odontoceti, probably because of the variable influence of the infraorbital vessels and nerves, and anterior parts of the **pterygoid sinus**.

= **antorbital maxillary tuberosity** (Kellogg, 1928:61, in *Hyperoodon*) = maxillary tubercle

* **antorbital notch** (Figures 1, 16a,d, Diagram 2; Table 5)

There is no antorbital notch in noncetacean mammals. The **infraorbital notch** (q.v.) in humans and some rodents may be analogous.

In *Tursiops* the antorbital notch is the notch formed laterally in the maxilla and lacrimal (lacrimojugal) at the base of the rostrum (Owen, 1866a:21, 34; Schulte, 1917:365, 373, 387–391, 400). The antorbital notch is medial to the **antorbital process** and transmits the facial nerve. In those odontocetes that develop a **prominential notch** (ziphiids), the prominential notch is anteromedial to the antorbital notch (Moore, 1963:424, fig. 14). Mitchell (1968:270, 271) described a situation in *Ziphius cavirostris* where the dorsal outline of the jugal did not coincide with the dorsal outline of the maxilla, and two notches were formed that Mitchell termed the internal antorbital notch (medial to the **antorbital tubercle** and jugal) and the external antorbital notch

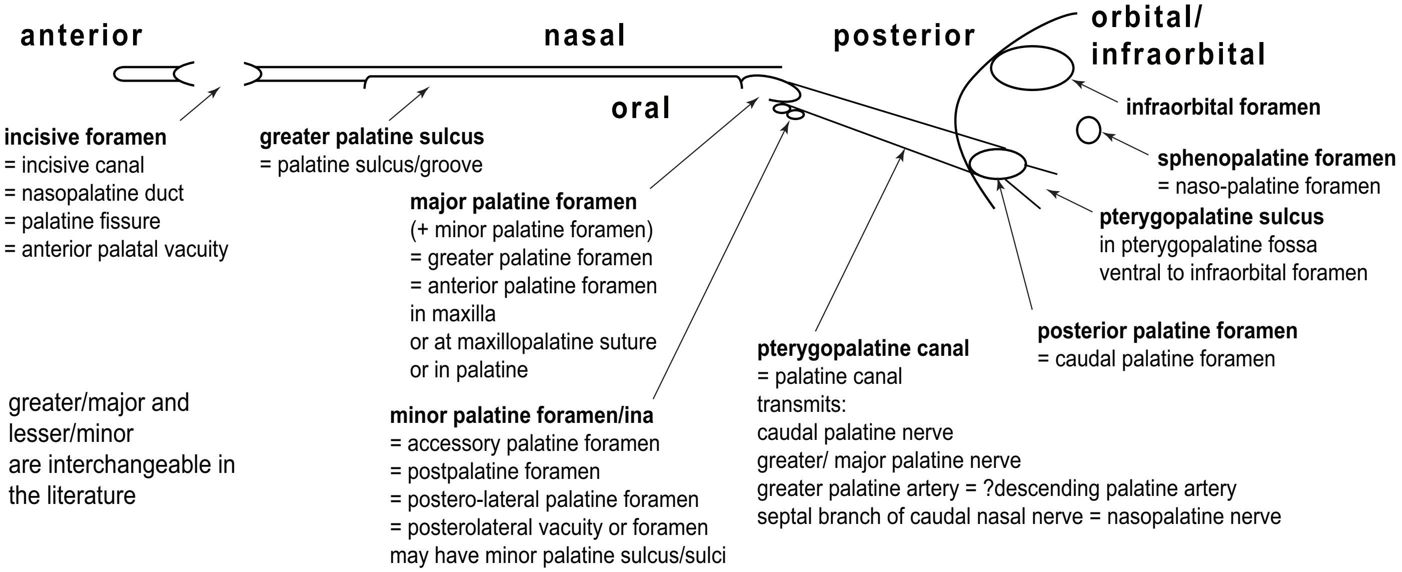


DIAGRAM 1. Schematic cross section of the rostrum and antorbital fossa, showing generalized distribution and names of features associated with the foramina of the palatine.

(lateral to the antorbital tubercle and jugal). Owen (1886a:34, 38, 39, 41; pl. 12: fig. 1k; pl. 13: fig. 1k) referred to the antorbital notch in *Kogia sima* as the malo-maxillary fissure).

* **antorbital process** (Diagram 2; Table 5; Figure 16a,c,d)

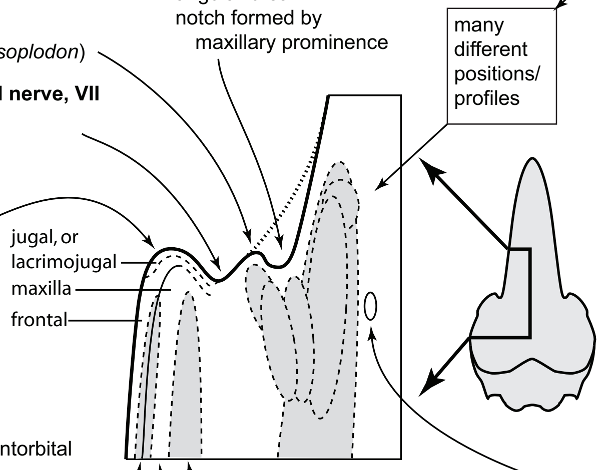
There is no antorbital process, in the cetacean sense, in non-cetacean mammals.

Tursiops has an antorbital process, which is the anterior projection of the skull lateral to the **antorbital notch**, involving the anterolateral portion of the maxilla and the underlying **lacrimojugal bone**. More broadly, the antorbital process in Cetacea is the anterior projection of one or more of maxilla, lacrimal, frontal, or jugal that lies lateral to the antorbital notch (path of facial nerve).

The literature reveals various combinations of antorbital and preorbital with the terms process, angle, and tubercle. The term "process" is preferred because it implies less about the shape and degree of projection than the terms angle, tubercle, or prominence, and "antorbital" is preferred over preorbital because of association with the path of the facial nerve at the antorbital notch.

There has been confusion regarding the nomenclature of the features around the antorbital process and antorbital notch. Table 5 and Diagram 2 summarize the terms that we use in this paper and the history of prior usage. The literature was reviewed to get a representative but not exhaustive idea of past use; anatomical use in recent cladistic literature was not checked in detail. In many cases, especially involving features medial to the antorbital notch, the original meaning was not clear, so we often give quotes and page numbers. Some new or significantly redefined terms are proposed for previously confused landmarks: **supraorbital crest**, supraorbital ridge, **maxillary crest**, **maxillary tubercle**, and rostral (or rostral maxillary) crest. The homology is not clear for the so-called maxillary crest in *Physeter* and *Kogia*.

Synonyms for antorbital process include antorbital eminence, antorbital tuberosity, antorbital prominence, **antorbital tubercle**, antorbital protuberance, preorbital apophysis, preorbital angle, preorbital process (not to be confused with the antorbital process in Mysticeti), large smooth tuberosity, round anterior extremity, and frontal protuberance (see Diagram 2).



Maxillary tubercle:
tubercle anterior to antorbital notch (*Mesoplodon)*
protuberance which projects into antorbital notch (*Mesoplodon*)
maxillary tubercle (*Mesoplodon, Indopacetus*)
maxillary prominence
antorbital tubercle (*Indopacetus*)
apex of maxillary prominence (*Mesoplodon*)

Prominential notch:
pseudo-notch (*Mesoplodon*)
inner notch (*Mesoplodon*)
second sinus (*Mesoplodon*)
angle formed by anterior margin
angular break
notch formed by maxillary prominence

Rostral [maxillary] ridge/crest: a feature medial to antorbital notch, associated with maxillary tubercle and prominential notch, or with rostrum in absence of tubercle and notch:
maxillary crest (*Hyperoodon, Berardius, Indopacetus*)
low roughed rugosity (*Ziphius*)
maxillary tuberosity (*Ziphius, Mesoplodon*)
rugose eminence (*Berardius*)
longitudinal ridge (*Mesoplodon, Hyperoodon*)
pronounced elevation (*Berardius*)
immense bony mass (*Hyperoodon*)
supraorbital ridge (*Hyperoodon*)
low maxillary ridge (*Mesoplodon*)
maxillary ridge 'behind" [medial to] antorbital notch (*Mesoplodon*)
dorsal maxillary tuberosity extending into maxillary tubercle (*Mesoplodon*)
maxillary prominence (*Mesoplodon*)
end of maxillary tubercle (*Mesoplodon*)
prominential crest (*Mesoplodon*)
maxillary eminence (*Parapontoporia*)

maxillary crest (*Physeter*) [homology uncertain]

Antorbital notch = path for facial nerve, VII
anteorbital notch
malo-maxillary fissure (*Kogia*)
preorbital notch
infraorbital notch?
maxillary notch

Antorbital process:
antorbital eminence
antorbital tuberosity
antorbital prominence
antorbital tubercle
antorbital protuberance
preorbital apophysis
preorbital angle
preorbital process = not same as antorbital process of Mysticeti
large smooth tuberosity (*Kogia*)
round anterior extremity (*Platanista*)
frontal protuberance

a large **dorsal infraorbital foramen** is commonly present medial to rostral ridge or crest

Supraorbital crest/ridge: feature lateral to antorbital notch developed on edge of maxilla and/or frontal:
lateral crest of maxilla (*Platanista*)
bony incurved crest (*Platanista*)
frontal plate (*Zarhachis*)
vertical crest of frontal plate of maxilla (*Inia*)
maxillary crest (Platanistidae)
pneumatic maxillary crest (*Platanista*)
crest of supraorbital process of frontal and maxilla (*Zarhachis*)
upward prolongation of maxilla (*Inia*)
vertical crest of maxilla (*Inia*)

Maxillary crest/ridge: feature lateral or posterior to antorbital notch developed on maxilla but not frontal:
posterior expanded plate of maxilla (*Kogia*)
longitudinal crest (*Pontoporia*)
incurved extremity of transverse crest (*Kogia*)
maxillary crest, non-pneumatized (*Pontoporia, Parapontoporia*)
supraorbital crest (*Parapontoporia*)

Maxillary groove, not bounded by crest (*Indopacetus*)

DIAGRAM 2. Schematic dorsal view of named osteological structures in and around the antorbital notch in Odontoceti.

TABLE 5. Terms used by selected authors to designate landmarks in the vicinity of the antorbital notch, with page and/or figure numbers given in parentheses for the citation in first column. A dash (–) indicates term not used in the indicated report; a question mark indicates a relationship that is questionable.

Author(s), date, taxa	Antorbital process	Supraorbital crest	Maxillary crest	Antorbital notch	Maxillary tubercle	Rostral [maxillary] crest	Prominential notch
Owen, 1866a, Delphinidae, *Kogia*	Antorbital process of the malar (25), large smooth tuberosity (38, *Kogia*)	—	Posterior expanded plate of the maxilla (38, *Kogia*)	Antorbital notch (21), malo-maxillary fissure (38, *Kogia*)	—	—	—
Flower, 1867, *Inia*, *Pontoporia*, Odontoceti	Antorbital process (89), antorbital eminence (91), antorbital tuberosity (108)	Large bony incurved crest [*Platanista*] (114)	Sharp, straight and nearly parallel crest . . . narrow upward prolongation of the maxilla [*Inia*] (91), longitudinal crest [*Pontoporia*] (108)	Antorbital notch (89)	—	—	—
Flower, 1868, *Physeter*	Antorbital process (319)	—	Elevated edge of broadly expanded maxilla, posteriorly continuous with but not the same as the occipital crest (314) [homology uncertain]	Antorbital notch (318)	—	—	—
Flower, 1872, *Berardius* and other Ziphiidae	—	—	—	Antorbital notch (207)	—	"Low roughed rugosities" (207), maxillary tuberosity [supposedly not in *Mesoplodon*] (209), rugose eminences on outer edge of upper surface of maxillae at base of rostrum [*Berardius*] (212), maxillary crest [of *Hyperoodon*, rostrum + cranium] (206)	—
Flower, 1878, *Mesoplodon* and other Ziphiidae	—	—	—	Antorbital notch (417)	Tubercle of maxilla in front of antorbital notch (417)	Longitudinal ridge on upper surface of maxilla [*Mesoplodon*], . . . pronounced elevation [*Berardius*], . . . immense bony mass [*Hyperoodon*]" (423)	—
Anderson, 1879, *Platanista*	"Round anterior extremity [of malar]" (524)	"Great lateral crests of the maxillary bones" (449)	—	Preorbital notch (363), = ? infraorbital notch (524)	—	—	—

(*continued*)

TABLE 5. (*Continued*)

Author(s), date, taxa	Antorbital process	Supraorbital crest	Maxillary crest	Antorbital notch	Maxillary tubercle	Rostral [maxillary] crest	Prominential notch
Flower, 1882, *Hyperoodon*	—	—	—	Antorbital notch (395)	—	= Supraorbital ridge (392), Maxillary crest (394)	—
Flower, 1885, *Globicephala*, *Physeter*, *Hyperoodon*	Antorbital prominence (212)	—	Maxillary crest [in *Physeter*] (218) [homology not clear]	Antorbital notch (213)	—	Thick high longitudinal ridge (218, *Hyperoodon*)	—
True, 1910, Ziphiidae	—	—	—	Antorbital notch (5), maxillary notch (13, 26, 65)	“Tubercle anterior to antorbital notch . . .” (5); protuberance which projects into antorbital notch (12, 26)	“Low maxillary ridge” (5) [*Mesoplodon*, apparently associated with tubercle], maxillary ridge behind [in lateral view, = medial to ?] antorbital notch (13)	“‘pseudo-notch’ . . .” (26)
True, 1913a, *Mesoplodon*	—	—	—	Antorbital notch (2)	Maxillary protuberance (2) [context not clear]	Maxillary prominence (1), = maxillary ridge (2)	Maxillary notch (1) [identity not clear, but apparently not = antorbital notch]
True, 1913b, *Mesoplodon*	—	—	—	Antorbital notch (653)	Apex of maxillary prominence (653)	Maxillary prominence (653, 654)	Maxillary notch (653) [context not clear]
Schulte, 1917, *Kogia*	Antorbital process (370)	—	“Incurved extremities of the transverse crest” (364)	Antorbital notch (373)	—	—	—
Kernan, 1918, *Ziphius*	Maxillary tuberosity (351)	—	—	Antorbital notch (351)	—	Maxillary prominence (353)	—
Harmer, 1924: 543, *Mesoplodon*	Antorbital tubercle: externally bounds the antorbital notch	—	—	Antorbital notch: bounded on medial side by maxillary tubercle	Maxillary tubercle: medial to antorbital notch; rostrum often separated from tubercle by the inner notch; not to be confused with rostral maxillary tuberosity sensu Harmer (544)	“Dorsal maxillary tuberosity . . . extends into . . . maxillary tubercle,” stated as homologous with maxillary crests of *Hyperoodon*	“Second sinus . . . [or] inner notch”

(*continued*)

TABLE 5. (*Continued*)

Author(s), date, taxa	Antorbital process	Supraorbital crest	Maxillary crest	Antorbital notch	Maxillary tubercle	Rostral [maxillary] crest	Prominential notch
Kellogg, 1924, *Platanista*, *Zarhachis*	—	“Vertical crest . . . of frontal plate of maxilla [*Inia*]” (7), “frontal plate [*Zarhachis*]” (13), maxillary crest (13)	—	Maxillary notch (5)	—	—	—
Kellogg, 1926, *Zarhachis*	Preorbital apophysis (11)	Combined crest of supra-orbital process of frontal and maxilla (3–4)	—	Antorbital notch (17)	—	—	—
Kellogg, 1936, Archaeoceti	Preorbital angle (21)	—	—	—	—	—	—
Fraser, 1945, *Hyperoodon*	Antorbital tubercle (24)	—	—	Antorbital notch (23, 24)	—	Maxillary crest (23, 25), as feature developed medial to antorbital notch	—
Fraser, 1955, *Mesoplodon*	Antorbital tubercle (626)	—	—	Antorbital notch (628)	—	Maxillary prominence [as an elevated feature] (625); = “end of maxillary tubercle” (625, table)	“Angle . . . formed by . . . anterior margin . . . angular break” (625)
Moore and Wood, 1957, *Mesoplodon*	Antorbital tubercle (12)	—	—	Antorbital notch (20)	“Anterior margin of each maxillary prominence protrudes” (10, 12, 23)	Maxillary prominence (compare 9, 10, 12, 23) = used in sense of prominential crest of later authors	“Notches . . . formed by maxillary prominences” (20)
Moore, 1960, *Mesoplodon*	Antorbital tubercle (16)	—	—	—	Protrusion of maxillary prominence (13)	Maxillary prominence (13, 18)	Notch associated with maxillary prominence (13)
Moore, 1963, Ziphiidae	Antorbital tubercle (407, fig. 14)	—	—	Antorbital notch (407)	“Apex of . . . maxillary prominence” (fig. 14)	Maxillary prominence (407, item 7) = used in sense of prominential crest of later authors	Prominential notch (406, fig. 14)
Mitchell and Houck, 1967, *Ziphius*	Preorbital process [of frontal] (2509)	—	—	Maxillary notch, = internal and external antorbital notches (2509)	Maxillary prominence (2510)	—	Prominential notch (2509)

(*continued*)

TABLE 5. (*Continued*)

Author(s), date, taxa	Antorbital process	Supraorbital crest	Maxillary crest	Antorbital notch	Maxillary tubercle	Rostral [maxillary] crest	Prominential notch
Azzaroli, 1968, *Indopacetus*	—	—	Not present, although a maxillary groove is shown posterior to antorbital process (fig. 5, 7)	Antorbital notch (fig. 5)	Maxillary tubercle (fig. 5), a projection medial to the antorbital notch, = antorbital tubercle of fig. 9	Maxillary crest (fig. 5)—a dorsal feature posterior to her maxillary tubercle; = maxillary ridge of fig. 7; bounded by maxillary groove (figs 5, 7)	—
Mitchell, 1968, *Ziphius*	Frontal protuberance, antorbital protuberance (271)	—	—	Antorbital notch: external antorbital notch, internal antorbital notch (271)	Maxillary prominence (271)	—	Prominential notch (269)
Moore, 1968, Ziphiidae	—	—	—	—	See rostral [maxillary] crest, right; maxillary tubercle sensu McCann = maxillary prominence sensu Moore (219 b, c)	Maxillary prominence of *Ziphius* and *Tasmacetus* = maxillary tubercle of *Mesoplodon* = maxillary crest of *Hyperoodon* (219, c; 274, 283, fig. 20)	Prominential notch (219)
Barnes, 1985, Pontoporiidae	Antorbital process (14)	—	Nonpneumatized maxillary crest on supraorbital process medial to margin of maxilla (3, 19, fig. 12)	Antorbital notch (4)	—	Maxillary eminence [anteromedial to antorbital notch] (14, 19)	—
de Muizon, 1988, Kogiidae, *Scaphokogia*	Preorbital process (66)	—	Maxillo-occipital crest [as in *Physeter*] (66, 69)	Preorbital notch (66)	—	—	—
Balcomb, 1989, *Berardius*	—	—	—	—	—	Maxillary crest [on rostrum] (281)	—
Heyning, 1989a, Ziphiidae	Antorbital tubercle (5; fig. 8)	Maxillary crest (5) to be used only for the elevated structures in *Platanista* and *Hyperoodon*	Maxillary ridge (5), different from maxillary crest sensu Platanista and *Hyperoodon*	Antorbital notch (5; fig. 8)	Maxillary prominence (5, under discussion of antorbital tubercle)	Maxillary tubercle (5, under discussion of maxillary ridge; also fig. 8); maxillary crest in *Hyperoodon* (5)	Prominential notch (5; fig. 8)
Mead, 1989a, *Hyperoodon*	—	—	—	—	—	Maxillary crest (327, 339)	—
Mead, 1989b, *Mesoplodon*	—	—	Maxillary prominence, associated with more lateral maxillary groove (393)	—	—	—	—

(*continued*)

TABLE 5. (*Continued*)

Author(s), date, taxa	Antorbital process	Supraorbital crest	Maxillary crest	Antorbital notch	Maxillary tubercle	Rostral [maxillary] crest	Prominential notch
Barnes, 1990, *Tursiops*	Preorbital process (22); is not same as antorbital process of maxilla in Mysticeti (21:9)	Maxillary crest (23)	Maxillary crest (23)	Antorbital notch, Odontoceti (21:10)	—	—	—
de Muizon, 1991, Ziphiidae, Odontoceti	Preorbital process (288)	—	Occipital crest in sense of maxillary crest of *Physeter* (294:20)	Antorbital notch (288)	—	Thickening on border between rostrum and cerebral skull in *Mesoplodon* (283)	—
Barnes, 1995, Pontoporiidae	Antorbital process (14)	—	Maxillary crest, non-pneumatized (3, 19)	Antorbital notch (4)	—	Maxillary eminence (14, fig. 6) [on maxilla on rostrum]	—
Messenger and McGuire, 1998	Antorbital tubercle = maxillary tubercle (117); context not clear	Pneumatic maxillary crest (117: 1421)	?Maxillae, low crest (117: 1421)	—	Antorbital tubercle = maxillary tubercle (117: 1425)	—	Antorbital notch (117: 1426); context could mean prominential notch

= antorbital tubercle = antorbital process

= antrum or Highmore's antrum = maxillary sinus (Gray, 1918:158, 999; Feneis, 1994:22.24)

No to be confused with **tympanic antrum** under "Periotic Bone" or **antrum** under "Tympanic Bulla."

*** ascending process of the maxilla** (Figures 3, 16a–e)

The ascending process of the maxilla is developed where the **frontal surface of the maxilla** is extended posterodorsally over the frontal bone, resulting in a squamous suture (Miller, 1923:5). This was also termed the ascending plates of the maxillaries (Anderson, 1879:510); fronto-nasal portion, fronto-nasal surface (Anderson, 1879:526); frontonasal region (Anderson, 1879:450); **suprafrontal process** (Schulte, 1917:380); suprafrontal extension (Schulte, 1917:398); facial plate, frontal plate, facial surface, superorbital plate, or **nasal plate** by Owen (1866a:28, 36, 38, 44); and frontal plate by Anderson (1879:522, 523).

In *Tursiops* and other odontocetes the ascending process is extremely well developed, with the maxillae extending over the anterior surface of the braincase and, in some species, contacting the interparietals in a developmental process known as "telescoping" (Winge, 1918; Miller, 1923).

– basirostral groove

The basirostral groove (Flower, 1878:417, 421; True, 1910:10) runs anteriorly along the lateral surface of the maxilla from a blind pit medial to the **antorbital notch** in *Mesoplodon grayi* and *M. layardii*. The basirostral groove continues anteriorly for a variable distance. It is thought to represent a vestigial **alveolar groove** (Harmer, 1924:542).

The basirostral groove (per se) is not present in *Tursiops*, although it is present in at least one delphinid that lacks upper teeth (i.e., *Grampus griseus*).

*** body of the maxilla** (*corpus maxillae*) (Figure 16a)

The body of the maxilla is the central portion of the maxilla (Feneis, 1994:22.3), including the **alveolar portion of the maxilla** (q.v.).

The body is differentiated from the **ascending process of the maxilla** in *Tursiops* and other odontocetes. Owen (1866a:28) referred to the body as the rostral part of the maxilla. Anderson (1879:524, 526, 528) calls the body the dental portion of the maxilla or the mandible.

– canine fossa (*fossa canina*)

The canine fossa of the maxilla lies lateral to the canine eminence formed by the roots of the canine tooth. The canine fossa gives origin to the *m. caninus* (Gray, 1918:158).

Because they lack a differentiated canine tooth, there is no distinct canine fossa in *Tursiops* or other odontocetes.

– caudal maxillary sinus (*sinus maxillaris caudalis*)

The caudal maxillary sinus is the posterior part of the **maxillary sinus** in animals where the sinus is separated by a maxillary septum (Schaller, 1992:32.5, 32.30, 36.35, 180.3; Sisson, 1910:73). It is also called the **posterior maxillary sinus** or the superior maxillary sinus (Sisson, 1910:73). **Paranasal sinuses** are not developed in cetaceans (Fraser and Purves, 1960:5, 75) and the caudal maxillary sinus is absent in *Tursiops*.

= cavity for the zygomatic articulation = zygomatic recess

– cerebral area (Schulte, 1917:389)

Schulte (1917:389) used the term "cerebral area" in describing the maxilla of *Kogia*: "The concavity of the **frontal process of the maxilla** is increased by sagittal flange which participates in the **facial crest**, the right being excluded by the premaxillary. Finally on the ventral surface the ridge between the cerebral and **lachrymal areas** is less pronounced."

Several things are unclear in this series of statements, one of which is the reference to "less pronounced." We think that cerebral area and lachrymal area might refer to those portions of the maxilla that abut directly on the brain and the lachrymal bone. See the following description of his usage of cerebral surface.

– cerebral surface of the maxilla (Schulte, 1917:389)

Schulte (1917:389) used the term "cerebral surface of the maxilla" in this description: "In this suture are the beginnings of arterial sulci, one passing mesad and one caudad to reach the cranial cavity by way of the fronto-maxillary suture and to be continued as branched systems of grooves on the cerebral surface of the maxilla. The remainder of the ventral surface consists of a cerebral surface entad and a broad marginal area for articulation with the lachrymal and frontal."

We interpret "cerebral surface" in that series of statements to mean the surface of the maxilla that is in direct contact with the brain. Schulte (1917:390) also uses cranial surface in the same way.

– circumnarial basin (Owen, 1866a:44)

Owen uses the term "circumnarial basin" to refer to the facial area of *Hyperoodon*, *Ziphius*, *Euphysetes* (*Kogia*), *Physeter,* and *Platanista*. These are members of the odontocete families Ziphiidae, Kogiidae, Physeteridae, and Platanistidae that have the lateral edges of the maxilla, sometimes also involving adjacent frontal, turned up. The elevated **supraorbital crest** (q.v.) or ridge may produce a basin. This structure has also been termed the **supracranial basin** (Flower, 1868:314).

Tursiops and other delphinids do not develop a circumnarial basin. Note that the exact contribution of maxilla and/or frontal to the supraorbital crest, or supraorbital ridge, varies with species (see Diagram 2).

– conchal crest [crest of the ventral concha] (*crista conchalis*)

The conchal crest lies on the medial surface of the palatine bone in humans, just dorsal to the **nasal surface of the palatine**. It forms a horizontal ridge for articulation with the inferior nasal concha (Gray, 1918:167). See **dorsal nasal concha** under "Ethmoid Bone."

The crest of the ventral concha in the dog lies on the **internal surface (nasal surface) of the maxilla**. The crest begins near the maxilla–premaxilla suture and ends just anterior to the opening of the **maxillary sinus** (Evans and Christensen, 1979:141).

Paranasal sinuses are not developed in cetaceans (Fraser and Purves, 1960:5, 75), and the conchal crest and maxillary sinus are absent in *Tursiops*.

= dental furrow (Anderson, 1879:524) = alveolar groove of the mandible

See "Mandible."

– diastema

The diastema in mammals is the interval or space between two consecutive teeth, or two kinds of teeth (Benbow et al., 2002). The term has wide use in comparative anatomy and vertebrate paleontology. Interdental space (q.v.) of veterinary anatomy is equivalent.

Tursiops and most other odontocetes lack a diastemata.

– dorsal ethmoidal crest of the maxilla (*crista ethmoidalis dorsalis*)

The dorsal ethmoid crest of the maxilla limits the **maxillary sinus** dorsally in the dog and marks the line of attachment of the lateral lamina of the ethmoid to the maxilla (Evans and Christensen, 1979:141).

There is no recognizable dorsal ethmoid crest or maxillary sinus in *Tursiops*, but the maxillomesethmoid suture within the bony nares may be excavated.

* **dorsal infraorbital foramen** (Diagram 2; Table 6; Figures 1, 16a,d)

In odontocetes the infraorbital foramina have become highly modified through telescoping of the maxillae, lengthening of the canals for infraorbital vessels and branches of the trigeminal nerve, and movement of some of the "infraorbital" foramina to various positions on the face and on the rostrum. As a result of changed relationships, the foramina have been referred to widely as maxillary and premaxillary foramina. This brings the difficulty of the duplication of the term "**maxillary foramen**." We follow Rommel (1990:36) in using the term "dorsal infraorbital foramen," or foramina, to refer to the distal openings on the maxilla: the maxillary foramina of some authors. **Premaxillary foramen** (q.v.) is retained.

We recommend that in *Tursiops* and other odontocetes, the foramina that were previously and widely known as the maxillary foramina (namely, foramina at the distal or facial end of the **infraorbital canal**) should be known as the dorsal infraorbital foramina.

= ectomaxillary groove (Owen, 1870:15) = alveolar groove of the mandible

– ethmoidal crest of the maxilla (*crista ethmoidalis*)

The ethmoidal crest of the maxilla lies on the internal (medial) surface of the **frontal process of the maxilla** (Gray, 1918:159f; Schaller, 1992:34.2). The ethmoidal crest is the line of attachment of the **dorsal nasal concha**.

The ethmoidal crest of the maxilla is not present in *Tursiops* and other delphinids due the loss of the nasal conchae.

– external plate of the maxilla (Anderson, 1879:524)

The external plate of the maxilla is the dorsal of the two plates that are produced by the pneumaticization of the maxilla in the region of the **antorbital notch** (Anderson, 1879:524).

Pneumaticization of the maxilla is restricted to *Platanista*.

* **external surface of the maxilla** (Figure 16a)

The external surface of the maxilla (dorsal surface of the maxilla) in the dog is smooth and forms a large part of the face (Evans and Christensen, 1979:140).

In *Tursiops* the external surface comprises both the ascending process and dorsal surface of the maxilla on the rostrum.

– **facial crest** (*crista facialis*)

The facial crest is a continuation of the **masseteric border of the jugal** onto the maxilla. The facial crest gives origin to the *m. masseter* (Schaller, 1992:32.10).

The facial crest is not present in odontocetes in the general mammalian sense due to the reduction of the *m. masseter* in odontocetes.

Schulte (1917:382, 387, 389) used the term "facial crest" for the prominent crest that is composed of right maxilla and the left premaxilla and that lies between the **nasal septum** and the **vertex**. Schulte also used mid-facial crest (1917:361, 362, 380, 400), **sagittal crest** (ibid., 371), sagittal facial crest (ibid., 372), mid-facial sagittal crest (ibid., 399), midcrest (ibid., 385) and mid-frontal crest (ibid., 402) for this structure.

* **facial fossa** (Figure 16a,d)

In horses (e.g., Woodburne and MacFadden, 1982: fig. 3), the facial fossa is a depression on the face anterior to the **orbit**, variably involving maxilla, lacrimal, and nasal. A comparable feature in some ruminants has been termed the **maxillary fossa** (q.v.).

In *Tursiops* and other odontocetes, the facial fossa is the concave surface of the **ascending process of the maxilla** that lies between the **nasal process of the premaxilla** and the **supraorbital margin of the maxilla** (Kernan, 1918; Heyning, 1989a:5). The facial fossa is present in all odontocetes and gives origin to the major nasofacial muscles. The facial fossa has also been called the **maxillary fossa** (Schulte, 1917:372).

= **facial process** (Wible and Gaudin, 2004:122)

Wible and Gaudin (2004:122) recognized the facial process in the yellow armadillo as comprising most of the external lateral surface of the maxilla, the bulk of the lateral wall and part of the roof of the nasal cavity. This is more or less equivalent to the facial surface or **external surface of the maxilla** of other authors.

= **facial surface of the maxilla** (*facies facialis*) = external surface of the maxilla

The facial surface of the maxilla in humans is that portion of the **external surface of the maxilla** that is lateral to the **external bony nares**, ventral to the **orbit**, and medial to the **zygomatic process** (Gray, 1918:158).

The facial surface in *Tursiops* and other delphinids is homologous with the external surface of the maxilla.

– **facial tuberosity** (*tuber faciale*)

The facial tuberosity is at the anterior end of the **facial crest** of the maxilla (Sisson and Grossman, 1953:137; Schaller, 1992:32.11). The facial tuberosity is only expressed in ruminants.

– **frontal plate of the maxillary** (Owen, 1866a:36)

Owen used "frontal or nasal plate of the maxillary" to indicate that portion of the maxilla immediately anterior to the **ventral infraorbital foramen** in *Kogia sima*.

It is debatable whether the maxillary border of the ventral infraorbital foramen is developed enough in *Tursiops* and other delphinids to warrant using this term. The feature probably represents part or all of the **anterior sinus fossa** (q.v.).

= **frontal process of the maxilla** (*processus frontalis*) = ascending process

The frontal process of the maxilla lies at the posterodorsal apex of the maxilla in the dog. It forms a squamous suture with the frontal (Evans and Christensen, 1979:141).

The frontal process of many mammals is equivalent to the **ascending process of the maxilla** of *Tursiops* and other odontocetes (Miller, 1923). Schulte (1917:389) used the term "frontal process" to refer to that portion of the left maxilla that contributed medially to the **facial crest** in *Kogia*. The facial crest (sensu Schulte) is present only in *Kogia*.

* **frontal surface of the maxilla** (Figure 16b)

The frontal surface of the maxilla is that portion of the maxilla that articulates with the frontal bone. It is the ventral surface of the ascending process.

Schulte (1917:388) uses frontal surface in just this way. He also used frontal portion (Schulte, 1917:386–388) and *pars frontalis* (Schulte, 1917:388) in exactly the same way, indicating that in his mind there was no difference between the three terms.

* **greater palatine foramen** (*foramen palatinum majus*) (Figures 2, 6f)

The greater palatine foramina lie at the posterior end of the **palatine sulcus** on the suture between the maxilla and palatine bones. In the dog the greater palatine nerve, coming off the maxillary nerve, and the descending palatine artery exit the **major palatine foramen** (Evans and Christensen, 1979:141; Schaller, 1992:12.24, 36.21; Feneis, 1994:30.22). Vesalius (1543:53; Vesalius et al., 1998:131) referred to the greater and **lesser palatine foramina** as the *ad palati sinem iuxta maxillae superioris sexta ossa, utrinque duo uisuntur foramina*.

In *Tursiops* the greater palatine foramen may have up to four apertures at or just anterior to the **maxillopalatine suture** near the midline. In mammals, smaller foramina associated with a greater palatine foramen have been named variously the **minor palatine foramen** or lesser palatine foramen or **accessory palatine foramen** or postpalatine foramen or posterolateral palatine foramen or posterolateral vacuity.

See **lesser palatine foramen**.

* **greater palatine sulcus** (*sulcus palatinus major*) (Diagram 1; Figure 16b)

The greater palatine sulcus lies on the posterior border of the maxilla in humans. The descending palatine artery and greater palatine nerve lie in this sulcus (Feneis, 1994:22.23). This sulcus was also known as the pterygopalatine sulcus (*sulcus pterygopalatinus*) (Feneis, 1994:22.23), and in humans it forms part of the wall of the **pterygopalatine canal** (Gray, 1918:168). The pterygopalatine canal originates in the **antorbital fossa** and terminates in the **greater palatine foramen** (Gray, 1918:185).

In *Tursiops* the mouth of the greater palatine sulcus lies in the **maxillopalatine suture** ventral to the **ventral infraorbital foramen**. The mouth of the greater palatine sulcus is frequently hidden by a flange of the maxilla that forms the anterior border of the ventral infraorbital foramen. The greater palatine sulcus then forms the pterygopalatine canal with the palatine and runs anteriorly along the palatomaxillary suture to exit on the **palatal surface of the maxilla** by the greater palatine foramen.

– great occipital crest

Flower's (1868:314) use of a "great occipital crest" did not refer to a structure on the maxilla in *Physeter* but to the bony elevation at the posterior of the **supracranial basin**. The **occipital crest** is continuous anteriorly with "the elevated edges of the broadly expanded maxillae." This is homologous with the **nuchal crest** of the rest of the odontocetes.

See also discussion under **supratemporal crest**.

* **hard palate** (*palatum osseum*) (Figure 16b)

The hard palate in most mammals is principally composed of the **palatine processes of the maxillae** and serves to separate the nasal cavity from the oral cavity (Evans and Christensen, 1979:141).

The palatine process of the maxilla has been interpreted as the roof of the oral cavity (Walmsley, 1938:142; Fraser and Purves, 1960:38) in mysticetes. We agree with Walmsley's interpretation. The whole of the oral surface of the maxilla in *Tursiops* is the palatine process (Anderson, 1879:497; Schulte, 1917:374, 375, 378, 381, 386, 388, 389, 393, 400), although the oral cavity no longer lies immediately dorsal.

See **palatine process of the maxilla**; see also **hard palate** under "Palatine bone."

* **incisivomaxillary canal** (Figure 16d)

The incisivomaxillary canal in the dog leaves the medial wall of the **infraorbital canal** within the **infraorbital foramen**, passes dorsally to the apex of the canine **alveolus**, with which it communicates, and enters the premaxilla. It continues anteriorly where it gives off branches to the incisor alveoli (Evans and Christensen, 1979:141).

The incisivomaxillary canal branches from the infraorbital canal at the level of the **antorbital notch** in *Tursiops*. It then passes to the premaxilla and continues through that bone to exit on the lateral surface of the alveolar part of the premaxilla.

= infrafrontal process (Schulte, 1917:380, 400) = infraorbital process

See also **orbital plate of the maxilla**.

– infraorbital border of the maxilla = infraorbital margin (*margo infraorbitalis*)

The infraorbital margin of the maxilla is that part of the maxilla that forms the ventromedial margin of the orbit in humans (Feneis, 1994:22.7).

"Telescoping" has modified the relationships of the maxilla, **antorbital notch**, **orbit**, and associated structures, so that the maxilla is removed from the orbit, and there is no infraorbital margin in *Tursiops* or other living odontocetes. An infraorbital border of the maxilla is present in a few archaic extinct odontocetes.

– infraorbital canal (*canalis infraorbitalis*) (Table 6)

The infraorbital canal in the dog and other noncetacean mammals begins proximally (posteriorly, within the **orbit**) at the **maxillary foramen** and terminates distally (anteriorly, facially) at the **infraorbital foramen** (Evans and Christensen, 1979:141). The distal (anterior, facial) opening in humans is also known as the infraorbital foramen (Gray, 1918: fig. 157).

The infraorbital canal carries the infraorbital nerve (infraorbital branch of the trigeminal) and infraorbital vessels. It lies entirely in the maxilla and usually lies lateral to the **maxillary sinus**.

The problem with the infraorbital canal in both odontocetes and mysticetes is the nomenclature of both the proximal and distal openings of the canal. The proximal (orbital/posterior) opening has been variously called infraorbital foramen, maxillary foramen (*trou dentaire superior*), suborbital foramen (*trou sous-orbitaire*), and the common inferior outlet. The distal (facial/anterior) opening has been called the **antorbital foramen**, infraorbital foramen, maxillary foramen, **supraorbital foramen** (*trou sous-orbitaire*). Table 6 gives some idea of the confused historical usage of the nomenclature of the openings of the infraorbital canal.

The only term that is used consistently and unambiguously is the infraorbital canal. The other terms are used variously to refer to either the distal/anterior or proximal/posterior opening. We therefore propose to use the term "**ventral infraorbital foramen**" in odontocetes and mysticetes to refer to the proximal (orbital/posterior) aperture and **dorsal infraorbital foramen** to refer to the distal (facial/anterior) aperture. Such a terminology has been used for *Tursiops* by Rommel (1990; Table 6 herein) and for the extinct dolphin *Australodelphis* by Fordyce et al. (2002:46, fig. 3).

The infraorbital canal is relatively large in *Tursiops* and other odontocetes. It begins on the **ventral surface of the hard palate** of the maxilla between the supraorbital process and the frontal, lacrimal, and posterior margin of the palatine. The canal may start within a distinct **antorbital fossa**. It branches immediately into the infraorbital canal and superior **alveolar canal**. The branches of the infraorbital canal exit onto the **facial surface of the maxilla** (dorsal infraorbital foramina) and premaxilla (premaxillary foramina) (q.v.) medial to the **antorbital notch**.

= infraorbital foramen (*foramen infraorbitale*) (Diagram 1; Table 6)

Vesalius (1543:48; Vesalius et al., 1998:131) referred to the infraorbital foramen as the *foramen, quo dictae minoris tertii paris nervorum cerebradicis soboles*.

See **infraorbital canal**, **dorsal infraorbital foramen**, and **maxillary foramen**.

= infraorbital fossa (Schulte, 1917:388) = ventral infraorbital foramen

See also comments under **antorbital fossa**.

– infraorbital notch = malar notch (*incisura malaris*)

In humans, the infraorbital notch (Callender, 1869; Lieberman, 1995: fig. 3; not in Gray, 1918) is a groove in the profile of the maxilla below the **orbit**, as seen in anterior view.

Tursiops and other delphinids lack an infraorbital notch in the human sense. The **antorbital notch** may be broadly equivalent.

Anderson (1879:524) used infraorbital notch for the antorbital notch in *Platanista*.

– infraorbital plates of the maxilla (Anderson, 1879:509)

Platanista is unique in developing and pneumaticizing the **maxillary crests** so that each crest develops two plates of the maxilla

TABLE 6. Terms used by selected authors for the antorbital canal and the distal and proximal openings of the canal. Definitions: a.c., antorbital canal; a.f., antorbital foramen; c.i.o., common inferior outlet; d.i.f., dorsal infraorbital foramen; i.c., infraorbital canal; i.f., infraorbital foramen; i.s., infraorbital sulcus; m.f., maxillary foramen; o.i.c., orifice of the infraorbital canal; p.i.f., posterior infraorbital foramen; s.f., supraorbital foramen; s.o.f., *trou sous-orbitaire* (suborbital foramen); t.d.s., *trou dentaire superior* (maxillary foramen); t.s.o., *trou sous-orbitaire* (supraorbital foramen); t.s.o.l., *trou sous-orbitaire* in *Physeter,* not referred to in any other species; v.i.f., ventral infraorbital foramen; a dash (–) = feature not treated; ? = questionable treatment.

Author, date	Proximal (orbital)	Distal (facial)	Canal
Barnes, 1978:15, 19	i.f.	m.f.	—
Bolk, 1967(II):588	—	i.f.	—
Cuvier, 1837(vol.5, part 1): 496	s.o.f.	t.s.o.l.	?
Davis, 1964:48	i.f.	i.f.	i.f.?
de Muizon, 1984:37	—	i.f.	i.c.
Feneis, 1976:22	i.s.	i.f.	i.c.
Flower, 1869:318	i.f.?	i.f.	i.f.?
Flower, 1878:417	—	m.f.	—
Flower, 1882:394	—	i.f.	—
Flower, 1885:138	—	i.f.	—
Forbes, 1893:221	—	m.f.	—
Fordyce, 1994:153, 155	i.f.	m.f.	—
Fordyce and de Muizon, 2001:196	—	p.i.f.	—
Fraser and Purves, 1960:51	m.f.	—	—
Jayne, 1898:187	?	i.f.	?
Kellogg, 1927:14, 18, 53	i.f.	m.f.	i.c.
Kellogg, 1936:108, 109	i.f.	a.f.	?
Kernan, 1918:369, 351	i.f.	m.f.	i.c.
Miller, 1923:7, 10, 47, 48	i.f.	a.f.	i.c.
Miller, 1979:151, 141	m.f.	i.f.	i.c.
Mivart, 1892:80	i.f.?	i.f.	i.c.
Moore, 1960:9	—	m.f.	—
Moris, 1969:699	t.d.s.	t.s.o.	—
Nishiwaki, 1958:68	—	m.f.	—
Owen, 1866a:38	c.i.o.	a.f.	?
Owen, 1869:10	—	a.f.	a.c.
Raven, 1937:6	—	m.f.	—
Romer, 1955:255	i.f.	—	i.c.
Rommel, 1990:36	v.i.f.	d.i.f.	i.c.
Schaller, 1992:32	m.f.	i.f.	i.c.
Schulte, 1917:373, 388, 389	o.i.c.	i.c.	i.c.
Sisson and Grossman, 1953:60	m.f.	i.f.	i.c.
Starck, 1967:510	?	i.f.	i.c.
True, 1910:9	—	—	m.f.
True, 1913:653	—	—	m.f.

that are separated by pneumatic spaces. Anderson (1879:509) called these two plates infraorbital plates of the maxilla.

Tursiops and other cetaceans do not have infraorbital plates of the maxilla.

Geisler and Sanders (2003:69) discussed the infraorbital plate as used in Miller (1923). In that paper, Miller (1923:7, 14, 55, pl. 1) discussed the same plate but called it the orbital plate (q.v.) not the infraorbital plate.

– infraorbital process = infraorbital plate (Kellogg, 1928:44)

The infraorbital, or orbital, process or plate of Mysticeti does not occur in *Tursiops* or other delphinids. Miller (1923:7) stated, of mysticetes: "the orbital portion of the body of the maxillary is present and well developed as a large 'horizontal ventral' plate projecting conspicuously behind and beneath the **infraorbital foramen**." Miller (e.g., 1923:8, 14) repeatedly used the term "orbital plate" (q.v.). Kellogg (1928:44) may have been the first to use infraorbital plate for the orbital plate of Miller. "Infraorbital" has come into wider use, and is preferred here. Geisler and Sanders (2003:69) stated that the presence of an infraorbital plate is not a mysticete synapomorphy, equating it with the **maxillary tuberosity** of other mammals.

= infraorbital sulcus (*sulcus infraorbitalis*) = infraorbital canal (Table 6)

The infraorbital sulcus lies on the posterior part of the orbital surface in humans and holds the infraorbital vessels and infraorbital nerve (Gray, 1918:159).

The infraorbital sulcus is closed in odontocetes and is known as the **infraorbital canal.**

*** infratemporal fossa** (*fossa infratemporalis*) = zygomatic fossa of the frontal bone (Figure 2)

In humans the infratemporal fossa is an irregularly shaped cavity situated on the skull base. The infratemporal fossa is bounded anteriorly by the **infratemporal surface of the maxilla** and the ridge that descends from the **zygomatic process of the maxilla;** posteriorly by the **articular tubercle** of the squamosal; dorsally by the **zygomatic process of the jugal** anterior to the articular tubercle, and the **alisphenoid;** and medially by the lateral **pterygoid plate** (Gray, 1918:184, fig. 189; Feneis, 1994:30.13).

The infratemporal fossa is not in Evans and Christensen (1979) but is in Schaller (1992:10.27), where no details are given. The best treatment of it we can find in a nonhuman subject is in the giant panda (Davis, 1964:48, fig. 17):

> In Ailuropoda the infratemporal fossa is separated from the **orbit** above by the well-marked inferior orbital ridge [*crista orbitalis inferior*] throughout most of its length. Behind the **orbital fissure** it is separated from the **temporal fossa** by an indistinct elevation extending from the superior orbital ridge in front of the orbital fissure to the anterior lip of the **glenoid fossa**. The infratemporal fossa is relatively small. The anterior half of the infratemporal fossa contains the entrance to the **infraorbital foramen,** the common foramen for the sphenopalatine (sphenopalatine artery and nerve; nasal branches of sphenopalatine ganglion) and pterygopalatine (descending palatine artery and

> nerve) canals. . . . The posterior half of the fossa, from which the pterygoid muscles arise, exhibits muscle rugosities. The areas of origin of the pterygoid muscles are sharply marked on the bone. The area of pterygoid origin is much reduced, both vertically and horizontally, as compared with Ursus.

Davis conceived of the lateral view of the skull, with the exclusion of the facial region, being composed of the temporal fossa, the orbit, and infratemporal fossa (1964: fig. 17). Given that concept, the infratemporal fossa is the remnant after the temporal fossa and orbital contents have been removed.

Wible (2003:153) indicated that the infratemporal fossa in *Monodelphis* is separated from the temporal fossa by the **infratemporal crest.** Alternatively, Meng and Wyss (2001) identified the **zygomatic fossa of the jugal** in lagomorphs as the distinctive, elongated fossa for attachment of the *m. masseter* lateralis on the lateral face of the jugal.

As "zygomatic fossa," the feature is only mentioned once in Anderson (1879:508): "From the upper border of the pterygomaxillary fissure, the ridge dividing the temporal and zygomatic fossae is prolonged backwards to the ***foramen ovale***." By following a "ridge" forward from the *foramen ovale* we have concluded that what Anderson meant by the "zygomatic fossa" in *Platanista* was the contents of the orbit.

In *Tursiops* and other delphinids the infratemporal fossa is bounded anteriorly by the medial surface of the **maxillary process of the jugal**, the anterior margin of the **anterior sinus fossa**, and the lateral edge of the **palatine surface of the pterygoids**. Medially the infratemporal fossa is bounded by the ventral edge of the pterygoids; and posteriorly by the posterior edge of the pterygoids and the crest that forms the posterior margin of the **fossa for the postorbital lobe of the pterygoid sinus**. Laterally the infratemporal fossa is bounded by the lateral margin of the **alisphenoid** and **orbitosphenoid**, and the lateral margin of the **antorbital fossa.** The infratemporal fossa contains the entire lateral surface of the pterygoid bone, the antorbital fossa (**pterygopalatine fossa**), and the anterior sinus fossa.

– **infratemporal surface of the maxilla** (*facies infratemporalis*)

In humans the infratemporal surface is the posterolateral portion of the **external surface of the maxilla** that lies just ventral to the **temporal fossa** (Feneis, 1994:22.14).

The maxilla in *Tursiops* does not lie ventral to the temporal fossa but, as a consequence of "telescoping," lies dorsal to the temporal fossa. Odontocetes do not have an infratemporal surface of the maxilla.

– **inner plate of the maxilla** (Anderson, 1879:524)

The inner plate of the maxilla is the ventral of the two plates that are produced by the pneumaticization of the maxilla in the region of the **antorbital notch** (Anderson, 1879:524).

Pneumaticization of the maxilla is restricted to *Platanista*.

* **interalveolar margin**

See "Mandible."

* **interalveolar septa** (Figure 16b)

See "Mandible."

– **interdental spaces**

The interdental spaces in the dog are spaces between the teeth when the teeth are set relatively far apart (Evans and Christensen, 1979:140). The interdental spaces grade into the **interalveolar margin** (q.v.). **Diastema** (q.v.) appears to be equivalent.

In *Tursiops* and other delphinids the teeth are set close together and interdental spaces do not occur.

– **interradicular septa**

See "Mandible."

– **lachrymal area** (Schulte, 1917:389)

See **cerebral area.**

– **lacrimal canal of the maxilla** (*canalis lacrimalis*)

The lacrimal canal of the maxilla in the dog continues from the lacrimal bone into the maxilla where it opens ventral to the **nasoturbinate crest** (Evans and Christensen, 1979:141; Schaller, 1992:30.32). The **lacrimal canal** carries the nasolacrimal duct (*ductus nasolacrimalis*).

The lacrimal canal is absent in *Tursiops* and other delphinids.

* **lacrimal margin of the maxilla** (*margo lacrimalis*) (Figure 16b)

The lacrimal margin of the maxilla is that portion of the bone that articulates with the lacrimal. It is on the medial border of the **orbit** and forms the posterior margin of the **frontal process of the maxilla** in humans (Gray, 1918:158f).

The lacrimal margin of the maxilla in *Tursiops* and other delphinids is centered on the **antorbital notch** and **antorbital tubercle.** The lacrimal margin is on the **ventral surface of the hard palate** of the maxilla posterior and lateral to the **zygomatic recess.**

– **lacrimal notch** (*incisura lacrimalis*)

The lacrimal notch is a crescentic notch at the entrance to the nasolacrimal duct (Feneis, 1994:22.27).

The lacrimal notch is absent in delphinids.

– **lacrimal sulcus** (*sulcus lacrimalis*)

The lacrimal sulcus lies on the medial or **nasal surface of the maxilla** and extends ventrally from the ventral angle of the **orbit** (Gray, 1918:159f; Feneis, 1994:22.19). It lodges the lacrimal sac (Gray, 1918:189; Feneis, 1994:334.21).

The lacrimal sulcus is lacking in delphinids.

See this term also under "Lacrimal Bone."

– **lacrimal tubercle** (Gray, 1918:164, fig. 157)

According to Gray (1918:164, fig. 157) the lacrimal tubercle is a structure of the maxilla in humans, contributing with part of the **lacrimal hamulus** to the upper opening of the **lacrimal canal.**

Tursiops does not have an obvious lacrimal tubercle and lacks the lacrimal canal. Novacek (1986:84, character 24) reported the lacrimal tubercle as absent in Cetacea.

* **lacrimojugal crest [new term]** (Figures 2, 16b)

In *Tursiops* the lacrimojugal crest is the prominent small ridge of maxilla that is exposed to ventral view in the **lacrimojugal cleft** of the fused lacrimal and jugal. The lacrimojugal crest is bounded anteriorly by the **maxillary process of the jugal** and posteriorly by the **medial process of the lacrimal**. The relationship of the lacrimojugal crest to the **anterior lacrimal crest of the maxilla** and to the **lacrimal sulcus** in humans is uncertain.

= **lamelliform extension** (Flower, 1885:212) = ascending process

= **lateral basirostral groove** = basirostral groove

= **malar process** = zygomatic process of the maxilla

= **malomaxillary fissure** = antorbital notch (Owen, 1866a:34, 38, 39, 41; pl. 12: fig. 1k; pl. 13: fig. 1k) as malo-maxillary fissure or malomaxillary fissure)

* **maxillary crest** (Diagram 2; Table 5; Figures 1, 16a,c,d)

In odontocetes "maxillary crest" normally refers to the structure located on the lateral part of the dorsal surface of the supraorbital part of the maxilla, lateral to the **antorbital notch** (Fraser and Purves, 1960:44, 83, 107). However, there has been considerable variation in the use of this term. For example, Harmer (1924:543) used it to refer to the crests in *Hyperoodon* that extend from the **maxillary prominences** medial to the antorbital notch. Further, the position, shape, and contribution of frontal to the maxillary crest varies among living species, and between living species and fossils, so that homologies are not always clear (particularly in *Physeter* and *Kogia*). Here we modify the use of Fraser and Purves: the maxillary crest (or maxillary ridge) is that feature developed lateral or posterior to the antorbital notch on the frontal but not involving the maxillo-frontal suture or the frontal itself. The terminology shown in Diagram 2 appears to deal satisfactorily with structures in living odontocetes other than *Physeter* and *Kogia*.

The maxillary crest in the broader sense is hypertrophied in *Physeter*. Flower (1868:314) referred to the **supracranial basin**, with the transverse occipital crest at the posterior boundary, and referred to the elevated edges of the maxillae without using the term "maxillary crest" and to the maxillary component of "the crest" (Flower, 1868:314, 317).

The maxillary crest in the broader sense is referred to as the great transverse crest (*crêtes frontales*) by Blainville in *Kogia breviceps* (Blainville, 1838:337; Schulte, 1917:371, 381). The great transverse crests form the *cirque faciale* of van Beneden and Gervais (1880:350; Schulte, 1917:371). Schulte (1917:372, 373) also referred to it as the maxillary crest and the transverse crest (1917:375, 376, 382, 391, 392, 400). See further discussion under **supraorbital crest** and **supratemporal crest**.

The maxillary crest in the broader sense is also hypertrophied in *Platanista* (Anderson, 1879:450, 496, 512, 525, 526) where it consists of two distinct plates, the external plate of the maxillary crest and the internal plate of the maxillary crest (Anderson, 1879:525, 526). Anderson (1879:449) also referred to this structure as the great lateral crests of the maxillary bones. **Supraorbital crest** (see Diagram 2) is the recommended term.

The maxillary crest is formed by the origin of the *externus* group of the facial muscles (*pars anteroexternus* and *pars posteroexternus* of the *m. maxillonasolabialis*) (Mead, 1975).

* **maxillary flange** (Figures 2, 16a)

The maxillary flange is the lateral portion of the maxilla that transitions between the rostrum and the ascending process. The maxillary flange is medial to the **maxillary prominences**, if present, and the **antorbital notch**. The term "maxillary flange" was used by Harmer (1924:544) where he said it was strongly developed in *Mesoplodon bidens* and lacking in *M. layardii*.

Maxillary flanges are variably developed in delphinids. They are relatively strong in *Tursiops*; in USNM 550403, each flange originates anteriorly level with the fourth or fifth last tooth, and extends posteriorly into the antorbital notch. Each flange has a thick rough projection; the homology is uncertain with the **maxillary tubercle** as seen in ziphiids. The maxillary flange is associated with the origin of the rostral muscle (Mead, 1975).

= **maxillary foramen** (*foramen maxillare*) = dorsal, ventral infraorbital foramina (Table 6)

The maxillary foramen, in the dog and other noncetacean mammals, lies on the **orbital surface of the maxilla** just medial to the **zygomatic bone**. It carries the branches of the infraorbital nerves and infraorbital vessels that exit via the superior **alveolar foramina** and infraorbital foramina (Evans and Christensen, 1979:141).

In cetaceans the term "maxillary foramina" has been used to refer to foramina on the facial or orbital surface of the maxilla (e.g., Fraser and Purves, 1960:51). We propose to follow Rommel (1990:36) and call the foramen on the orbital surface of the maxilla, the "**ventral infraorbital foramen**" and the foramina on the facial surface "dorsal infraorbital foramina." See the discussion under **infraorbital canal** for more details.

= **maxillary fossa** (Schulte, 1917:372) = facial fossa

A maxillary fossa occurs on the face anterior to the **orbit** in various land mammals including Perissodactyls (e.g., Holbrook, 1999:336). See also **antorbital fossa**, **facial fossa**.

For maxillary fossa in Cetacea, see **facial fossa**.

– **maxillary groove** (Azzaroli, 1968:75; Mead, 1989b:393) (Diagram 2)

The maxillary groove is a deep **longitudinal groove** on the lateral surface of the **ascending process of the maxilla** (Azzaroli, 1968:75). The anterior extent of the maxillary groove is clearly limited by a pit dorsal to the lacrimal bone. Posteriorly the maxillary groove disappears gradually. The maxillary groove has been reported only from specimens of *Indopacetus pacificus*. Besharse (1971:303) reported a maxillary groove in *Mesoplodon densirostris*, but the feature could not be discerned in the published figures.

– **maxillary hiatus** (*hiatus maxillaris*)

The maxillary hiatus is the large opening in the medial wall of the **maxillary sinus** (Feneis, 1994:22.22). The maxillary sinus communicates with the nasal cavity through the maxillary hiatus.

Paranasal sinuses are not developed in cetaceans (Fraser and Purves, 1960:5, 75), and the maxillary hiatus is absent in *Tursiops*.

= **maxillary notch** (Kernan, 1918) = antorbital notch

True (1910:19), Kellogg (1924:10) and Brimley (1943:200) used maxillary notch for **antorbital notch** (not in Schaller, 1992; not in Feneis, 1994).

= **maxillary plate** (Moore, 1960:16) = ascending process

Following True (1910:21; Moore, 1963), maxillary plate has had some use for odontocetes (e.g., Moore, 1960:16; Dalebout et al., 2002:595; Kemper, 2004:31). Ascending process is preferred here.

The maxillary plate was also used by Fraser and Purves (1960:46) to refer to the following structure in *Inia*: "As in *Stenodelphis* there is a posteriorly projecting, but in this genus much fenestrated, maxillary plate. This plate was considered by Flower (1889 [sic, 1867]) to be a portion of the palatine fused anteriorly to the maxilla, but the lateral suture between the palatine and the maxillary plate is situated in the deep fossa formed between the aforementioned plate and the palatine."

We have examined an ontogenetic series of *Pontoporia* (*Stenodelphis* in the sense of Fraser and Purves) and determined that Flower was correct. In USNM 482712 the sutures for the maxilla and palatine are clearly visible and it is the palatine that forms the lateral wall of the **pterygoid sinus fossa**.

– maxillary process of the zygomatic arch

The term "maxillary process of the zygomatic arch" has been used for the posterolateral extension of maxilla that bounds the **temporal fossa** in monotremes and the extinct Multituberculata (see comment by Wible and Rougier, 2000:83). It is distinct from the **maxillary process of the jugal**, also confusingly known as the maxillary process of the zygomatic, as seen in some mammals including primates ("maxillary process of the **zygomatic bone**": Begun, 1994:43; Nishimura et al., 2005).

Tursiops and other Cetacea lack a maxillary process of the zygomatic arch.

– maxillary prominence

In the odontocete family Ziphiidae, there develops a feature medial to the **antorbital notch** and on the posterolateral surface of the rostrum that has been termed the "maxillary prominence" (True, 1913a:653; Moore, 1960:13). The maxillary prominence projects into the antorbital notch dividing it into an anteromedial **prominential notch** and a posterolateral antorbital notch. **Tubercle of the maxilla** or **maxillary tubercle**, of Flower (1878:417) appears to be the oldest available name for the maxillary prominence of later authors. See the discussion under **maxillary tuberosity**.

= maxillary protuberance = antorbital process (True, 1910:20, 21)

= maxillary recess (*recessus maxillaris*) = maxillary sinus

The maxillary recess is synonymous with the **maxillary sinus** in carnivores (Sisson and Grossman, 1953:61; Evans and Christensen, 1979:141, 159; Schaller, 1992:14.13, 180.5). Rossie (2006) discussed issues of homology and nomenclature for the maxillary recess in primates.

– maxillary sinus (*sinus maxillaris*)

The maxillary sinus or **maxillary recess** is a paranasal sinus, a large lateral diverticulum of the nasal cavity, that lies medial to the **infraorbital canal** and **lacrimal canal** in most mammals, both of which protrude slightly into the sinus. The lateral wall of the maxillary sinus is formed largely by the maxilla with the addition of the palatine posteriorly. The medial wall of the maxillary sinus is formed by the lateral lamina of the ethmoid bone. The maxillary sinus opens into the nasal cavity through the **nasomaxillary opening** (Evans and Christensen, 1979:159). The sinus may expand laterally and be subdivided as in equids into a **posterior maxillary sinus** (*sinus maxillaris caudalis*) and an **anterior maxillary sinus** (*sinus maxillaris rostralis*) (q.v.) (Sisson and Grossman, 1953:80; Schaller, 1992:32.5, 29; 180.2, 3). The **sphenopalatine foramen** opens near the posterior limit of the sinus in canids. The **maxillopalatine suture** lies within the sinus.

Paranasal sinuses are not developed in cetaceans (Fraser and Purves, 1960:5, 75), and the maxillary sinus is absent in *Tursiops*. The situation of the paranasal sinus system in nondelphinid cetaceans is not well known. The paranasal sinus system is present in archaeocetes (Kellogg, 1928:199; Uhen, 2004).

– maxillary tubercle (Diagram 2; Table 5)

Flower (1872:209) used **maxillary tuberosity** to refer to the rugosity at the anterior end of the "**maxillary crests**" of *Hyperoodon* but later (Flower, 1878:417) referred to the "**tubercle of the maxilla**" in *Mesoplodon grayi* and *M. densirostris*. "Tubercle" in the latter sense, and our preferred use, is the prominence medial to the **antorbital notch** and apparent in dorsal or ventral view (see Diagram 2). The maxillary tubercle should be differentiated from any elevation that may develop on the maxilla posterior and dorsal to the maxillary tubercle; such a crest is the rostral [maxillary] ridge or crest.

Past use of tubercle and tuberosity is confusing. For example, Schulte (1917:371, 373, 400) used "maxillary tuberosity" to refer to the anterior end of the maxillary crests in *Kogia*, namely, for structures lateral to the antorbital notch. Harmer (1924:543) used "maxillary tubercle" to indicate a rugosity at the anterior end of his maxillary tuberosity. See Table 5 and discussion under "**antorbital process**" for the complex history of names for what we here term the rostral (maxillary) ridge or crest of the face.

Tursiops lacks a maxillary tubercle.

– maxillary tuberosity (*tuber maxillae* / *eminentia maxillae*)

The maxillary tuberosity or tuber in mammals is a posterior projection of the maxillary portion of the **maxillary sinus** associated with the posterior molars, and often developed in the floor of the **orbit** (Sisson, 1910:58; Gray, 1918:159; Evans and Christensen, 1979:141; Feneis, 1994:22.17; Wible and Gaudin 2004:123, **orbital process** of the maxilla).

Tursiops lacks a maxillary tuberosity in the sense of terrestrial mammals.

Maxillary tuberosity should not be confused with the dorsal feature on the face of ziphiids, termed "**maxillary tubercle**" (q.v.).

– maxillopalatine suture (Owen, 1866a:29)

The maxillopalatine suture is the serrate joint between the maxillae and the palatine bones. In Cetacea this joint has become relatively large. Fusion of the elements does not take place with age.

– maxilloturbinal = maxilloturbinate

In many terrestrial mammals the maxilloturbinal (maxilloturbinate; **ventral nasal concha** of veterinary anatomy) is one of several scrolls that occupy the anterior part of the nasal cavity and are attached to the *crista conchalis* on the medial surface of the maxilla (Flower, 1885:130; Evans and Christensen, 1979:512). Wible and Gaudin (2004:121) commented on the maxilloturbinal in the armadillo. Uhen (2004:46) described **turbinals** in the archaeocete *Dorudon atrox*.

In *Tursiops* and other odontocetes the turbinals are not developed in the normal mammalian manner, as discrete bony structures in adults. Cave (1988) indicated that the maxilloturbinal may be present in highly modified and vestigial form as the bilateral Meckelian ossicle, which may be a distinct bone in adults including *Tursiops*.

= maxilloturbinate
See **maxilloturbinal**.

* **mesorostral canal**
See "Premaxilla."

* **nasal crest of the maxilla** (*crista nasalis*) (Figure 16b,c,e)

The nasal crest of the maxilla is the anterior edge of the medial border of the **palatine process of the maxilla**, which is raised into a ridge (Gray, 1918:163; Schaller, 1992:36.23; Feneis, 1994:24.2) for reception of the vomer.

Modifications of the relationships among the bones of the rostrum in cetaceans have produced some drastic changes. The nasal crest of the maxilla is that surface of the maxilla that is in contact with the vomer. The nasal crest has broadened considerably and is the ventromedial portion of the maxilla that is in direct contact with the vomer (i.e., is not overlain by the premaxilla).

* **nasal notch of the maxilla** (*incisura nasalis*) (Figure 16a)

The nasal notch of the maxilla is that portion of the maxilla that forms the lateral border of the **external bony nares** (Gray, 1918:158; Feneis, 1994:22.11).

The nasal notch of the maxilla is represented by the posteromedial surface of the maxilla that borders the external bony nares in delphinids.

= nasal process of the maxilla (Gray, 1918:161) = frontal process of the maxilla

* **nasal surface of the maxilla** (*facies nasalis*) (Figure 16a)

The nasal surface of the maxilla is the medial surface of the maxilla in the dog that forms the wall of the nasal cavity (Evans and Christensen, 1979:141).

The nasal surface of the maxilla in delphinids is the posteromedial portion of the **ventral surface of the hard palate** of the maxilla that forms the anterodorsal wall of the nasal cavity.

= nasomaxillary opening (*aditus nasomaxillaris*) = maxillary hiatus

– occipital crest
See **great occipital crest**.

– orbital plate of the maxilla (Miller, 1923:7, 14)

The orbital plate of the maxilla (Miller, 1923:7, 14, 55, pl. 1) is the posterior part of the maxillary border that projects obliquely downward and backward under the anterior margin of the **supraorbital process of the frontal** bone in mysticete telescoping (Miller, 1923:4, 55). Miller (1923:8) also called this the horizontal ventral plate. Kellogg (1928:44) may have been the first to use the term "infraorbital" plate or process, which has come into common use and is preferred here for the feature in Mysticeti (see **infraorbital process**). The orbital plate overlies (is dorsal and posterior to) the **ventral infraorbital foramen**. Schulte (1917:380, 400) terms this feature the infrafrontal process and states that it may be present in a reduced condition in some *Kogia* skulls.

In *Tursiops* and probably most delphinids the surface of the maxilla anterior to the ventral infraorbital foramen is smooth and shows no sign of an orbital plate.

= orbital process
See "Palatine Bone," "Jugal Bone."

– orbital surface of the maxilla (*facies orbitalis*)

The orbital surface of the maxilla is the part of the maxilla that lies within the orbit in humans (Gray, 1918:159; Feneis, 1994:22.4).

The maxilla does not take part in the formation of the **orbit** in odontocetes. See discussion under **maxillary tuberosity** and **infraorbital process**.

– palatal groove

Bilateral palatal grooves (Perrin et al., 1981:593) occur in the maxillae of the delphinids, *Delphinus*, *Stenella*, and *Lagenodelphis*, on the ventral surface of the rostrum. Each groove holds a rostral extension of the **anterior sinus** (Fraser and Purves, 1960:72 "deep groove in maxilla"). True (1889:44) termed these the **lateral grooves** in the palate. Gray (1846:41) also referred to the "deep grooves." Palatal grooves are absent in *Tursiops*.

See also **anterior sinus fossa**.

* **palatal surface of the maxilla** (Owen, 1866a:38) (Figure 2)

The palatal surface of the maxilla is the **ventral surface of the hard palate** that forms part of the palate. The palatal surface is homologous with the **palatine process of the maxilla**.

= palatine fissure (*fissura palatina*)
See "Premaxilla."

* **palatine grooves of the maxilla** (*sulci palatinae*) (Figure 16b)

The palatine grooves or **palatine sulci** are depressions leading from the **greater palatine foramen** on the surface of the palate that contain branches of the greater palatine nerve and descending palatine artery (Schaller, 1992:34.6; Feneis, 1994:24.7). In some mammals the greater palatine groove (*sulcus palatinus major*) of the maxilla forms the greater **palatine canal** with the greater palatine groove of the palatine bone (Schaller, 1992:32.27, 36.7).

* **palatine process of the maxilla** (*processus palatinus*) (Figures 2, 16b)

The palatine process of the maxilla, in the dog and other mammals, is a transverse shelf of bone medial to the teeth that forms most of the **hard palate** (q.v.) (Evans and Christensen, 1979:141; Schaller, 1992:34.4; Feneis, 1994:24.1; Wible and Gaudin, 2004:122). The palatine process is in contact with the oral cavity and encompasses all of the maxillary surface medial to the tooth row.

The palatine process of the maxilla has been interpreted as the roof of the oral cavity (Walmsley, 1938:142) in mysticetes. We agree with Walmsley's interpretation. The whole of the oral surface of the maxilla in odontocetes is the palatine process. Owen (1866a:27, 29) referred to the palatine process as the palatine plate of the maxillary.

* **palatine prominence** (Figure 16c)

"[The palatine] receives in a groove on its upper and anterior border the palatine prominence of the upper maxillary bone. The maxillary expands from its palatine prominence—the essential point of the suspension—backwards, outwards, but chiefly forwards, where it gradually diminishes to an obtuse point." (Owen, 1853:443).

The palatine prominence, as described by Owen and confirmed on a newborn *Physeter catodon* skull (USNM 49488), lies on the ventromedial margin of the maxilla, just anterior to the anterior edge of the palatine. The palatine prominence forms a low but pronounced buttress on which the palatine bone sits. This is a feature of the palatomaxillary articulation and is only expressed in those mammals that have a wide palatomaxillary suture. This suture occurs on the **hard palate** of noncetacean animals, which is normally smooth (without prominences).

The palatine prominence can be seen in *Tursiops* as the change in orientation of the ventral margin of the maxilla where the palatine articulates with the maxilla. Schulte (1917:388, 393) called this the **pterygoid elevation** or pterygoid eminence (Schulte, 1917:394) in *Kogia*. A **palatal ridge** or **palatal crest** (q.v.) may develop on the palatine, posterior to the palatine prominence.

– **palatine sinus** (*sinus palatinus*)

The palatine sinus excavates the palatal process of the maxilla in ruminants (Schaller, 1992:34:8). See also **palatine sinus** under "Palatine Bone."

Cetacea do not develop a palatine sinus in the maxilla.

– **palatine spines** (*spinae palatinae*)

In humans the palatine spines are bony ridges along the **palatine grooves of the maxilla** (Feneis, 1994:24.6).

Palatine spines are not developed in the palatine grooves of odontocetes.

* **palatine sulcus** (*sulcus palatinus*) (Figures 2, 6f)

The palatine sulcus or palatine groove lies on the **ventral surface of the hard palate** (or oral surface) of the **palatine process of the maxilla** and extends anteriorly from the greater palatine foramina to the **palatine fissure** (**incisive foramen**) (Evans and Christensen, 1979:141, 152, 672; Schaller, 1992:34.6; Feneis, 1994:24.7). The palatine sulcus contains the greater palatine nerve and greater palatine artery. In some mammals the greater palatine groove (*sulcus palatinus major*) of the maxilla forms the greater **palatine canal** with the greater palatine groove of the palatine bone (Schaller, 1992:32.27, 36.7).

The palatine sulcus in *Tursiops* is reduced to a series of short grooves that radiate anteriorly from the greater palatine foramina; minor palatine foramina and sulci may be developed in some Cetacea. The palatine fissure (**incisive canal**, sometimes known as the **incisive foramen**) is not present in *Tursiops*, and dolphins reportedly lack the nasopalatine nerve that in other mammals runs through the incisive canal / incisive foramen.

= **posterior infraorbital foramen** (Fordyce, 1981:text-fig. 2; Fordyce and de Muizon, 2001:196, fig. 12) = dorsal infraorbital foramen (Table 6)

– **posterior maxillary sinus** (*sinus maxillaris caudalis*)

The posterior maxillary sinus is the posterior part of the **maxillary sinus** (Schaller, 1992:32.5, 180.3).

Paranasal sinuses are not developed in cetaceans (Fraser and Purves, 1960:5, 75), and the posterior maxillary sinus is absent in *Tursiops*.

* **posterior palatine foramen** (*foramen palatinum caudale*) (Diagram 1; Figures 16b, 18e)

The posterior palatine foramen in the dog is situated in the **antorbital fossa** next to the **sphenopalatine foramen** (Evans and Christensen, 1979:144, figs. 4–38) and is the entrance to the **palatine canal**, which transmits the greater palatine nerve and the greater palatine artery (Sisson and Grossman, 1953:61; Schaller, 1992:12.22). This is also known as the caudal palatine foramen.

The posterior palatine foramen (Fraser and Purves, 1960:26) in delphinids is the communication between the **infraorbital canal** and the **greater palatine sulcus**. It lies at the posterior end of the greater palatine sulcus and is entirely covered by the palatine bone. The posterior palatine foramen in *Tursiops* opens on the posterior wall (nasal surface) of the **ethmoidal crest of the palatine** just anteroventral to the sphenopalatine foramen. It communicates with a canal for palatine vessels and nerves, which opens at major palatine foramina and minor palatine foramina. In adult *Tursiops* the posterior palatine foramen may be confluent with the opening of the sphenopalatine foramen.

– **postnarial cavity** (Owen, 1866a:37, 38, 42)

Owen used postnarial cavity (1866a:37, 42), postnarial tract, or spermacetic cavity (1866a:38) to refer to the paired cavities that are formed by the maxillae posterior to the nasals in *Kogia*. These are formed in the **facial fossa**e of the maxilla by dorsal proliferation of the bones surrounding the facial fossa, primarily the frontals. This is correlated with the unusual development of the spermaceti organ and associated tissues in *Kogia* (Schenkkan and Purves, 1973).

* **premaxillary surface of the maxilla** (Figure 16d)

The premaxillary surface of the maxilla (Anderson, 1879:526) is the surface of the maxilla that articulates with the premaxilla.

In delphinids the premaxillary surface is the dorsomedial surface that extends from the anterior extremity of the maxilla to nearly the posteromedial corner of the ascending process. The premaxillary surface is defined dorsally by strong lateral angles that are formed between the premaxillary and dorsal surfaces of the maxilla. The premaxillary surface is defined ventrally by a ridge and corresponding sulcus for reception of the ventral portion of the premaxilla. The medial surface of the maxilla consists of the premaxillary surface and the **vomerine shelf.**

= **preorbital notch** (Anderson, 1879:363) = antorbital notch

– prominential crest of the maxilla [new term]

The prominential crest of the maxilla in cetaceans is the crest that extends posteriorly along the dorsal surface of the maxilla from the **maxillary prominence**. See the discussion under antorbital prominence. The prominential crest is formed by the origin of the -internus group of the facial muscles (*pars anterointernus*, *pars posterointernus* of the *m. maxillonasolabialis*) (Mead, 1975).

A prominential crest is not present in delphinids but is a marked feature of some ziphiids.

– prominential notch (Diagram 2; Table 5)

The prominential notch is formed between the **maxillary prominence** and the base of the rostrum in ziphiids (Moore, 1963:406, fig. 14). Harmer (1924:543) referred to the prominential notch as the inner notch.

A prominential notch is not present in delphinids but is a marked feature of some ziphiids.

– pterygoid elevation (Schulte, 1917:388) = palatine prominence

– pterygoid process of the maxilla (*processus pterygoideus*)

The pterygoid process of the maxilla is a small pointed spur located on the **palatal surface of the maxilla** posteromedial to the **alveolus** for the last tooth. In the dog the pterygoid process and the palatine bone form a notch, rarely a foramen, through which the minor palatine vessels pass (Evans and Christensen, 1979:141, 151; Schaller, 1992:250.36 unlabeled).

There is no distinct pterygoid process of the maxilla in *Tursiops*.

= pterygopalatine fossa (*fossa pterygopalatina*) = antorbital fossa

In humans the pterygopalatine fossa is a small triangular space associated with the orbit, medial to the **infratemporal fossa.** It is bounded dorsally by the **body of the sphenoid** and by the **orbital process of the palatine**; anteriorly by the **infratemporal surface of the maxilla**; posteriorly by the base of the **pterygoid process of the sphenoid** and the **alisphenoid**; and medially by the vertical portion (including orbital and sphenoid processes) of the palatine (Gray, 1918:185; Feneis, 1994:30.14; Daniels et al., 1998: "Determining the exact margins of the PPF [pterygopalatine fossa] is problematic, because they are not strictly defined even in the anatomic literature"). In humans, it is distinct from the adjacent **temporal fossa** and infratemporal (or zygomatic) fossa. Vesalius et al. (1998:131) referred to the pterygopalatine fossa as the structure that is indicated by the symbol ϕ. In this translation of pages 47–55 of Book I of Vesalius (1543)—the section on the foramina in the bones of the head and upper jaw—Richardson and Carman indicate that ϕ occurs but do not give any other relevant facts.

The pterygopalatine fossa in humans communicates with the orbit by the **inferior orbital fissure**, with the nasal cavity by the **sphenopalatine foramen**, and with the infratemporal fossa by the pterygomaxillary fissure. The **foramen rotundum**, **pterygoid canal**, and the pharyngeal canal open into the posterior wall of the pterygopalatine fossa; the sphenopalatine foramen opens into its medial wall; and the **pterygopalatine canal** opens into its ventral wall. The pterygopalatine fossa contains the maxillary nerve, the sphenopalatine ganglion (Schulte, 1917:378), and the terminal part of the internal maxillary artery (Gray, 1918:185).

Owen (1866a:27) called the pterygopalatine fossa the superorbital fossa.

There is confusion in application to carnivores. For the dog Evans and Christensen (1979:150) used the term in a broad sense for those structures ventral to the **ventral orbital crest** between the **maxillary foramen** and the posterior end of the pterygoid. Conversely, in the panda Davis (1964: fig. 17) identified the area ventral to the ventral orbital crest as the infratemporal fossa. Davis's terminology more closely follows that of Gray (1918).

For the horse, Sisson and Grossman (1953:72) also used pterygopalatine fossa in the broader sense, namely, the fossa bounded by the pterygoid process of the sphenoid, the **perpendicular plate** of the palatine, and the **maxillary tuberosity** of the maxilla. The maxillary foramen, sphenopalatine foramen, and **posterior palatine foramen** open into the pterygopalatine fossa.

McFarland et al. (1979:11) define the pterygomaxillary region (*regio pterygomaxilaris*) as a "region at the base of the skull encompassing the pterygoid process of the sphenoid bone (a perpendicular process extending down from the junction of the **greater wing** and **body of the sphenoid** bone) and the maxilla, the upper jaw bone." The pterygomaxillary region is another part of the complex anatomy of the pterygopalatine fossa. Fraser and Purves (1960:65) probably had the pterygopalatine fossa in mind when they referred to the pre-orbital concavity and the preorbital recess (1960:53, 54, 58).

In and around the **orbit** in *Tursiops* the maxilla, frontal, palatine, and sphenoid have been so modified by changes in topography, particularly involving fossae for the pterygoid air sinuses, that the pterygopalatine fossa is no longer identifiable, and the term cannot be applied clearly. The superorbital fossa (q.v.) of Owen (1866a:28) is here used for the main depression associated with the maxilla anterior to the orbit.

*** pterygopalatine surface of the maxilla** (*facies pterygopalatina*) (Figure 16b)

The pterygopalatine surface of the maxilla is that part of the posterior surface maxilla that borders the **pterygopalatine fossa** (**antorbital fossa**) (q.v.) (Schaller, 1992:32.17).

The pterygopalatine surface of the maxilla cannot be identified clearly in *Tursiops* or other delphinids.

– rostral maxillary sinus (*sinus maxillaris rostralis*)

The rostral maxillary sinus is the anterior part of the **maxillary sinus** in animals in which the sinus is separated by a maxillary septum (Sisson, 1910:72, 73, 126, 146; Schaller, 1992:32.29, 180.2). The rostral maxillary sinus is also called the **anterior maxillary sinus** or the inferior maxillary sinus (Sisson, 1910:73).

Paranasal sinuses are not developed in cetaceans (Fraser and Purves, 1960:5, 75), and the rostral maxillary sinus is absent in *Tursiops*.

*** rostral portion of the maxilla** (Schulte, 1917:386–388) (Figure 16a)

The rostral portion of the maxilla lies anterior to the **antorbital notches**, and thus it contributes to the formation of the rostrum.

*** rostral surface of the maxilla** (Schulte, 1917:389) (Figure 16a)

The rostral surface of the maxilla consists of the **external surface** of the **rostral portion of the maxilla**.

– septum of the maxillary sinus (*septum sinuum maxillarium*)

The septum of the **maxillary sinus** separates the **caudal maxillary sinus** from the **rostral maxillary sinus** in equids (Schaller, 1992:32.31, 180.4).

Paranasal sinuses are not developed in cetaceans (Fraser and Purves, 1960:5, 75), and the septum of the maxillary sinus is absent in *Tursiops* .

= socket = dental alveolus

= sphenomaxillary fossa (Schulte, 1917:373, 378, 387) = pterygopalatine fossa (Osborn, 1979) = antorbital fossa

= suborbital canal (Owen, 1870:7) = infraorbital canal

= subvomerine shelf (Schulte, 1917:388) = vomerine shelf

= supracranial basin (Flower, 1868:314) = circumnarial basin (Owen, 1866a:44)

= suprafrontal process (Schulte, 1917:380) = ascending process

= supraorbital crest (Barnes, 1984:9) = maxillary crest (Diagram 2; Table 5)

A supraorbital crest is reported in various mammals, forming, for example, the thickened rim of the frontal in the fossil mammal *Kryptobaatar* (see Wible and Rougier, 2000:22) and *Matutinia* (see Ting et al., 2002:12).

In Cetacea, crests on the maxilla have received several different names (Diagram 2). Crests are not normally considered present in mysticetes, although Ridewood (1922:224) commented, about a fetus of *Megaptera novaeangliae*, "The supraorbital crest is already strongly developed." For the extinct dolphin *Parapontoporia*, Barnes (1984:9) stated that the "supraorbital crest on the maxilla is in the same location as in *Pontoporia blainvillei*," and later (Barnes, 1985:3, fig. 12) emphasized that the crest in *Pontoporia* and *Parapontoporia* is a non-pneumaticized structure located medial to the margin of the maxilla, termed the **maxillary crest**.

We recognize the supraorbital crest as the structure developed on the lateral margin of the maxilla at the suture with the frontal, and involving a contribution of frontal. The supraorbital crest or ridge in this sense does not occur in *Tursiops* or other delphinids but is seen in *Platanista* (as an elevated pneumaticized crest) and in *Inia*.

*** supraorbital margin of the maxilla** (Figure 16b)

The supraorbital margin of the maxilla is the lateral margin of the maxilla that overlies the **supraorbital process of the frontal** bone in *Tursiops* and other odontocetes.

= supraorbital plate (Anderson, 1879:364) = supraorbital process of the maxilla

*** supraorbital process of the maxilla** (Figure 16b)

The maxilla does not extend over the **orbit** in most mammals.

The supraorbital process of the maxilla is that part of the **ascending process of the maxilla** in odontocetes that lies over the supraorbital process of the frontal and the orbit (Schulte, 1917:369; Fordyce, 1994:153).

– supratemporal crest = supratemporal ridge

The supratemporal crest is the crest that lies on the dorsolateral surface of the maxilla in *Kogia* (Schulte, 1917:376, 392). It is continuous with the **nuchal crest**. Delphinids have not developed a supratemporal crest per se, limiting the crest development on the maxilla to the **maxillary crest**. The anterior portion of the supratemporal crest is homologous with the maxillary crest. This feature has also been called the supratemporal ridge.

The supratemporal crest should not be confused with Flower's (1868:314) "**great occipital crest**" in *Physeter*, which is a feature posterior to the **supracranial basin**. The posterior part of this crest seems to be homologous with the crest in *Kogia*, but the anterior part is not. In *Physeter* the **occipital crest** terminates anteriorly at a position medial to the **antorbital notches** (Flower, 1868: pl. 57). In *Kogia* the anterior portion of the crest terminates lateral to the antorbital notch (Schulte, 1917:371, 373, pls. 35, 36). Clearly additional work needs to be done on the physeterids before the homologies are straightened out.

= tubercle of the maxilla (Flower, 1878:417) = maxillary tuberosity

– ventral ethmoidal crest of the maxilla (*crista ethmoidalis ventralis*)

The ventral ethmoidal crest of the maxilla in the dog is a small sagittofrontal crest that serves as an attachment for the **floor plate** or transverse lamina of the ethmoid bone (Evans and Christensen, 1979:140, 141). The ventral ethmoidal crest lies on the ventromedial surface of the maxilla just anterior to the **maxillary tuberosity** (not in Schaller, 1992).

Due to the elongation of the rostral elements and the posterodorsal movement of the bony nares in odontocetes, the ethmoid no longer contacts the maxilla and the ventral ethmoidal crest has disappeared.

*** ventral infraorbital foramen** (Figures 16b,c,e, 30; Table 6)

In odontocetes the foramen that was previously known as the **maxillary foramen**, at the proximal end of the **infraorbital canal**, is now known as the ventral infraorbital foramen (Rommel, 1990:36). This foramen was also known as the **infraorbital fossa** (Kernan, 1918:388) and the preorbital foramen (Fraser and Purves, 1960:67–69, 71, 73), and the **antorbital foramen** (Fraser and Purves, 1960:137, pl. 9ff.).

See discussion under **infraorbital canal**.

– ventral surface of the hard palate (*facies palatina*)

The ventral surface of the **hard palate** in the dog forms part of the roof of the mouth (Evans and Christensen, 1979:141).

The ventral surface of the hard palate in odontocetes is composed of the **palatine process of the maxilla** (q.v.).

*** vomerine shelf** (Figure 16e)

The vomerine shelf is a sharp ridge that delimits the ventral border of the premaxillary surface on the ventromedial aspect of the maxilla (Kernan, 1918:368).

– zygomaticomaxillary suture (*sutura zygomaticomaxillaris*)

The zygomaticomaxillary suture is the sutural connection between the maxilla and **zygomatic bone**, here known as jugal bones (Gray, 1918:189; Evans and Christensen, 1979:142, 143; Schaller, 1992:76.26; Feneis, 1994:22.13, 54.19). Vesalius (1543:23) referred to the zygomaticomaxillary suture as merely the *sutura*.

As noted under discussion of jugal, the homologies of parts of the jugal and lacrimal in *Tursiops* are difficult to establish. The presumed jugal in *Tursiops* (namely, that part of the lacrimojugal immediately dorsal to the fused anterior of the **styliform part**) sutures with the maxilla dorsally just below the **antorbital notch**, while the medially developed **maxillary process of the jugal** projects into the **zygomatic recess** of the maxilla. The anterior end of the jugal bone in odontocetes lies in the zygomatic recess and is not suturally connected with the maxilla.

– zygomatic process of the maxilla (*processus zygomaticus*)

The zygomatic process of the maxilla in mammals is on the posterolateral aspect of the **external surface of the maxilla** (Wible and Gaudin, 2004:122). It is bounded both dorsally and ventrally by the jugal. It contributes to the strength of the **zygomaticomaxillary suture** (Evans and Christensen, 1979:140, 141, 151). The zygomatic process of the maxilla extends along the margin of the **orbital plate of the maxilla** from the posterolateral angle of the plate to a point distinctly above the **antorbital foramen** (Miller, 1923:9, 10, pl. 3; as **malar process**). Hopson et al. (1989) described the zygomatic process of the maxilla in the extinct Multituberculata. This is a posterolateral process from the maxilla, that bounds the **temporal fossa** and contacts the squamosal posteriorly. Simpson (1937) earlier referred to the zygomatic process as the zygomatic root of the maxilla.

Due to the change in relationship between the zygomatic and maxilla, the zygomatic process of the maxilla has disappeared in *Tursiops* and other odontocetes.

* **zygomatic recess [new term]** (Figure 16b,c)

The **cavity for the zygomatic articulation** lies posteroventral to the **frontal process of the maxilla** on the **external surface of the maxilla**. It receives the articulation of the zygomatic (jugal) (Evans and Christensen, 1979:140).

The zygomatic recess in *Tursiops* is a small groove or recess on the **ventral surface of the hard palate** just medial to the **antorbital notch**, and anterior to the **lacrimojugal crest** (q.v.). The **maxillary process of the jugal** fits into the zygomatic recess. In very old specimens of *Tursiops* the anterior portion of the jugal becomes fused to the maxilla.

NASAL BONE

Os Nasale

FIGURES 1, 3, 4, 6A,C,D, 17

The nasal bone is a paired midline bone that forms the dorsal margin of the external bony nares, hence its name. The nasal bone in generalized mammals articulates with the premaxilla, maxilla, and frontal.

The evolutionary movement of the nasal passage posterodorsally with the elaboration of the facial region has led to a change in the relationships and shape of the nasal bone in cetaceans, particularly odontocetes. In *Tursiops* and other delphinids the nasals are nodular, elevated, and anteroposteriorly compressed, rather than plate-like and dorsoventrally thin. They have come to form part of the posterior wall of the nasal passage and the nucleus of the bony mass that forms the vertex. The nasals keep their articulation with the frontals, now sutured at extensive surfaces rather than thin borders, but their articulation with the premaxillae and maxillae becomes variable. It is difficult to identify homologues for some of the features seen in other mammals. Mysticetes and the extinct archaeocetes have nasals more like those of other mammals.

– anterior border of the nasal [new term]

The anterior border of the nasal bone is equivalent to the **inferior border of the nasal** in humans (Gray, 1918:156), the most anterior transverse border of the nasal, which does not articulate with other elements. The anterior border of the nasal bone is present in other mammals but does not seem to have been named (Evans and Christensen, 1979:139; ICVGAN, 1983:A23; Schaller, 1992:30).

Tursiops and other delphinids lack an anterior border in the sense of other mammals, but the border is present in some fossil Cetacea (Archaeoceti, and certain Neoceti) in which the nasals retain a dorsoventrally thin plate-like form. The anterior border is probably equivalent to the rounded **anterodorsal border** (q.v.) **of the nasal**, at the junction of the external (dorsal) and internal (anterior) faces as seen in *Tursiops* and more obviously in extinct dolphins such as *Kentriodon* and *Delphinodon*.

– anterior process of the nasal

The anterior process (e.g., Novacek, 1986:27) of the nasal bone appears to be that part that protrudes beyond the point of contact with the anterior edge of the premaxilla. Alternatively, Evans and Christensen (1979:139) used the term "**nasal process**" for the lateral part of the anterior end of the nasal. "Anterior process of the nasal" seems preferable.

Tursiops and other delphinids lack an obvious anterior process of the nasal.

* **anterodorsal border of the nasal** or **anterodorsal crest of the nasal [new term]** (Figure 17a,c,d)

The anterodorsal border (or anterodorsal crest, if markedly elevated) of the nasal bone in *Tursiops* runs from a point on the ventrolateral margin of the nasal bone to a point on the dorsomedial margin. The anterodorsal border divides the internal (anterior) surface of the nasal from the external (dorsal) surface of the nasal.

* **anterodorsal groove [new term]** (Figure 17a,d)

The **anterodorsal crest of the nasal** delimits an oblique groove immediately dorsal to it, the anterodorsal groove. This groove appears to be more evident in younger specimens. In the newborn specimen that we illustrated (USNM 504560), the anterodorsal groove is distinct when the specimen is properly lighted.

* **central caudorostral ridge** (Figure 4)

Kernan, in his description of the skull of a fetal *Ziphius* (1918:389, paragraph 3), delineated a central caudorostral ridge.

In examining USNM 504732, which is a partly disarticulated calf, the complex terminology of Kernan can be worked out. *Ziphius* differs from delphinids in that the **internal surface of the nasal** is rather well developed and the central caudorostral ridge is formed on the medial border of the internal surface where it abuts the contralateral nasal bone.

The central caudorostral ridge appears in some adult *Tursiops* and other delphinids.

– dorsal nasal meatus (Wible and Gaudin 2004:120)

Wible and Gaudin (2004:120) identified the dorsal nasal meatus in armadillos and the dog as a deep longitudinal trough on the ventral surface of the lateral part of the nasals, in which the ossified **nasoturbinal** is present.

Tursiops and other delphinids lacks the dorsal nasal meatus.

– ethmoidal crest of the nasal bone (*crista ethmoidalis*)

The ethmoidal crest of the nasal bone in the dog lies on the **internal surface of the nasal** bone and articulates with the **dorsal nasal concha** (Gray, 1918:161; Evans and Christensen, 1979:156).

Tursiops and other odontocetes have reduced their olfactory functions and nasal elements. The ethmoidal crest is nonexistent in *Tursiops* and other odontocetes.

– ethmoidal fossa (*sulcus ethmoidalis*)

The ethmoidal fossa in the dog is located on the posterior part of the ventral surface of the nasal bone and bounds the dorsal part of the ethmoid (Evans and Christensen, 1979:139). Rowe et al. (2005:320) identified the ethmoid fossa in *Monodelphis* as an endocranial feature.

Tursiops and other odontocetes have reduced their olfactory functions and nasal elements. The ethmoidal fossa is nonexistent in *Tursiops* and other odontocetes.

*** external surface of the nasal** (Figure 17a,c,d)

In most mammals (Evans and Christensen, 1979:139; Schaller, 1992:30.14), including the extinct archaeocete cetaceans, the external surface of the nasal bone is readily identifiable as the convex surface that faces dorsally, or anteriorly in humans (outer surface of the nasal bone, Gray, 1918:156).

In *Tursiops* and other delphinids the external surface is presumed to be the most dorsal part of the nasal bone, which contributes to the **vertex**. The **anterodorsal border of the nasal** (q.v.) separates the external surface of the nasal from the now anteriorly facing **internal surface of the nasal**. The relationship of the external surface to the internal surface is clearer in extinct kentriodontids (*Kentriodon*, *Delphinodon*) in which the former faces dorsally and the latter faces anteriorly.

*** frontal margin of the nasal** (Figure 17b,c,e)

The frontal margin of the nasal is that part of the nasal bone that articulates with the frontal. In most mammals, this is the posterior margin of the nasal. It includes the **frontal process of the nasal** (q.v.).

Homologies are not clear with *Tursiops* and other delphinids, in which both the posterior and ventral surfaces of the nasal bone broadly contact the frontal bone.

See also **frontonasal suture**.

– frontal process of the nasal

In the dog the frontal process of the nasal is the normally pointed posterior part of the nasal near the mid-sagittal plane (Evans and Christensen, 1979:139; not in Schaller, 1992). The frontal processes of the nasals are bounded posteriorly and laterally by frontals. Although the nasal bears the same relationship to the frontal in humans, the frontal process is not named (Gray, 1918:157; Feneis, 1994:20).

Tursiops and other delphinids lack a frontal process in the sense of other mammals.

– frontonasal suture

The frontonasal suture lies on the posterior part of the nasal bone and articulates with the frontal bone.

The frontonasal suture is well developed in odontocetes (e.g., Owen, 1872:175). The frontonasal suture is visible along the posterior of each nasal as viewed dorsally in *Tursiops* and other delphinids. In young animals, in which the maxilla and **mesethmoid** do not contact the nasal bone, the posterior, lateral, and anteroventral surfaces of the nasal contact the frontal bone, forming an extensive frontonasal suture in the broader sense. It lies on the **internal surface of the nasal** bones. The frontonasal suture at the anteroventral part of the nasal is obliterated during ontogeny, as the mesethmoid grows to contact the nasal bone.

– groove for nasociliary nerve

In humans (Gray, 1918:157, 881: fig. 771, 888) the inner surface of the nasal carries a fine groove for the passage of a branch of the nasociliary nerve.

The anterior face of the nasal (equivalent to **internal surface of the nasal**) in *Tursiops* carries a relatively open groove that may be subvertical to oblique. Whether the feature is related to the groove for the nasociliary nerve in humans, to the epicranial sinuses (nasal diverticula), or to some other structure is uncertain.

= inferior border of the nasal = anterior border of the nasal

In humans the inferior border of the nasal bone (Gray, 1918:156) is the most anteroventral part of the nasal that does not articulate with other elements. The term "**anterior border of the nasal**" (q.v.) is more applicable to most mammals.

*** internal surface of the nasal** (Figure 17a,c,d)

In the dog and other mammals, the internal surface is the ventral part of the nasal, which is covered with mucus membrane (Evans and Christensen, 1979:139).

Because of dramatic changes in the shape of the delphinid nasal, the homologous surface in *Tursiops*, namely, the surface that is in direct contact with the epithelium of the nasal cavity, now faces anteriorly. It forms the anteroventral portion of the nasal bone. The internal surface is, however, identifiable in mysticetes and extinct archaeocete cetaceans, forming the ventral border of the bone.

= internarial groove (Fraser, 1945:24) = internasal gap

– internasal gap (Fraser, 1945:24)

Fraser (1945:24) commented, of *Hyperoodon*, that the premaxillae at the **vertex** form massive "narial prominences" which are "separated from each other [medially] by a parallel-sided gap bounded by the nasals." The internasal gap diverges to the left, and has parallel sides. The name apparently refers to the gap between the adjacent medial faces of the massive **premaxillary crests** above the nares on the vertex. Fraser (1945:24) used **internarial groove** as an apparent synonym for internasal gap. "Internasal" is preferred, because "internarial" could be taken to mean a feature at the nares.

Because the premaxillae do not approach each other medially above the nares, *Tursiops* lacks an internasal gap.

* **internasal suture** (Figure 4)

The internasal suture lies on the medial surface of the nasal bones and articulates with the contralateral nasal bone (e.g., Owen, 1872:178).

Tursiops and other delphinids (e.g., *Australodelphis*; Fordyce et al., 2002:47, nasal) may have a well-developed internasal suture on the medial edge of each nasal bone. In young delphinids, the nasals may be separated to the extent that the internasal suture is not developed.

* **maxillary margin of the nasal** (Figure 4)

The maxillary margin of the nasal bone is that portion of the nasal bone that articulates with the maxilla. In *Tursiops* the extent of the maxillary margin is extremely variable (depending on the contact of maxilla and nasal) and it occupies the lateral surface of the nasal bone. The maxillary margin is conspicuous in some archaeocetes.

* **medial margin of the nasal** (Figure 17a,d,e)

The medial margin of the nasal bone is that part of the nasal bone that articulates with the contralateral nasal bone at the **internasal suture** (q.v.). The medial margin occupies the medial surface of the nasal bone.

* **mesethmoid margin of the nasal** (Figure 17a–e)

The mesethmoid margin of the nasal bone is on the anteroventral surface of the nasal bone where it contacts the **mesethmoid**. The margin develops ontogenetically, as the **frontonasal suture** becomes obscured. The mesethmoid may come to overlie the anteroventral border of the nasal bone.

– **nasal foramen**

In some mammals, including the dog and armadillo, the nasal is pierced by one or more nasal foramina of uncertain vascular or nervous function (Gray, 1918: fig. 155, "foramen for vein"; Wible and Rougier, 2000; Wible and Gaudin, 2004:161, and citations therein).

Tursiops does not appear to have nasal foramina. Clarke (2003:249) used the term "nasal foramina" as a synonym for the external bony nares in *Kogia*.

See **external bony nares**.

= **nasal process** (Evans and Christensen, 1979:139, 140) = anterior process of the nasal

This use of nasal process here should not be confused with the **nasal process of the maxilla** or the **nasal process of the premaxilla**.

See **anterior process of the nasal**.

– **nasomaxillary suture**

The nasomaxillary suture lies on the ventrolateral surface of the nasal bones and articulates with the maxilla.

The posteromedial edge of the maxilla in *Tursiops* and other delphinids sometimes does not contact the nasal bone or it comes to rest over the nasal bones without a sutural attachment. In some odontocetes, including many fossil species, the maxilla is separated from the nasal by the premaxilla, so the suture cannot form.

– **nasoturbinate crest**

The nasoturbinate crest is a thin shelf of bone that gives rise to the nasal turbinate (**dorsal nasal concha**). It is located on the **internal surface of the nasal** bone. Evans and Christensen (1979:136, figs. 4–25) illustrated this shelf in the dog but did not name it.

Tursiops and other delphinids lack development of the turbinate complex.

– **septal process of the nasal** (*processus septalis*)

The septal process on the nasal bone lies at the anterior end of the **internal surface of the nasal** and contributes to the **bony nasal septum** (Schaller, 1992: 28:27, 30:17).

The odontocetes have reduced their olfactory functions and nasal elements. The **nasal septum** is composed solely of the **mesethmoid** and vomer and the septal process of the nasal is nonexistent in odontocetes.

PALATINE BONE

Os Palatinum

FIGURES 3, 6B,C, 18, 31A, 32

The palatine takes part in the formation of the back of the mouth, the hard palate, and the nasal passage in mammals. It is one of the rostral bones that does not appear on the surface of the skull (Gray, 1918:166–169; Evans and Christensen, 1979:143, 144; Schaller, 1992:3.1–26; Feneis, 1994:24.15–33). The horizontal lamina, with distinct oral and nasal surfaces, usually forms the bulk of the bone. Vesalius (1543:23) referred to the palatine as *sextis superioris maxill' ossibus* (sixth bone of the upper jaw).

In delphinids, with the movement of the nasal passage from subhorizontal (as in most mammals) to subvertical, the relationships of the palatine to the nasal passage and palate cavity between the oral and nasal cavities but is dorsoventrally deep and somewhat short anteroposteriorly.

In delphinids, the posterior portion of the hard palate, at the opening of the internal bony nares, is now formed mainly by the pterygoid instead of the palatine, but the palatine forms much of the middle part of the anterior wall of the nasal passage. The palatine is exposed on the palate between the pterygoid and the maxilla, and in *Tursiops* and other delphinids forms the anterodorsal and dorsolateral walls of the fossa for the hamular lobe of the pterygoid sinus. Because of radical changes in topography, it is hard to apply some terms used for the palatine in other mammals. The palatine is bounded by the maxilla, frontal, vomer, and pterygoid. See Gray (1918:166–169), Schulte (1917:375, 378, 383, 386, 393, 399, 400); Fraser and

Purves (1960:8, 13, 18, 33, 35, 38–41, 46–57, 60, 61, 69, 84, 87, 89, 100), Evans and Christensen (1979:143, 144), Schaller, 1992:36:1–26), Feneis (1994:15–33).

= **accessory palatine foramen** (Wible and Gaudin, 2004)
See **minor palatine foramen**.

= ***ala palatina*** = perpendicular process

Boenninghaus used "*ala palatina*" in a caption for his illustration of *Phocoena* (1904: pl. 12, figs. 3–4, 5(19); Fraser and Purves, 1960:13, pl. 1b). Those figures illustrated the palatal aspect of the body of the palatine bone, specifically the **lateral lamina of the palatine**.

* **base of the palatine** (Fraser and Purves, 1960:26) (Figure 18c)

Fraser and Purves (1960:26) refer to the base of the palatine as that portion of the palatine that is exposed on the palatal view of the skull, which we recognize as the **horizontal portion of the palatine**, contributing to the **hard palate**. In the human, from which the terms "horizontal lamina" and "perpendicular lamina" were derived, it would seem to us useful to have a term for the part of the palatine bone that represents the junction of the horizontal and perpendicular laminae. We according define the base of the palatine to consist of that junction. In the loose palatine of delphinids, the bone is seen to be thick ventrally and ventrolaterally so that the horizontal portion and **lateral lamina of the palatine** merge without distinct boundary. If developed, a **palatal crest** or **palatal ridge** approximates the base of the palatine.

= **choanal border** = nasal surface of the palatine

– **conchal crest** [crest of the ventral concha] (*crista conchalis*)

The nasal conchae are not developed in *Tursiops* or other odontocetes. See **conchal crest** under "Maxilla."

* **ethmoidal crest of the palatine** (*crista ethmoidalis*) (Figure 18a,b,d,e)

The ethmoidal crest of the palatine in most mammals occurs at the juncture of the ethmoid bone to maxilla, palatine, or nasal (Evans and Christensen, 1979:141, 144; Schaller, 1992:30.18, 34.2; Daniels et al., 1998: fig. 3B). It forms the point of attachment of the **dorsal nasal concha**. The ethmoidal crest of the palatine is a thin, irregularly convex border near the anterior edge of the **perpendicular plate** of the palatine bone. It borders the **maxillary sinus** dorsally and bears the **sphenopalatine foramen** (Evans and Christensen, 1979:144).

The ethmoidal crest in *Tursiops* has been displaced anteriorly with the posterodorsal movement of the narial passage. It no longer contacts the ethmoid but, with the vomer, forms the anteromedial wall of the nasal passage.

* **free border of the palatine** (*margo liber*) (Figures 2, 18e)

The free border of the palatine bone is the posterior edge that bears the **soft palate** and that borders the nasopharynx (Schaller, 1992:36.18). It is also known as the caudal border of the palatine.

The free border of the palatine in Odontoceti is restricted to the median portion of the posterior edge of palatine bone that is not bounded posteriorly by the pterygoid. In *Tursiops* and other delphinids, the free border is small to nonexistent because the **pterygoid hamulus** expands medially to form the posterior margin of the **hard palate** and the border of the internal bony nares (e.g., Flower, 1883: figs. 1–9).

= **free lamina of the palatine** (Owen, 1866a:28) = free border

= **greater palatine foramen** = major palatine foramen
See **greater palatine foramen** of "Maxilla."

– **groove for sphenopalatine artery**

The groove for the sphenopalatine artery lies on the anteromedial surface of the palatine bone, just ventral to the **ethmoidal crest of the palatine** (Evans and Christensen, 1979:143). The sphenopalatine artery is a branch of the maxillary artery that leaves the **pterygopalatine fossa** (**antorbital fossa**) by passing through the **sphenopalatine foramen**. The terminal branches of the sphenopalatine artery are the caudal lateral nasal arteries (Evans and Christensen, 1979:674).

In delphinids the groove for the sphenopalatine artery is confluent with the **greater palatine sulcus** on the maxilla. It did not groove the palatine bone in the *Tursiops* specimens examined.

= **groove for the sphenopalatine canal** = greater palatine sulcus

– **hard palate** (*palatum osseum*)

The hard palate forms the division between the oral cavity and the nasal cavity in mammals. The anterior portion is formed by the premaxilla, the middle portion, the maxilla and the posterior portion, the palatine (Evans and Christensen, 1979:143). The surface of palatine in the hard palate is the **oral surface of the palatine**.

The oral or ventral or **palatine surface of the palatine** forms a small part of the hard palate in *Tursiops* and other delphinids. However, in the sense of "roof of mouth," the delphinid hard palate is formed mainly by the maxilla. The **nasal surface of the palatine** no longer lies immediately dorsal to most of the hard palate but is prolonged into a subvertical surface in the nasal passage. In most dolphins, the medially apposed pterygoid hamuli form the posterior of the hard palate.

See **horizontal lamina of the palatine** and **horizontal portion of the palatine**. See also **hard palate** under "Maxilla."

– **horizontal lamina of the palatine** (*lamina horizontalis*)

The horizontal lamina of the mammalian palatine is a thin and usually long sheet of bone that forms the posterior portion of the **hard palate**, bordering the oral cavity and nasal cavity (Evans and Christensen, 1979:143; Schaller, 1992:36:15; Feneis, 1994:24:27). The horizontal lamina usually has two closely parallel surfaces: oral (ventral, palatine) and nasal (dorsal).

In *Tursiops* and other delphinids, the equivalent of the horizontal lamina is so thickened that it no longer forms a true lamina [viz., a thin layer], and the term "**horizontal portion of the palatine**" (q.v.) is preferred.

* **horizontal portion of the palatine [new term]** (Figure 18a,c,e)

Due to the radical transformation of the nasal passage, the palatine no longer forms a thin **horizontal lamina** between the nasal cavity and oral cavity in *Tursiops* and other delphinids. Whereas in most mammals, the oral and nasal surfaces are opposite surfaces of a sheet-like horizontal lamina, the equivalents in *Tursiops* are perpendicular to each other. The term "horizontal portion" is used here for the dorsoventrally thick part of the palatine that is exposed ventrally on the **hard palate**, between the maxilla and **pterygoid hamulus**.

The horizontal portion bears the **oral surface of the palatine**. Posteriorly, the horizontal portion ends at the free border where the palatine is bounded by the pterygoid. Laterally, in *Tursiops*, the horizontal portion passes into the **lateral lamina** via the **base of the palatine**; this junction may be marked by the development of a **palatal crest** or ridge.

= **internal-orbital foramen** = sphenopalatine foramen

Kellogg (1936:110) indicated that the terms internal-orbital foramen and **sphenopalatine foramen** are synonyms. Internal-orbital foramen in this sense should not be confused with the "internal orbital foramen" as mentioned by Wible et al. (2005:103), namely, a feature internal to the **optic foramen** in some rodents and not known to occur in Cetacea.

* **lateral lamina of the palatine** (Fraser and Purves, 1960:18, 48, 59, 65) (Figure 18b–e)

The lateral lamina of the palatine is unique to odontocetes. In *Tursiops* the palatine posterodorsal to the **horizontal portion** is split, by development of the **hamular fossa**, into the lateral and **medial laminae of the palatine**. Fraser and Purves (1960:18, 48, 59, 65) used "lateral lamina," while de Muizon (1988:3) used both "lateral" and "medial laminae" (q.v.) for the duplications of the palatine characteristic of the Delphinida (Delphinoidea + *Pontoporia* + *Inia* + *Lipotes*). The perpendicular lamina is thus present dorsally but not ventrally.

In *Tursiops* and other delphinids, the lateral lamina is a posterolateral extension of the palatine over the hamular sinus. Ventrally, the lateral lamina of the palatine joins the **lateral lamina of the pterygoid** (the latter forming the ventral half of the wall of the hamular fossa). Posteriorly, the lateral lamina has a free margin at the entrance to the fossa for the hamular sinus. The lateral lamina thus separates the hamular fossa from the region of the **antorbital fossa**. Anteroventrally, the lamina merges with the diffuse region comprising the **base of the palatine** and the **maxillary process of the palatine**. Dorsally, above the level of the hamular fossa, the lateral and medial laminae of the palatine meet to form the thin perpendicular lamina that separates the nasal passage from the region of the antorbital fossa.

In *Tursiops*, *Delphinus*, and other delphinids, the lateral lamina is the origin for part of the internal and external pterygoid muscles (Fraser and Purves, 1960:17, 18; Seagars, 1982:50–56, fig. 10c). In land mammals (dog, Evans and Christensen, 1979:143; giant panda, Davis, 1964: fig. 17) the perpendicular lamina forms the origin for the external and much of the internal pterygoid muscles; lateral lamina and perpendicular lamina are thus homologous.

The boundaries of the lateral lamina may be difficult to trace (particularly for *Inia* and *Pontoporia*), which may explain why the lateral lamina of the palatine has sometimes been mistaken for maxilla (e.g., Miller, 1923:34, "freely-projecting plate-like process" of maxilla; 51, "backwardly projecting **maxillary plate**"). Owen (1866a:27) referred to the **perpendicular plate** as the orbital plate of the palatine; Flower (1867:93) named it the **projecting plate of the palatine**. Lateral lamina should not be confused with **lateral palatal lobe of the palatine** (q.v.).

– **lateral palatal lobe of the palatine**

In some odontocetes the ventral exposure of the palatine on the **hard palate** is split into two, the medial lobe and the lateral lobe (Arnold and Heinsohn, 1996: fig. 10, *Orcaella*) by the contact of the pterygoid and maxilla. See also, e.g., Fraser and Purves, 1960: pls. 9 (*Berardius*), 16 (*Kogia*), and 32 (*Orcaella*).

Tursiops lacks such a double ventral exposure. To avoid confusion with the **lateral lamina of the palatine** (q.v.), we propose a slight modification of the Arnold and Heinsohn term thus: lateral palatal lobe of the palatine.

= **lesser palatine foramen** = minor palatine foramen

* **major palatine foramen** = greater palatine foramen (Diagram 1)

See **greater palatine foramen** in "Maxilla."

– **maxillary fossa**

The maxillary fossa is part of the anterior portion of the nasal part of the **perpendicular lamina of the palatine** bone. This fossa forms a posterior portion of the **maxillary sinus** (Evans and Christensen, 1979:144).

The maxillary fossa is not developed in odontocetes since the **paranasal sinuses** are not developed (Fraser and Purves, 1960:5, 75).

See also **maxillary fossa of the ethmoid bone**.

* **maxillary process of the palatine** (*processes maxillaris*) (Figure 18a–e)

The maxillary process of the palatine bone is the anteroventral portion of the perpendicular lamina that articulates with the maxilla (Evans and Christensen, 1979:144). In humans (Gray, 1918:168), the maxillary process is a lamina associated with part of the opening of the **maxillary sinus**. It is also known as the **maxillary surface of the palatine**.

The maxillary process of *Tursiops* and other delphinids is greatly expanded because the suture with the maxilla has become larger. The maxillary process consists of the bone between the nasal passage and the anterodorsal border of the palatine bone that is exposed between the **antorbital fossa** and the **hard palate**. The suture is fully apparent only in the disarticulated palatine; otherwise, in contrast to many other mammals, the maxillary process is not a distinct part of the palatine bone.

= **maxillary recess** = maxillary fossa

See **maxillary recess** under "Maxilla."

= **maxillary surface of the palatine** (*facies maxillaris*) = maxillary process of the palatine (*processes maxillaris*)

– **medial lamina of the palatine**

De Muizon (1988:3) noted that a unique characteristic of the Delphinida is the duplication of the palatine into lateral and medial laminae. Fraser and Purves (1960), who used lateral lamina extensively, apparently did not name the medial lamina. In

Tursiops most or all of the medial border of the **hamular fossa** (and the adjacent lateral wall of the nasal passage) is formed by pterygoid, not palatine. In *Lagenorhynchus obscurus*, in which the hamular sinus is anteromedially deeper than in *Tursiops*, a medial lamina more clearly separates the hamular fossa from the nasal passage. The nasal surface (q.v.) of the medial lamina thus forms some of the nasal passage. Dorsally, above the level of the hamular fossa, the lateral and medial laminae of the palatine in delphinids meet to form the perpendicular lamina that separates the nasal passage from the region of the **antorbital fossa**.

The medial lamina is conspicuous in *Inia* (USNM 239667) and *Pontoporia* (USNM 482708).

See also **lateral lamina of the palatine**.

– median palatal lobe of the palatine

In some odontocetes the ventral exposure of the palatine on the **hard palate** is split into two, the medial lobe and lateral lobe (sensu Arnold and Heinsohn, 1996: fig. 10, *Orcaella*) by the contact of the pterygoid and maxilla.

Tursiops lacks such a double ventral exposure. To avoid confusion with the **medial lamina** (q.v.), we propose a slight modification of the Arnold and Heinsohn term thus: medial palatal lobe of the palatine.

See also **lateral palatal lobe of the palatine**.

= mesial portion = median palatal lobe of the palatine

= middle palatine foramen (Novacek, 1986)

See **minor palatine foramen**.

– minor palatine canals (*canales palatini minores*)

The minor palatine canals lead from the **palatine canal** to the minor palatine foramina and transmit branches of the palatine artery, palatine vein, and palatine nerve (Evans and Christensen, 1979:143; Feneis, 1994:24.22).

Minor palatine canals have not been distinguished in odontocetes.

* **minor palatine foramen** (*foramina palatina minora*) (Figure 18a)

The minor palatine foramen lies just posterior to the **major palatine foramen**. There are frequently several lesser palatine foramina that transmits branches of the minor palatine nerve and minor palatine vessels (Evans and Christensen, 1979:143). These minor palatine foramina lie within the palatine not at the palatomaxillary suture. The minor palatine foramen is also known as the **lesser palatine foramen** or accessory palatine foramina.

The minor palatine foramina appear to be irregularly developed in delphinids. There are none in the *Tursiops* we have used, but there is a large foramen in the body of the palatine in a specimen of *Orcaella* (USNM 284430) in its anterodorsal aspect that would be considered (topographically) a minor palatine foramen. See also Arnold and Heinsohn (1996: figs. 10, 12) on *Orcaella*.

= narial process of the palatine = nasal surface of the palatine

Miller (1923:47) said, of *Inia*, "narial process of palatine [is] well developed and forming an important part of the anterior wall of the nasal passage."

* **nasal crest of the palatine** (*crista nasalis*) (Figure 18a,b,e)

The nasal crest of the palatine is that surface of the palatine bone adjacent to the medial palatine suture and raised into a crest that articulates with the vomer (Evans and Christensen, 1979:143; Schaller, 1992:34.5). It forms the basis for attachment of the **nasal septum**.

In *Tursiops* and other delphinids the nasal crest is markedly reduced to the anterior one-quarter to one-third of the medial portion of the palatine that lies in the midline between the pterygoid bones and the vomer, immediately adjacent to the suture with the vomer.

* **nasal spine of the palatine** (*spina nasalis*) (Figures 2, 18b,e)

The nasal spine of the palatine bone is the posterior midline portion of the **hard palate**. It forms the posterior margin of the nasal crest (Gray, 1918:167; Evans and Christensen, 1979:143; White and Folkens, 1991:77). The nasal spine has also been termed the **postpalatine spine** (e.g., Novacek, 1986:34, fig. 14, in *Leptictis*; Asher, 1999:244, in tenrecs).

The nasal spine of the palatine bone in *Tursiops* and other delphinids is situated between the pterygoid bones and usually does not have a free projection into the palatal surface.

* **nasal surface of the palatine** (*facies nasalis*) (Figure 18e)

The nasal surface of the palatine bone consists of the dorsal surface of the **horizontal lamina of the palatine** bone. This surface forms the posterior floor of the nasal cavity (Evans and Christensen, 1979:143). The nasal surface is also called the **choanal border**.

Due to the radical transformation of the nasal passage, the palatine no longer forms a thin horizontal lamina between the nasal cavity and oral cavity in *Tursiops* and other delphinids, and the nasal surface is not applied closely to what we recognize as the **horizontal portion of the palatine**. The nasal surface in *Tursiops* comprises all the surface of the palatine that lines the nasal passage. Given that perpendicular lamina (as recognized here for *Tursiops*) may bound the nasal passage, this concept of nasal surface is broader than that used for the dog (above), in which the nasal surface is horizontal but not lateral. Ventrally, the nasal surface lies partly on the **medial lamina of the palatine** (that is, on the medial wall of the **hamular fossa**). Ventromedially, the nasal surface in *Tursiops* ends at the vestigial **free border of the palatine**, or at the medial margin of the pterygoid. Dorsally, beyond the limit of the medial and lateral laminae, the nasal surface lies on the perpendicular lamina.

Miller (1923:47) said, of *Inia*, "**narial process of palatine** [is] well developed and forming an important part of the anterior wall of the nasal passage." Narial process in this sense embodies the nasal surface and the perpendicular lamina.

* **nasopharyngeal duct** (*meatus nasopharyngeus*) (Figure 31a)

The nasopharyngeal duct or nasopharyngeal meatus in mammals (Wible and Gaudin, 2004) is the air passage rostral to the **choanae**. Together with the sphenoethmoid recess (or olfactory recess), the nasopharyngeal duct forms the nasal cavity (Rowe et al., 2005).

Tursiops has a nasopharyngeal duct between the **external bony nares** and choanae, although as in other odontocetes, the geometric relationship with the palate is dramatically different from other mammals. Cetacean literature makes little mention of the nasopharyngeal duct. Less specialized terms, such as nasal passage, are commonly used (e.g., Raven and Gregory, 1933; Messenger and McGuire, 1998; Houser et al., 2004). We consider the latter acceptable for Odontoceti. Ridewood (1922:221) termed the nasopharyngeal duct the **postnasal passage** (in part) and the **oro-nasal passage**.

= **oral surface of the palatine** = palatine surface of the palatine

* **orbital process of the palatine** (*processus orbitalis*) (Figure 18a–e)

The orbital process of the palatine is barely distinct in the dog but is well developed in humans; it is the dorsal part of the bone lying dorsal to the **ethmoidal crest of the palatine** and **sphenopalatine foramen**, rising anterodorsally from the latter. It is separated from the body of the palatine by a thin neck. It consists of five surfaces, some of which are articulating, which enclose an air cell in humans. The articulating surfaces are: anterior or maxillary, posterior or sphenoidal, medial or ethmoidal. The nonarticulating surfaces are: superior or orbital, and lateral (Gray, 1918:167, 168; Schaller, 1992:36.12; Feneis, 1994:24.25).

In adult *Tursiops* the **orbital process**, which has the sphenopalatine foramen at the base, is a small part of the palatine that projects laterally and slightly anterodorsally toward the **antorbital fossa**. Limits may be obscure in adult *Tursiops* but are more clear in e.g., *Cephalorhynchus*.

= **oro-nasal passage** (Ridewood, 1922:221) = nasopharyngeal duct

= **palatal crest** = palatal ridge

* **palatal ridge** (Fordyce, 1994:149) (Figure 17b–d)

The palatal crest is defined (Schaller, 1992:36:24) as a ridge on the palatal face of the palatine, occasionally present in suids.

Palatal ridge and palatal crest (a synonym) were mentioned in passing by Fordyce for the rostrum in the extinct dolphin *Waipatia* (1994:149 “Palatal ridges are indistinct”). Fordyce used crest to indicate a more pronounced elevation, as seen in the long sharp palatal crests in the extinct delphinid *Australodelphis* (see Fordyce et al., 2002:45). In *Tursiops* the palatal ridge separates the ventral and lateral faces of each palatine; the feature is better developed in some other delphinids (e.g., Fraser and Purves, 1960: pls. 43, 47).

Judging from the account of Seagars (1982:50–56, fig. 10) on pterygoid muscles in delphinids, the palatal ridge or crest probably marks the anteroventral limit of insertion of the internal pterygoid muscle.

See also **palatine crests**.

* **palatine canal** (*canalis palatinus major*) (Figure 18d)

In the dog the palatine canal runs through the palatine bone from the **antorbital fossa** posteriorly to the major palatine foramina and minor palatine foramina anteriorly. It carries the major palatine branches and minor palatine branches of the maxillary nerve and the palatine vessels (Evans and Christensen, 1979:143).

The palatine canal in *Tursiops* lies along the palatomaxillary suture. It runs anteriorly from near the **sphenopalatine foramen** in the antorbital fossa to exit via the major palatine foramina and minor palatine foramina.

– **palatine crests** (*crista palatina*)

The palatine crests are variably expressed features on the ventral surface of the horizontal plate just posterior to the anterior margin (Schaller, 1992:36.24; Feneis, 1994:24.33). (The palatine crests are not discussed in Sisson, 1910; Gray, 1918; Evans and Christensen, 1979; or White and Folkens, 1991.)

There do not appear to be structures that are homologous with the palatine crests in Cetacea. The **palatal ridge** or **palatal crest** (q.v.) of some odontocetes appears not to be homologous with the feature in land mammals.

= **palatine foramen**

See **major palatine foramen** and **minor palatine foramen**.

– **palatine sinus** (*sinus palatinus*)

The palatine sinus excavates the *pars perpendicularis* in horses and the *pars horizontalis* (**soft palate**) of the palatine in ruminants (Schaller, 1992:36.25, 180)

Paranasal sinuses are not developed in cetaceans (Fraser and Purves, 1960:5, 75), and the palatal sinus is absent in *Tursiops*.

– **palatine sinus septum** (*septum sinuum palatinorum*)

The palatine sinus septum is a median septum that separates the right and left palatine sinuses in ruminants (Schaller, 1992:34.9, 36.26).

Paranasal sinuses are not developed in cetaceans (Fraser and Purves, 1960:5, 75), and the palatal sinus is absent in *Tursiops*.

= **palatine sulci**

See **greater palatine sulcus** in “Maxilla.”

* **palatine surface of the palatine** (*facies palatina*) (Figure 18b,c)

The palatine surface of the palatine bone forms the posterior roof of the oral cavity, namely, part of the **hard palate**. In the dog, it lies posterior to the ventral exposure of the maxilla (Evans and Christensen, 1979:143). The palatine surface is also known as the **ventral surface of the palatine** or **oral surface of the palatine**.

The palatine surface of the palatine bone in *Tursiops* and other delphinids is the surface of the **horizontal portion** that is exposed between the maxilla anteriorly and the pterygoid posteriorly. The palatine surface is the same as the oral surface of the palatine and ventral surface of the palatine, and is the palatine contribution to the hard palate. It extends posteriorly as far as the **free border of the palatine** and/or the suture with the **pterygoid hamulus**.

* **perpendicular lamina of the palatine** (*lamina perpendicularis*) (Figure 18b–e)

In the dog the perpendicular lamina of the palatine bone forms the lateral wall of the **nasopharyngeal duct** and the medial wall of the **antorbital fossa** (q.v. under maxilla). It joins the **horizontal lamina of the palatine** nearly at right angles (Evans and Christensen, 1979:143). Externally, the perpendicular lamina forms the wall of the **infratemporal fossa** (e.g., in the panda, Davis, 1964: fig. 17), which provides origins for the internal and external pterygoid muscles.

In *Tursiops* and other Delphinidae, the palatine is extensively modified by development of the hamular lobe of the **pterygoid sinus**. The resulting lateral and medial laminae are neomorphic structures partly equivalent to the perpendicular lamina. See discussion of pterygoid muscle origins under **lateral lamina of the palatine.**

In *Tursiops* we recognize the perpendicular lamina as that part of palatine present dorsal to the lateral and medial laminae (that is, dorsal to the **hamular fossa**), forming a thin surface between the lateral wall of the nasal passage and the antorbital fossa.

See also **nasal surface of the palatine** and **medial lamina of palatine.**

= posterior nasal spine = nasal spine of the palatine

The posterior nasal spine is at the posterior end of the **nasal crest of the palatine.** The posterior nasal spine projects dorsally into the back of the nasal cavity (Gray, 1918:167; Evans and Christensen, 1979:143; White and Folkens, 1991:77).

= posterior palatine canal

See **palatine canal.**

* **posterior palatine foramen**

See "Maxilla."

– posterior wing of the lateral lamina

In the delphinid *Orcaella*, the posterior part of the **lateral lamina of the palatine** carries a wing-like horizontal flange that is directed outward and back toward foramina associated with the **orbit**. Arnold and Heinsohn (1996:149, 156, fig. 11) termed this the wing-like process, wing-like posterior extension, and posterior wing of the lateral palatine.

Tursiops lacks a posterior wing of the lateral lamina.

= postnasal passage (Ridewood, 1922:221) = nasopharyngeal duct

= postpalatine spine (Novacek, 1986:34, fig. 14; Asher, 1999:244) = nasal spine of the palatine

– postpalatine torus

McDowell (1958:127) described the postpalatine torus as the transverse bony thickening at the rear of the bony palate. See also Novacek (1986: fig. 14).

Tursiops and other delphinids lack a postpalatine torus.

= projecting plate of the palatine (Flower, 1867:93) = lateral lamina of the palatine

– pterygoid fossa of the palatine

In humans (Gray, 1918:166) the pterygoid fossa for origin of the internal pterygoid muscle is developed in part on the posterior face of the palatine. For leptictid insectivores Novacek (1986:45) used the name **ectopterygoid fossa** for the origin of the internal pterygoid muscle, noting that the **entopterygoid crest** forms the internal wall of the pterygoid fossa.

In *Tursiops* and many other odontocetes the internal pterygoid muscle arises on the **lateral lamina of the palatine** (q.v.) and **lateral lamina of the pterygoid** (the latter forming the ventral half of the wall of the **hamular fossa**). The **pterygoid sinus fossa** of Odontoceti and Mysticeti, and the extinct Archaeoceti, is not homologous with the pterygoid fossa of many land mammals.

See also **pyramidal process of the palatine** and **pterygoid fossa of the sphenoid.**

= pterygopalatine canal = palatine canal (Gray, 1918:168) (Diagram 1)

= pterygopalatine fossa

See **antorbital fossa** under "Maxilla."

* **pyramidal process of the palatine** (*processus pyramidalis*) (Figures 3, 18b,c,e)

The pyramidal process of the palatine bone in humans projects posterolaterally from the junction of the **horizontal lamina of the palatine** and vertical laminae. It articulates with the pterygoid bones and forms part of the origin of the internal pterygoid muscle (Gray, 1918:168; Feneis, 1994:24.21). In domestic animals it is a posteroventral process inserted between the **pterygoid process of the basisphenoid** (**alisphenoid**) and the pterygoid bone (Schaller, 1992:36.9). It is absent in dogs.

The pyramidal process in delphinids extends posteriorly forming the most posterolateral extension of the palatine bone. Its boundaries may be marked by variably developed ridges that produce a semicircular to triangular region, concave posteriorly, on the **lateral lamina of the palatine**. The pyramidal process does not form the wall of the **pterygoid sinus**. The pyramidal process gives origin to part of the internal pterygoid muscle (Seagars, 1982:51–56, fig. 10c). The pyramidal process may be the feature that is called the palatal process of the pterygoid by Fraser and Purves (1960:13).

– ridge impressions (*impressiones rugae*)

The ridge impressions are found on the **ventral surface of the hard palate** and are caused by the **palatal ridges**. The palatal ridges are hard ridges of non-bony tissue that lie transversely on the roof of the **hard palate** (Evans and Christensen, 1979:413, 414; Schaller, 1992:140.31).

Palatal ridges and ridge impressions are not developed in cetaceans.

– soft palate (*palatum molle*) (Gray, 1918:167, 1112)

The soft palate is the posterior continuation, in soft tissue, of the **hard palate** (*palatum durum / palatum osseum*) (Evans and Christensen, 1979:141, 143, 413; Schaller, 1992:140.14, 12.23; Feneis, 1994:108.17). In humans the lower border of the soft palate is free and hangs like a curtain between the mouth and the pharynx. It is called the palatine vellum (*velum palatinum*).

The soft palate is absent in odontocetes, the space that it would occupy having been taken over by the pterygoid bones (Fraser and Purves, 1960:19, 20, 22, 82). The soft palate persists in mysticetes.

* ***sphenoethmoid lamina* of the palatine** (*lamina sphenoethmoidalis*) (Figure 18d)

The *sphenoethmoid lamina* of the palatine bone comes off the **perpendicular lamina of the palatine** and articulates with the vomer (Evans and Christensen, 1979:144; Schaller, 1992:36.11).

In *Tursiops* the *sphenoethmoid lamina* is reduced to a vertically oriented ridge on the medial surface of the palatine bone. It forms the posterior margin of the vomeropalatine suture.

* **sphenoidal process** (*processus sphenoidalis*) (Figure 18b,c,e)

The sphenoidal process is the posterior portion of the perpendicular lamina between the pterygoid bone medially and the sphenoid bone laterally (Evans and Christensen, 1979:144; Schaller, 1992:36.13). In humans, the sphenoidal process lies posterior and slightly dorsal to the **sphenopalatine foramen** (Gray, 1918: figs. 168, 169).

In *Tursiops* the sphenoidal process is the indistinctly bounded part of the palatine posterodorsal to the sphenopalatine foramen. The sphenoidal process, which has the sphenopalatine foramen at the base, is a small part of the palatine that projects laterally and slightly anterodorsally toward the **antorbital fossa**. Limits may be obscure in adult *Tursiops* but are more clear in e.g., *Cephalorhynchus*.

= **sphenoidal sinus** (*sinus sphenoidalis*)
See "Sphenoid Bone."

= **sphenopalatine canal** or **sphenopalatine opening**
See **sphenopalatine foramen**.

* **sphenopalatine foramen** (*foramen sphenopalatinum*) (Diagram 1; Figures 18e, 30)

In the dog (Evans and Christensen, 1979:674) the sphenopalatine foramen lies at the anterior margin of the sphenopalatine lamina of the palatine, in the **pterygopalatine fossa** (**antorbital fossa**) (Evans and Christensen, 1979:144; Schaller, 1992:14.12, 36.6). It is also known as the sphenopalatine foramen in humans (Feneis, 1994:32.11, 322.20). It transmits the sphenopalatine artery and caudal nasal nerve from the pterygopalatine fossa [antorbital fossa] to the **nasopharyngeal duct**. In some armadillos (Wible and Gaudin, 2004:164), the sphenopalatine foramen and caudal **palatine foramen** (opening of the **palatine canal**) may be confluent.

In *Tursiops* the sphenopalatine foramen lies in the antorbital fossa anterior to the **orbit**, close to the **ventral infraorbital foramen**, and opens medially into the bony narial passage. The sphenopalatine foramen lies just anterior to the middle of the **ethmoidal crest of the palatine** on the medial (vomerine) surface of the palatine bone.

Schulte (1917:373) referred to the sphenopalatine foramen in *Kogia* as the naso-palatine foramen.

For the archaeocete *Zygorhiza*, Kellogg (1936:110) indicated that the **internal-orbital foramen** or sphenopalatine foramen is the foramen at junction of palatine, maxilla, and frontal. The name internal-orbital foramen (q.v.) should not be used because of confusion with a foramen in some rodents (see Wible et al. 2005:103).

– **sphenopalatine notch of the palatine** (*incisura sphenopalatina*)

The sphenopalatine notch of the palatine bone lies between the **orbital process of the palatine** and **sphenoidal processes** (Gray, 1918:169; Feneis, 1994:24.19). Gray noted that in humans the notch may be bridged by the orbital and sphenoidal processes to form a complete **sphenopalatine foramen**. The sphenopalatine notch lies on the posterodorsal aspect of the palatine bone and is part of the sphenopalatine foramen (Schaller, 1992:36.5).

The topography of the palatine bone has changed dramatically in cetaceans. The sphenopalatine foramen is now entirely within the palatine bone and the notch is closed over.

= **ventral surface of the palatine** = palatine surface of the palatine

PARIETAL BONE

Os Parietale

FIGURES 1, 3–5, 6A,C, **19**, 32

The parietal bone forms the lateral walls of the cranium and, in most mammals, meets with the contralateral bone in the midline (Gray, 1918:133; Evans and Christensen, 1979:124; Schaller, 1992:26.1; Feneis, 1994:16.24). Vesalius (1543:21,23) referred to the parietal as *dextrum uerticis os*, *sinstrum uerticis os*, or *verticis sinistrum os*. The parietal in most mammals is bounded by the frontal, basisphenoid, squamosal, interparietal, and supraoccipital. The exoccipital normally is excluded from contacting the parietal by the squamosal. Cetaceans are unusual in that the interparietal ossification is discrete and forms the midline ossification of the cranial walls, excluding the parietals from the midline. The parietal is bounded by the frontal, alisphenoid, squamosal, interparietal, supraoccipital, and exoccipital (Schulte, 1917:370, 375, 376, 382, 383, 391–393).

* **alisphenoid border of the parietal** (Figure 19b,c)

The alisphenoid border of the parietal is the border that articulates with the **alisphenoid** part of the sphenoid bones. It lies on the anteroventral surface of the parietal bone, posterior and ventral to the **frontal border of the parietal**.

– **caudal frontal sinus** (*sinus frontalis caudalis*)
See "Frontal Bone."

– **dorsal sagittal sinus sulcus** (*sulcus sinus sagittalis dorsalis*)
See "Interparietal Bone."

* **exoccipital border of the parietal** (Figure 19a–c,e)

The exoccipital border of the parietal is that portion of the parietal margin that articulates with the exoccipital. It is located ventromedially on the posterior border of the parietal (lateral and ventral to the occipital border).

– **external sagittal crest** (*crista sagittalis externa*)

The external **sagittal crest** is formed by the medial borders of the **temporal fossae** on the dorsal surface of the skull (Schaller, 1992:16:30, 18:3, 26:6).

Because the parietals do not meet in the midline in cetaceans and the dorsal **temporal line** is situated laterally on the skull, the external sagittal crest is not a feature of extant cetacean skulls.

* **external surface of the parietal** (*facies externa*) (Figure 19a–e)

The external surface of the parietal bone is that surface the bone that is external to the cranial cavity; the outside of the parietal bone.

* **free border of the parietal [new term]** (Figure 19b)

The free border of the parietal bone lies between the **alisphenoid border of the parietal** and the exoccipital border. It is the border that projects into the **posterior lacerate foramen** in odontocetes. The parietal bone does not participate in the posterior **lacerate foramen** of most mammals.

– frontal angle of the parietal (*angulus frontalis*)

The frontal angle is the craniometric angle formed by the intersection of a line from the center of the orifice of the **external auditory meatus** to the *ophryon* and a line from the *ophryon* (the middle of the supraorbital line, which, drawn across the narrowest part of the forehead, separates the face from the cranium) to the bregma (Whitney, 1889–1910:[vol. 2]1331). The frontal angle is the angle formed at the bregma by the sagittal and **frontal borders of the parietal** (White and Folkens, 1991:61, 62).

Because the parietals do not meet in the midline, this feature is not found on the cetacean skull.

*** frontal border of the parietal** (*margo frontalis*) (Figure 19a–d)

The frontal border of the parietal is the border that articulates with the frontal bones. It lies on the anterior surface of the parietal bone (Schaller, 1992:26.13).

The frontal border of the parietal is present in cetaceans.

*** inferior anterior external angle of the parietal** (Anderson, 1879:504) (Figure 19c)

Anderson (1879:504) describes the inferior posterior external angle of the parietal as "being external to that process with the **frontal process of the pterygoid** external to it and excluding it from appearing in the outer wall of the skull, although in the **temporal fossa** it is close behind the superior border of the isolated portion of the pterygoid, that is wedged in between the frontal, parietal and squamosal." In determining the location of this structure it became apparent that is was on the anterior not the posterior angle of the parietal.

The inferior anterior external angle of the parietal is present in delphinids.

– internal sagittal crest (*crista sagittalis interna*)

See **occipital bone** and "Interparietal Bone."

*** internal surface of the parietal** (*facies interna*) (Figure 19d,e)

The internal surface of the parietal bone is the medial or cranial surface of that bone.

*** interparietal border of the parietal** (*margo interparietalis*) (Figure 19a,c,d)

The interparietal border of the parietal is the border that articulates with the interparietal bone. It lies anteromedially on the dorsal surface of the parietal bone.

– mastoid angle (*angulus mastoideus*)

The mastoid angle is the angle formed at the *asterion* by the occipital border and temporal borders of the parietal (White and Folkens, 1991:61, 62).

It appears that this measurement is possible but difficult in Cetacea.

*** nuchal plane** (*planum nuchale*) (Figure 5)

The nuchal plane is the caudal surface of the skull formed by the exoccipitals, **supraoccipital**, and mid-ventrally by the basioccipital with its intracondyloid closure. It is limited by the **nuchal crest** (Evans and Christensen, 1979:154; Schaller, 1992:26.20).

In cetaceans the nuchal plane has been modified to include the interparietal, which bears the median portion of the nuchal crest. It is limited laterally by the **temporal crests** and ventrally by the ventral border of the exoccipital bones. The nuchal plane is more planar in adults than juveniles.

– occipital angle (*angulus occipitalis*)

The occipital angle of Broca is the craniometric angle formed by the intersection of the lines drawn from the ***opisthion*** (the middle point of the posterior border of the ***foramen magnum***) to the ***basion*** (the middle point of the anterior margin of the *foramen magnum*) and *nasion* or nasal points (the middle of the **frontonasal suture** at the root of the nose) (Whitney, 1889–1910:[vol. 2]1331).

The occipital angle of Daubenton is the angle that the line of Daubenton (a line drawn through the *opisthion* and the projection, on the medial plane of the skull, of the lower border of the **orbit**) makes with a line joining the *basion* (the middle point of the anterior margin of the *foramen magnum*) and the *opisthion* (the middle point of the posterior border of the *foramen magnum*) (Whitney, 1889–1910:[vol. 2]1331).

The occipital angle is the angle formed at lambda by the sagittal and occipital borders (White and Folkens, 1991:61, 62).

Because the parietals do not meet in the midline, this feature is not found on the cetacean skull.

= occipital border of the parietal (*margo occipitalis*)

The occipital border is that portion of the parietal margin that articulates with the occipital. It is located posteromedially on the dorsal border of the parietal. In delphinids it is composed of the **supraoccipital border** and the exoccipital border.

– parietal eminence (*tuber parietale*)

The parietal eminence is the feature on the **external surface of the parietal** that indicates where the parietal ossification began.

The parietal eminence is not evident in *Tursiops* or other odontocetes.

– parietal foramen (*foramen parietale*)

Gingerich et al. (2005: fig. 4) show a parietal foramen opening at the junction of parietal, squamosal, and occipital in the archaeocete *Makaracetus*.

See this term under "Interparietal Bone."

= parietal plane (*planum parietale*) = temporal fossa (adult)

The parietal plane is bounded by the **temporal line** and the **external sagittal crest** medially and the **nuchal line** posteriorly (Evans and Christensen, 1979:150). It is equivalent to the **temporal fossa**.

*** parietointerparietal suture** (Figure 5)

The parietointerparietal suture is the suture between the parietal and interparietal centers of ossification. In delphinids the parietointerparietal suture occurs on the interparietal border on the anterodorsal aspect of the parietal and on the parietal margin on the posterolateral aspect of the interparietals.

*** parietosupraoccipital suture** (Figure 5)

The parietosupraoccipital suture is the suture between the parietal and supraoccipital centers of ossification. In delphinids the parietosupraoccipital suture occurs on the **supraoccipital border** on the posterodorsal aspect of the parietal and on the parietal margin on the anterolateral aspect of the **supraoccipital**.

– postparietal foramen (Uhen, 2004:132)

Some archaeocete whales may have a prominent postparietal foramen opening dorsally in the parietal, in the wall of the **temporal fossa** (Kellogg, 1936: fig. 31c; Uhen, 2004:132). Uhen identified the postparietal foramen as for passage of a vessel from the otic region.

Tursiops lacks a postparietal foramen.

– sagittal border of the parietal (*margo sagittalis*)

The sagittal border of the parietal is the border that articulates with the contralateral bone.

Because the parietals do not meet in the midline, the sagittal border of the parietal is not a feature of the cetacean skull.

– sagittal sinus

See this term under "Frontal Bone" and "Interparietal Bone."

– sagittal suture (*sutura sagittalis*)

The sagittal suture is formed by the right and left parietal bones in the midline of the skull (Gray, 1918:178; Evans and Christensen, 1979:125; Schaller, 1992:76.3; Feneis, 1994:54.3). Vesalius (1543:23, 25) and Eustachius and Lancisius (1714:111) referred to the sagittal suture as the *sagittalis sutura*.

Because the parietals are excluded from the midline in modern Cetacea, the sagittal suture does not occur.

– septum of the frontal sinus (*septum sinuum frontalium*)

See "Frontal Bone."

– sphenoidal angle (*angulus sphenoidalis*)

The sphenoidal angle is the angle between the lines drawn from the ***basion*** (the middle point of the anterior margin of the ***foramen magnum***; Whitney, 1889–1910:[vol. 2]1331) and *nasion* (the middle of the **frontonasal suture** at the root of the nose; ibid.) to a point in the median line where the sloping anterior surface of the ***sella turcica*** passes over into the horizontal surface of the olivary eminence (a small rounded transverse process of the **body of the sphenoid** bone, just in front of the **pituitary fossa,** in relation with the optic chiasma; also called the olivary process or ***tuberculum sellae***; ibid., [vol. 5]4103).

The sphenoidal angle is the angle formed at *pterion* by the frontal and sphenoid borders (White and Folkens, 1991:61, 62). It appears that this measurement is possible but difficult in Cetacea.

*** squamous border of the parietal** (*margo squamosus*) (Figure 19c)

The squamous border of the parietal is the portion of the parietal margin that articulates with the squamosal. It is located ventromedially in cetaceans.

– sulci for intracranial extensions of spinal meningeal arteries

See "Exoccipital Bone."

*** sulcus for the middle meningeal artery** (Figure 31a)

The sulcus for the middle meningeal artery starts at the posterior-ventral angle of the parietal and branches over its **internal surface of the parietal** (Evans and Christensen, 1979:124). The sulcus for the middle meningeal artery is also called the **groove for the middle meningeal artery**

In *Tursiops* the sulcus for the middle meningeal artery appears to start on the **alisphenoid** and extend laterally onto the parietal. Two major branches of the sulcus are preserved on the parietal, the sulcus having divided on the alisphenoid.

*** sulcus for the transverse sinus** (transverse sulcus) (*sulcus sinus transversi*) (Figure 31b)

The sulcus for the transverse sinus (Evans and Christensen, 1979:122; Schaller, 1992:16.37, 18.6; Feneis, 1994:8.32) is located on the **supraoccipital** bone and the parietal bone. The sulcus is formed by one of the endocranial venous sinuses, the **transverse sinus.**

The sulcus for the transverse sinus in *Tursiops* occupies the area of the **internal surface of parietal** bone just lateral to the **tentorial process**. The transverse sinus broadens remarkably here compared to the situation in the dog (Evans and Christensen, 1979:124). The sulcus for the transverse sinus appears to be approximately 2 cm wide laterally (USNM 571695).

*** supraoccipital border** (Figure 19a,c,e)

The supraoccipital border of the parietal bone is that border of the parietal that abuts the **supraoccipital**. The supraoccipital border of the parietal lies between the **exoccipital border of the parietal** and the **interparietal border of the parietal**.

*** temporal line** (*linea temporalis*) (Figures 6c, 19c)

The temporal lines bound the **temporal fossa**. They are a continuation of the **sagittal crest** in dogs (Evans and Christensen, 1979:124; Schaller, 1992:16.31, 26.7). The temporal fascia is attached to the temporal line. In humans the temporal line is differentiated into a superior temporal line (*linea temporalis superior*), to which the temporal fascia is attached, and the inferior temporal line (*linea temporalis inferior*), to which the temporal muscle is attached (Feneis, 1994:16.28, 16.29). In other animals in which this differentiation occurs, the superior temporal line is known as the dorsal temporal line and the inferior temporal line is known as the ventral temporal line. **Temporal crest** and **supratemporal crest** have been used for comparable features in other mammals (e.g., Novacek, 1986). In humans the temporal line continues onto the frontal bone (Feneis, 1994:18.12).

In *Tursiops* the dorsal temporal line (q.v.) forms the posterior limit of the temporal fossa, which constitutes the posteromedial margin of the **external surface of the parietal** bone. Dorsally the temporal line comes to lie on the parietal only. Anterodorsally it continues onto the **postorbital process of the frontal bone**, where ventrally it runs onto the **zygomatic process of the squamosal** bone. The ventral temporal line is not developed. The dorsal temporal line becomes the temporal crest of adults.

The situation is different in some other Cetacea, especially archaic forms with an intertemporal constriction in which parietals and interparietal broadly separate face from **supraoccipital**. In *Simocetus*, each parietal is smooth with two indistinct subparallel parasagittal temporal crests (Fordyce, 2002).

– temporal plane (*planum temporale*)

The temporal plane is the temporal surface of the cranium (Whitney, 1889–1910:[vol. 6]4528), essentially the **temporal fossa**.

= tentorial process (*processus tentoricus*)
See "Exoccipital Bone."

= *tentorium* (tentorial ossification) (*tentorium cerebelli osseum*)
See "Exoccipital Bone."

= transverse sulcus = sulcus for the transverse sinus

PREMAXILLA

Os Incisivum

FIGURES 1, 3, 4, 6C,D, 20

The premaxilla forms the most anterior part of the skull, contacting the contralateral bone in the midline. It is one of three dentulous (tooth bearing) bones, the other two being the maxilla and mandible. The premaxilla bears the incisor teeth and forms the anterior part of the canine alveolus (alveolus for the canine tooth). The premaxilla also forms the floor of the anterior nasal passage. The premaxilla is bounded by the maxilla, vomer, and the nasal.

The premaxilla in odontocetes has been modified from the basic mammalian plan by the movement of the bony nares posteriorly and the accompanying development of the ascending process of the maxilla. The premaxilla forms most of the anterior border of the external bony nares. The premaxilla is bounded by the maxilla and vomer. The premaxilla rarely, if ever, contacts the nasal and frontal (Schulte, 1917:362, 365, 371, 372, 374, 377, 378, 380–383, 385–389, 400).

= alveolar border (*arcus alveolaris*)
See "Mandible."

= alveolar juga (*juga alveolaria*)
See this term under "Mandible."

= alveolar margin (*margo alveolaris*)
See **alveolar margin of the maxilla** under "Maxilla."

= alveolar process (*processus alveolaris*)
See **alveolar process of the maxilla** under "Maxilla."

= alveolar walls
See "Mandible."

– alveolus for the canine tooth
The alveolus for the canine tooth in most terrestrial mammals lies between the premaxilla and maxilla and forms an oval depression in both bones.

The teeth in odontocetes are homodont, i.e., there is no differentiated canine tooth. There is usually a small tooth whose **alveolus** lies between the premaxilla and maxilla.

– anterior nasal spine (*spina nasalis anterior*)
The anterior nasal spine of the premaxilla is the prolongation of the **incisor crest** anteriorly to form a spine that projects dorsally into the external narial aperture (Gray, 1918:158, 163; Feneis, 1994:22.12). This is commonly located on the maxilla in humans since the premaxillary ossification fuses in utero at an extremely early stage and is not recognized as a separate ossification.

The anterior nasal spine appears to be a neomorph in humans and is not present in Cetacea or domestic animals.

*** anteromedial sulcus** (Figure 20a)
The anteromedial sulcus lies on dorsal surface of the **nasal process of the premaxilla**. It contains the **premaxillary foramen** and forms the boundary between the anterior portion of the **premaxillary sac fossa** medially and the dorsal portion of the **rostral process** laterally (Fordyce, 1981: fig. 2; 1994:153).

– body (*corpus ossis incisivi*)
The premaxillary bone.

= dental groove = alveolar gutter = alveolar groove of the mandible
See **alveolar groove of the mandible** under "Mandible."

– dorsal sulcus (*sulcus septi nasi*)
The dorsal sulcus of the premaxilla is formed by the **palatine process of the premaxilla**, which, together with the contralateral palatine process, forms a groove for the **cartilaginous nasal septum** (Evans and Christensen, 1979:139).

The palatine process of the premaxilla is not developed in *Tursiops*.

*** external bony nares** (*apertura nasi ossea*) (Figures 1, 4)
The external bony nares form the anterior opening of the nasal cavities in the skull (Schaller, 1992:14.3). In most terrestrial mammals the external bony nares is formed by the premaxillae ventrally and the nasals dorsally (Evans and Christensen, 1979:508). It is known as the piriform aperture (*apertura piriformis / apertura nasalis anterior*) in humans (Feneis, 1994:32.3).

In delphinids the external bony nares are bounded by the premaxillae anteriorly and the nasals posteriorly. Depending on individual variation and type of preparation of bony specimens, the **mesethmoid** may be considered as forming part of the posterior border, the frontals, and the maxillae part of the lateral border, and a small slip of the maxilla may form part of the anterior border of the external bony nares. Clarke (2003:249) used the term "nasal foramina" as a synonym for the external bony nares in *Kogia*.

– frontal process of the premaxilla (Schulte, 1917:387)
Schulte used the term "frontal process of the premaxilla" to denote the contribution of the right premaxilla into the **facial crest** in *Kogia*. The facial crest (sensu Schulte) is present only in *Kogia*.

– incisive canal (*canalis incisivus*)
The incisive canals (foramina of Stenson) open into the **incisive foramen** in humans and carry the terminal branch of the descending palatine artery and the nasopalatine nerve (Gray, 1918:162; Evans and Christensen, 1979:139; Schaller, 1992:466.27; Feneis, 1994:24.4; Wible and Gaudin, 2004). The incisive canal lies in the interincisive suture.

The incisive canal is lacking in Neoceti because of the apparent lack of a nasopalatine nerve.

– incisive foramen (*foramen incisivum*) (Diagram 1)

The incisive foramen in humans is a shallow opening in the ventral midline of the palatal surface of the premaxilla and maxilla just posterior to the incisor teeth. It contains the apertures of the **incisive canals**, or foramina of Stenson (Gray, 1918:162, 180; Feneis, 1994:24.14). The incisive foramen is also known as the palatal fissure (Evans and Christensen, 1979:139; Schaller, 1992:12.25). Vesalius (1543:53; Vesalius et al., 1998:131) referred to the incisive foramen as the *foramen hoc iuxta posteriorem dentium incisoriorum*.

The incisive foramen is not developed in Neoceti.

– incisive suture (*sutura incisiva*)

The incisive suture is the suture between the right and left premaxillae.

The right and left premaxillae often bear a sutural relationship in delphinids.

– incisor crest

The incisor crest is a continuation of the **nasal crest of the maxilla** on the dorsomedial aspect of the premaxilla (Gray, 1918:163). The incisor crest continues anterodorsally where it forms the **anterior nasal spine**.

The incisor crest is not developed in delphinids due to the lack of fusion of the premaxilla medially.

*** infraorbital canal** (Table 6; Figure 20b,c,e)

See discussion under **premaxillary foramen** under "Premaxilla."

= infraorbital foramen

See "Maxilla."

= interalveolar margin (*margo interalveolaris*)

See "Mandible."

= interalveolar septa (*septa interalveolaria*)

See "Mandible."

= interradicular septa (*septa interradicularia*)

See "Mandible."

*** labial surface of the premaxilla** (*facies labialis*) (Figure 20a)

The labial surface of the premaxilla is that part of the anterior surface that faces the lips.

In odontocetes, this term is applicable to the anteroventral margin of the premaxilla.

*** lateral nasal crest [new term]** (Figure 20a,c)

The lateral nasal crest forms the functional border of the narial region laterally and differentiates it from the rest of the facial region. It is asymmetrically developed, being most prominent on the left side. The lateral nasal crest lies on the lateral edge of the **nasal process of the premaxilla** immediately lateral to the **external bony nares**. The lateral nasal crest lies lateral to the **premaxillary cleft** and medial to the **posterolateral plate** of the premaxilla (when developed). The lateral nasal crest also lies posteromedial to the **posterolateral sulcus**, and passes back into the "crest on maxilla" (sensu Fordyce, 1994:153).

= major palatine foramen (*foramen palatinum majus*)

See "Palatine Bone."

*** mesorostral canal** (Figure 1)

The mesorostral canal or groove is a characteristic feature of cetaceans. It lies dorsal to the vomer, medial to the maxilla and premaxilla, and anterior to the **mesethmoid** (Kernan, 1918, Rommel, 1990; Fordyce 1994). The mesorostral groove becomes occupied by the **mesorostral ossification** with age in ziphiids (Flower, 1878; Fraser, 1942; Heyning, 1984).

*** nasal portion** (Owen, 1866a:28) (Figure 20b)

The nasal portion of the premaxilla is that part of the bone lined by extensions of the nasal epithelium that cover the premaxillary sac and the inferior **vestibule** (Mead, 1975:6–8, fig. 2). The nasal portion is posterior to the rostral portion.

*** nasal process of the premaxilla** (*processus nasalis*) (Figure 20a,b,d,e)

The nasal process of the premaxilla is the posterodorsal portion of the premaxilla. The free rostral border of the nasal process forms part of the **external bony nares** (Evans and Christensen, 1979:139; Schaller, 1992:34.28).

The nasal process of the premaxilla in delphinids is that portion of the premaxilla that lies posterior to the anterior margin of the external bony nares. It is equivalent to the **spiracular surface of the vertex** in ziphiids (Heyning, 1989a) and has also been called the naso-frontal plate (Owen, 1866a:42) and **nasal plate** (Owen, 1866a:30). Schulte (1917:372, 373) referred to the nasal process as the postnarial process in *Kogia*.

= *os rostrale* = premaxilla

– palatine fissure (*fissura palatina*)

The palatine fissure is an oval opening formed at the junction of the **palatal surfaces of the maxilla** and premaxilla. The palatine vessels anastomose with the infraorbital vessels and nasal vessels through the palatine fissure (Evans and Christensen, 1979:141, 154). It also contains the bulk of the vomeronasal organ in most mammals (Evans and Christensen, 1979:510).

Schulte (1917:373) stated: "somewhat more caudally at the junction of the maxilla, pterygoid and frontal is the naso-palatine foramen." We are unable to find any other reference to the naso-palatine foramen, but the nasopalatine nerve goes through the palatine fissure (Schaller, 1992:466.27), and that structure could have been what Schulte had in mind. The foramen that Schulte describes is the **sphenopalatine foramen**.

The palatine fissure is absent in delphinids, as is the vomeronasal organ.

= palatine foramen

See "Palatine Bone."

*** palatine process of the premaxilla** (*processus palatinus*) (Figure 2)

The palatine process of the premaxilla is a pointed and laterally compressed process extending posteroventrally. This process, together with the opposite one, forms the **dorsal sulcus** into which the dorsal part of the **cartilaginous nasal septum** fits (Evans and Christensen, 1979:139). The palatine process is the contribution of the premaxilla to the palate (Evans and Christensen, 1979:152).

In *Tursiops* the palatine process is the anteroventral portion of the premaxilla that projects onto the palate. The palatine process is equivalent to the **palatine surface of the premaxilla**.

= palatine sulcus (*sulcus palatinus*)
See "Maxilla."

* **palatine surface of the premaxilla** (*facies palatina*) (Figure 20b,d)

The palatine or **ventral surface of the premaxilla** is that portion of the premaxilla that is exposed on the palate. It is the most anteromedial surface of the premaxilla. The palatine surface of the premaxilla is equivalent to the **palatine process of the premaxilla.**

* **porcelanous part** (Figure 1)

The porcelanous part is the dorsal surface of the **rostral process** of the cetacean premaxilla. Because the porcelanous part has no muscular insertions on it, the external surface is extremely smooth (Lawrence and Schevill, 1956: fig. 23).

= posteroexternal plate (Fordyce and de Muizon, 2001:196, fig. 12) = posterolateral plate

= posterointernal plate (Fordyce and de Muizon, 2001:196, fig. 12) = posteromedial splint

– posterolateral plate

The posterolateral plate of the premaxilla is the most posterolateral portion of the **nasal process of the premaxilla.** It is bounded medially by the **premaxillary cleft** (Fordyce, 1994:153). The posterolateral plate was described in a fossil platanistoid, *Waipatia.*

* **posterolateral sulcus** (Figure 20a,d)

The posterolateral sulcus lies on the dorsal surface of the **nasal process of the premaxilla**, posterior to the **premaxillary foramen.** It is a continuation of the **anteromedial sulcus** and forms the boundary between the **premaxillary sac fossa** medially and the lateral portion of the premaxilla that is a continuation posteriorly of the dorsal surface of the **rostral process** (Fordyce, 1994:153). The posterolateral sulcus was described in a fossil platanistoid, *Waipatia.*

– posteromedial splint

The posteromedial splint of the premaxilla, when developed, is the most posteromedial portion of the **nasal process of the premaxilla.** It is limited by the **external bony nares** medially, the frontal or maxillary posteriorly, and the **premaxillary cleft** laterally (Fordyce, 1994:153). The posteromedial splint was described in a fossil platanistoid, *Waipatia*, and is not developed in *Tursiops.*

* **posteromedial sulcus** (Figure 20a,d)

The posteromedial sulcus lies medial to the **premaxillary foramen** and forms the boundary between the **premaxillary sac fossa** and the rugose area immediately anterior to it, which is the area of origin of the nasal plug muscle (**prenarial triangle**) (Fordyce, 1994:153).

The posteromedial sulcus was described in a fossil platanistoid, *Waipatia*, and is developed variably in delphinids. It is developed in *Tursiops.*

– premaxillary cleft

The premaxillary cleft lies on the posterodorsal surface of the **nasal process of the premaxilla.** It lies between the **premaxillary sac fossa** and the **posterolateral plate** (if present) of the premaxilla. The premaxillary cleft lies posteromedial to the **posterolateral sulcus** (Fordyce, 1994:153).

The premaxillary cleft was described in a fossil platanistoid, *Waipatia.* The premaxillary cleft is not developed in delphinids.

– premaxillary crest

The premaxillary crest is formed by the elevation of the premaxillaries to form a distinct crest on the nasal **vertex** in ziphiids (Moore, 1968:255). The nasals and maxillae commonly take part in the formation of the premaxillary crest.

The premaxillary crest is absent in modern delphinids. Cowan's (1944:300) use of the term "premaxillary crest" was in reference to the **premaxillary eminence** on *Phocoenoides dalli.*

– premaxillary eminence (Barnes, 1984:19, 1985:151)

The premaxillary eminence or premaxillary boss is an abruptly raised elongate structure that makes up most of the **premaxillary sac fossa** in Phocoenidae and the extinct family Albireonidae. The medial **premaxillary foramen** and associated sulci may be involved. Hamilton (1941:232) used the term "**prenasal protuberance**" for premaxillary eminence; de Muizon (1983:1205) called it the posterior swelling of the premaxilla (*renflement postérieur du prémaxillaire*).

In *Tursiops* and most other Odontoceti, the premaxillary sac fossa is concave to flat, without a premaxillary eminence. However specimens of *Grampus* show a swelling that could be considered a premaxillary eminence.

* **premaxillary foramen** (Figures 1, 20a)

The premaxillary foramina in odontocetes are part of the infraorbital nerve complex. The **infraorbital canal** begins at the **ventral infraorbital foramen** and ends at the **dorsal infraorbital foramen** and premaxillary foramen. The premaxillary foramina are located on the dorsal surface of the **nasal process of the premaxilla** at or near the anterior apex of the **premaxillary sac fossa.**

* **premaxillary sac fossa** (Figure 20a,d)

The premaxillary sac fossa is located on the posterodorsal surface of the premaxilla (Fordyce, 1981, 1994:149) and is well developed in *Tursiops.* This shallow fossa outlines the anterior extent of the premaxillary sac but extends posterodorsally beyond the limits of the premaxillary sac. Owen (1866a:30) referred to this portion of the premaxilla as the "prenarial plate of the right maxillary," when he really meant the right premaxilla. Heyning (1989a:5) used spiracular sac for this structure. As we note in the discussion concerning structures associated with the nares, we prefer not to use the term "spiracular" because it has many anatomical meanings.

The premaxillary sac fossa is the only bony fossa for any part of the epicranial sinuses or nasal diverticula, which otherwise are contained within soft tissues of the odontocete face (Mead, 1975; Heyning, 1989a; Cranford et al., 1996). We follow Heyning (1989a:2) in use of the term "epicranial sinuses."

= **premaxillary sulci**
See **anteromedial sulcus**, **posterolateral sulcus**, and **posteromedial sulcus**.

= **premaxillary tubercle**
See **tubercle of the premaxilla**.

– **prenarial basin**
The prenarial basin is a feature limited to adult males of *Ziphius cavirostris* (Heyning, 1989b:297). The prenarial basin is an excavation on the premaxillae, maxillae, and vomer immediately anterior to the **external bony nares**. Heyning has found that the prenarial basin is filled with the enlarged right nasal plug. The prenarial basin has also been called the pre-nasal fossa (Turner, 1872) and the prenarial fossa (Owen, 1870).

* **prenarial triangle** (Figure 20a)
The prenarial triangle in delphinids is situated on the dorsal surface of the premaxilla between the posteromedial and anteromedial **premaxillary sulci** and the medial border of the premaxilla (Perrin et al., 1987). The prenarial triangle has a relatively rugose surface, particularly in comparison to the dorsal surface of the **rostral portion of the premaxilla**, which it borders. The prenarial triangle serves as the direct bony origin for the nasal plug muscle and overlaps both the rostral portion anteriorly and the **nasal portion** posteriorly.

= **prenasal protuberance** (Hamilton, 1941:232) = premaxillary eminence

– **prespiracular plate**
The prespiracular plate is that part of the external surface of the premaxilla immediately anterior to the **spiracular plate** (**premaxillary sac fossa**) in ziphiids (Mitchell, 1968:271).

The prespiracular plate appears to be homologous with the most anterior end of the premaxillary sac fossa in delphinids. Mitchell (1968:270) defined the **prespiracular plate groove**, which we have homologized with the **posteromedial sulcus**, as lying on the prespiracular plate. There does not seem to be differentiation of those two areas on the premaxillary sac fossa in delphinids.

– **prespiracular plate flange**
The prespiracular plate flange is a "slight, broadly arcuate flange (called the prespiracular plate flange herein) proximally, with a slight emargination distally (called the **prespiracular plate notch** herein) on the medial margin of the right premaxillary in the area of the **prespiracular plate**." (Mitchell, 1968:270, fig. 2; 271).

The prespiracular plate flange appears to be restricted to ziphiids and may be restricted to *Ziphius*.

– **prespiracular plate groove** = posteromedial sulcus (Mitchell, 1968:270, 271)

– **prespiracular plate notch**
See **prespiracular plate flange**.

– ***prosthion***
The *prosthion* is the craniometric point at the anterior end of the interincisive suture.

The premaxillae do not fuse in an interincisive suture in delphinids. The position of the *prosthion* can only be estimated in delphinids.

* **rostral portion of the premaxilla** (Schulte, 1917:386) (Figure 20a,b,d,e)
The rostral portion is the portion of the premaxilla that lies anterior to the **antorbital notches**, that is, that contributes to the formation of the rostrum (Schulte, 1917:386).

* **rostral surface of the premaxilla** (Schulte, 1917:389) (Figure 20a)
The rostral surface of the premaxilla is the external surface of the premaxilla on the rostrum. The middle portion of the rostral surface is known as the **porcelanous part** (q.v.) in cetaceans where the surface of that portion is extremely smooth and hard.

= **sockets** = alveoli (*alveoli dentales*)
See "Mandible."

= **spiracular plate** (Moore, 1963) = premaxillary sac fossa

= **spiracular surface of the vertex** = nasal process of the premaxilla

– **tubercle of the premaxilla** (Schulte, 1917:372, 380) = premaxillary tubercle
In *Kogia* the **nasal process of the right premaxilla** is expanded posteriorly into a ridge that ends at the **vertex** and is known as the tubercle of the premaxilla (Schulte, 1917:372, 380). Schulte also referred to this structure as the tuberosity of the premaxilla.

Tursiops and other delphinids have not developed a premaxillary tubercle.

= **ventral surface of the premaxilla**
See **palatine surface of the premaxilla**.

PTERYGOID BONE

Os Pterygoideum

FIGURES 3–5, 6B–D, **21**, 31A, 32

The pterygoid is a paired bone that forms the back of the hard palate (Evans and Christensen, 1979:145). In most mammals that have an extensive soft palate, there is no contact with the pterygoid of the opposite side. The pterygoid forms the lateral and part of the dorsal walls of the nasal passage. The pterygoid is bounded by the basisphenoid, presphenoid, and the palatine.

In humans the pterygoid is recognized, not as a separate bone, but as the pterygoid process of the sphenoid (Gray, 1918:151; Feneis, 1994:121.1–5). The pterygoid may fuse with adjacent bones in other mammals (e.g., Novacek, 1986:45), which has resulted in misleading early accounts of homologies for the cetacean pterygoid. Ridewood (1922:260) gave a useful review of issues.

In odontocetes the pterygoid bridges the floor (namely, anteroventral part) of the choanae and sometimes there contacts its contralateral element. The pterygoid also forms the lateral wall of the choanae, contacting the vomer dorsally. The other bones that the pterygoid contacts are the basioccipital, basisphenoid, palatine, and the presphenoid. See Schulte (1917:373–375, 378–384, 387–389, 393, 394, 398–401) and Fraser and Purves (1960:8, 10, 12–14, 16, 18, 22, 33–41, 42, 44–51, 53–55, 57, 58, 60, 61, 63, 64, 68, 71, 73, 74, 76, 82–89, 100, 101, 132, 136).

To ensure that osteological features are clearly defined, we consider details of some soft tissues involving the pterygoid sinus system in the broad sense. This approach should resolve some inconsistencies in the work of Fraser and Purves (1960), such as the interchangeable use of cavity, lobe, sac, and sinus for parts of the pterygoid sinus complex. Table 7 illustrates the components of the air sinus complex in odontocetes.

– **accessory air sinuses** (Fraser and Purves, 1960:4, 16)

The accessory air sinus system is unique to cetaceans and is an extension of the middle ear cavity. This system has sometimes been referred to as the Eustachian apparatus (Anderson, 1879:455) or the guttural pouch (Anderson, 1879:452, 453, pl. 37, fig. 7), Eustachian system (Anderson, 1879:454), Eustachian sacs (Fraser and Purves, 1960:7), or pterygoid sinus system (Fraser and Purves, 1960:19, 20, 26, 30, 34, 35, 39, 41, 42, 53, 119). Flower (1867:93, 113; see also Gill, 1871:728) referred to the pterygoid sinus complex as the postpalatine sinus, a term that seems to have been forgotten. The accessory air sinuses cover most of the basicranium and, in some species, are adjacent to the maxilla, palatine, frontal, lacrimal, pterygoid, **alisphenoid**, **basisphenoid**, squamosal, basioccipital, exoccipital, **tympanic bulla**, and periotic. The anterior portion of the system arises from the **auditory tube** near the opening of the tympanic **bulla**. It consists of the **pterygoid sinus** proper, with the hamular lobe, postorbital lobe, preorbital lobe, and anterior lobe in some species. The pterygoid sinus also gives rise to the **basisphenoidal sinus** in phocoenids. Posteriorly the **tympanic cavity** gives rise to the **middle sinus**, **peribullary sinus**, and the **posterior sinus**.

– **alisphenoidal portions of the external plate** (Anderson, 1879:509)

Alisphenoidal portions of the **external plate of the pterygoid** are those portions of the lateral plate of the pterygoid that, in *Platanista*, lie external to the **alisphenoid** (Anderson, 1879:509).

Tursiops and other delphinids do not develop their lateral plate such that it extends over the alisphenoids.

= **anterior air sinus system** (Fraser and Purves, 1960:62)

In the course of discussion, Fraser and Purves only once used the term "anterior air sinus system" (1960:62) for what they otherwise identified as the **pterygoid sinus**. Given this single mention, we recommend that the term "anterior air sinus system" not be used. Similarly, Fraser and Purves (1960:12) only once used the term "**anterior pneumatic cavities**," which we likewise recommend discarding.

= **anterior pneumatic cavities** (Boenninghaus, 1904; Fraser and Purves, 1960:12) = anterior air sinus system

= **anterior pterygoid sinus** = pterygoid sinus

Luo and Gingerich (1999:28, 38) proposed the term "anterior pterygoid sinus" for part of the **pterygoid sinus fossa** in archaeocete whales. In *Tursiops* the equivalent structure is probably homologous with part of the **pterygoid sinus** (sensu stricto).

We recommend that the term "anterior pterygoid sinus" not be used because of confusion with the **anterior sinus**, which is a rostral extension of part of the pterygoid sinus complex (Fraser and Purves, 1960).

– **anterior sac** (Beauregard, 1894; Fraser and Purves, 1960:8, 9, 100)

The term "anterior sac" was used by Beauregard (1894) to mean that portion of the pterygoid sinus complex that lay anterior to the **falciform process**, that is, the anterior lobe, hamular lobe, postorbital lobe, preorbital lobe, and the **pterygoid sinus** (sensu stricto) (Fraser and Purves, 1960:8). Fraser and Purves (1960:8) modified Beauregard's concept, restricting the term anterior sac "to that part of the system projecting beyond the posterior limit of the rostrum." This definition of anterior sac conflicts with Fraser and Purves' (1960:62) definition of the same feature under the name of **anterior sinus** (q.v.).

Tursiops and some other delphinids have an anterior sac, for which we prefer the term "anterior sinus."

= **anterior sinus**

See treatment under "Maxilla."

– **bony nasopharynx**

Fraser and Purves (1960:12) quoted Boenninghaus' (1904) study of *Phocoena* and stated that the bony nasopharynx is filled by the naso-pharyngeal muscle mass that rises into the nose through the "**false choanae**."

See also **nasopharyngeal duct** under "Palatine Bone."

* **choanae** (Figure 2)

The choanae are posterior openings between the nasal cavity and the nasopharynx (Whitney, 1889–1910:[vol. 2]972; Schaller, 1992:14.11, 176.5; Feneis, 1994:136.3), also known as the internal bony nares.

The choanae in odontocetes consist of the posterior borders of the pterygoids and the vomer.

= **choanal fossa** = interpterygoid fossa (McDowell, 1958:203)

* **dorsal lamina of the pterygoid** (Fraser and Purves, 1960:100, 102) (Figures 21a,c,d, 30)

The dorsal lamina of the pterygoid is that part of the pterygoid bone that forms a dorsal bridge between the **lateral** and **medial laminae of the pterygoid**.

Fraser and Purves also referred to the dorsal lamina as the superior **lamina of the pterygoid** (1960:35, 38–40, 49–61, 83–85, 87, 89, 100, 102, 107, 108, 138, pl. 43), superior lamina of the **pterygoid hamulus** (1960:64, 87), and superior lamina of the **pterygoid plate** (1960:85). Schulte (1917:373) called it the lateral process of the pterygoid in *Kogia*.

TABLE 7. Components of the accessory air sinus complex in odontocetes.

Name of sinus (plus selected synonyms)	Position and comments	Main bony elements
Basisphenoidal sinus	In ventral part of skull medial to the alisphenoid, and within the basioccipital. Arises as a medial to posteromedial lobe of the pterygoid sinus. Occurs in phocoenids only.	Basioccipital, basisphenoid.
Anterior lobe	Rostral or antorbital extension of the frontal may form pterygoid sinus, anterior to the preorbital lobe. Originates from preorbital lobe. An anterior lobe has probably evolved convergently in several different groups of odontocetes.	Maxilla, palatine; lacrimal and frontal may form some of the fossa.
Hamular lobe	In hamular fossa, ventral and immediately anterior to the bony nares. Originates from pterygoid sinus at about the level of the Eustachian notch.	Pterygoid, palatine.
Middle sinus	In tympanosquamosal recess of the squamosal. Originates as lateral projection from the tympanic cavity via the epitympanic hiatus.	Squamosal only.
Peribullary sinus	Between basioccipital crest, paroccipital process, tympanic bulla, and periotic, extending dorsally around the periotic.	Originates from basioccipital crest, paroccipital process, tympanic bulla, and periotic.
Posterior sinus [= *sinus pneumaticus paroccipitalis* = posterior pterygoid sinus]	Posterior to the tympanic bulla, in the space between bulla and paroccipital process. Originates from the tympanic cavity via the elliptical foramen.	Tympanic bulla and paroccipital process.
Posterolateral lobe of peribullary sinus [= posterior sinus of some authors]	Between tympanic bulla, periotic, and paroccipital process, and possibly squamosal. Originates as a posterolateral extension of the peribullary sinus.	Tympanic bulla, periotic and paroccipital process; possibly squamosal.
Postorbital lobe	In the orbit posterior to postorbital ridge. Originates from pterygoid sinus posteroventral to the optic foramen but anterior to foramen ovale. There is a postorbital diverticulum in *Cephalorhynchus*.	Frontal, alisphenoid.
Preorbital lobe	In orbit around ventral infraorbital foramen, anterior to preorbital ridge. Originates from pterygoid sinus anteroventral to optic foramen.	Frontal, maxilla; may have some contribution from lacrimal and palatine
Pterygoid sinus (in the strict sense) [= anterior pterygoid sinus; = middle pterygoid sinus]	In ventral part of skull lateral to basioccipital crest and to pharyngeal crest (in part, medial lamina of pterygoid). Passes back into tympanic cavity. Ultimately originates as a diverticulum of Eustachian tube immediately anterior to the tympanic bulla.	Pterygoid, alisphenoid, basioccipital
Tympanic cavity	In tympanic cavity of tympanic bulla and epitympanic recess of periotic.	Tympanic bulla, periotic

The dorsal lamina is best understood with reference to cetaceans in which the **pterygoid sinuses** do not invade the **orbit**, such as the Monodontidae and the Balaenopteridae. There, the **pterygoid sinus fossa** has a distinct bony roof or dorsal lamina. The situation is complicated—and homologs often uncertain—in delphinids because the pterygoid sinus is expanded dorsally and/or anteriorly. Fraser and Purves noted (1960:100) that the dorsal or superior lamina is vestigial in *Tursiops*. They labeled the dorsal lamina in various delphinids as the narrow strip of pterygoid anteromedial to the path of orbital nerves, sometimes ventral to the **orbitosphenoid**.

– ectopterygoid crest

In some mammal groups the pterygoid includes two components, the ectopterygoid crest and the **entopterygoid crest**, that delimit the **ectopterygoid fossa** (Novacek, 1986:45). The ectopterygoid fossa forms the origin for the internal pterygoid muscle (Novacek, 1986).

To consider the situation in *Tursiops*, it is helpful to review other Cetacea. In Neoceti (Mysticeti and some Odontoceti) and the basilosaurid Archaeoceti, the pterygoid includes **lateral laminae** and **medial laminae** that bound the **pterygoid sinus** (Fraser and Purves, 1960). The presence of a pterygoid sinus bounded by lateral laminae and medial laminae is a synapomorphy for Neoceti and Basilosauridae; more-basal Cetacea lack the sinus and bounding laminae. Accordingly, the **pterygoid laminae** in Neoceti and Basilosauridae are probably not homologous with the ectopterygoid and entopterygoid crests of some other mammals. Developmental studies would help to resolve matters.

Thus, in *Tursiops* and many other Delphinidae, the terms "ectopterygoid" and "entopterygoid" are not clearly applicable.

– ectopterygoid fossa

As noted under **ectopterygoid crest** (q.v.), the ectopterygoid crest and **entopterygoid crest** in mammals delimit the ectopterygoid fossa (Novacek, 1986:45) for the internal pterygoid muscles. In humans (e.g., Gray, 1918:151) the fossa is commonly referred to as the **pterygoid fossa of the palatine** and it may include a significant component from the palatine.

See discussion under **pterygoid fossa of the palatine**, where we outline why the **pterygoid sinus fossa** of Odontoceti and Mysticeti, and the extinct Archaeoceti, is not homologous with the pterygoid fossa of many land mammals. Ridewood (1922:260ff) also offered pertinent comment.

Tursiops and other delphinids do not have an ectopterygoid fossa in the sense of other mammals. The internal pterygoid muscle originates from the lateral lamina associated with the **pterygoid hamulus**, the palatine, and adjacent structures (Seagars, 1982:51).

– entopterygoid crest

In some mammal groups the pterygoid includes two components, the **ectopterygoid crest** and the entopterygoid crest, that delimit the **ectopterygoid fossa** (Novacek, 1986:45). Details are given under ectopterygoid crest.

Wible and Gaudin (2004:127) noted that in armadillos and other mammals, the paired entopterygoid crests form the lateral walls of the basipharyngeal canal.

There is no evidence at present to suggest that, in *Tursiops*, the **medial lamina of the pterygoid** (sensu Fraser and Purves, 1960) is homologous with the entopterygoid in the sense of Novacek (1986).

* **Eustachian notch** (Figures 21a,c, 30, 32)

The Eustachian notch in *Tursiops* and other delphinids is on the dorsal corner of the free edge of the **medial lamina of the pterygoid**, dorsal to the **pterygoid hamulus**. The Eustachian notch passes the **Eustachian tube** (**auditory tube**). Schulte (1917:374, 394) referred to it as the **tubal notch** in addition to the Eustachian notch (Schulte, 1917:394).

= external lamina [of the pterygoid] (Owen, 1866a:28) = lateral lamina of the pterygoid

= external plate of the pterygoid (Owen, 1866a:38; Anderson, 1879:507–509; Schulte, 1917:399) = lateral lamina of the pterygoid

= external reduplication of the pterygoid = lateral lamina of the pterygoid (Miller, 1923:33)

= false choanae = bony nasopharynx (Fraser and Purves, 1960:12)

– frontal process of the pterygoid (Anderson, 1879:504)

Anderson (1879:504) stated:

> The anterior division of the **alisphenoid** is applied by its front margin to the **orbitosphenoid**, while by its thickened superior rough surface it articulates with the inferior thickened rough angle of the parietal; it also rests on the external surface of the inferior posterior external angle of the parietal, i.e., being external to that process with the frontal process of the pterygoid external to it and excluding it from appearing in the outer wall of the skull, although in the **temporal fossa** it is close behind the superior border of the isolated portion of the pterygoid, that is wedged in between the frontal, parietal and squamosal.

We attempted to discern this structure but were unsuccessful. This feature appears to be unique to *Platanista* and may not have homologues in other cetaceans.

– groove of the pterygoid hamulus (*sulcus hamuli pterygoidei*)

The groove of the pterygoid hamulus is located at the base of the **pterygoid hamulus** (Schaller, 1992:20.29, 152:16; Feneis, 1994:12.11). It contains the tendon of the *m. tensor veli palatini*.

The nasopharynx of cetaceans is considerably modified from terrestrial mammals. A large palatal sphincter holds the larynx up into the nasopharynx and effectively isolates the respiratory and gustatory functions. Because of this modification the small muscles of the pharyngeal area, including the *tensor veli palatini* muscle, have probably been lost. However, Boeninghaus (1904) (*fide* Fraser and Purves, 1960:10, 11) mentioned the *tensor veli palatini* muscle in *Phocoena* and Fraser and Purves mentioned it in a number of families (1960:10–12, 19, 22, 26, 29, 31, 76, 82–84, 132.

* **hamular crest** [**new term**] (Figure 2)

The hamular crest lies on the ventral surface of the pterygoid and extends from the **pterygoid hamulus** forward to the anterior margin of the pterygoid where it continues as the **palatal crest**. The hamular crest is well developed in adult *Tursiops* and variable in other delphinids. It is well shown on ventral photographs of some delphinids (Fraser and Purves, 1960: pls. 43, 47).

= hamular fossa = pterygoid sinus fossa

The hamular fossa (Fraser and Purves, 1960:22) is the bilateral fossa for the hamular lobe of the **pterygoid sinus**. The hamular fossa is equivalent to the **pterygoid sinus fossa** (q.v.). The term has been used by de Muizon (1991:290) and Fordyce et al. (2002).

= hamular process (Schulte, 1917:375, 394, 399; Fraser and Purves, 1960:10, 44, 82) = pterygoid hamulus

= hamulus = pterygoid hamulus

= inferior lamina of the pterygoid = ventral lamina of the pterygoid

= inner lamina of the pterygoid = medial lamina of the pterygoid

= inner plate of the pterygoid (Owen, 1866a:28) = medial lamina of the pterygoid

= internal plate of the pterygoid = medial lamina of the pterygoid

– internal superior plate of the pterygoid (Anderson, 1879:506)

Anderson (1879:506) referred to the internal superior plate of the pterygoid in the following paragraph:

> The posterior division of the wing of the **orbitosphenoid** articulates by its extremity with the frontal anteriorly, and by its outer and under surface (which is broadly and deeply grooved for the branches of the fifth nerve passing out by the **sphenoidal fissure**) with the outer extremity of the **alisphenoid**; this is overlapped by the pterygoid and by the under surface of the base of the wings with the internal superior plate of the pterygoid; the body of the bone being supported by the vomer (consult pl. XL, fig. 1, etc.)

Anderson's plate XL shows two views of disarticulated pterygoid bones (figs. 13 and 14). The topography of those bones is extremely complicated and not adequately explained by the caption. We cannot locate the internal superior plate of the pterygoid.

– interpterygoid fossa = choanal fossa

McDowell (1958:125) described the interpterygoid fossa in insectivores as the "continuation of the choanal passage between the **pterygoid laminae** posterior to the false palate." McDowell (1958:203) also used **choanal fossa** as a synonym. Novacek (1986:45) described the fossa in leptictids.

Tursiops and other delphinids have an interpterygoid fossa, sensu McDowell, formed by the nasopharyngeal surface, and comprising part of the basipharyngeal canal; the fossa continues posteriorly, without interruption, between the **basioccipital crests**. The term apparently has no past use for *Tursiops*.

See **pharyngeal crest [new term]** under "Basioccipital Bone" and see also "Basipharyngeal Canal" within "Multi-Element Complexes."

= lamina of the pterygoid

The laminae of the pterygoid are the plate-like vertical parts of the pterygoid that connect the **hamulus** to the **dorsal lamina of the pterygoid** or to other dorsal structures such as the **lateral lamina of the palatine**. The medial wall of the **medial lamina of the pterygoid** is the nasopharyngeal surface. Fraser and Purves (1960:59) referred to the **pterygoid laminae** as the hamular laminae.

See also **medial lamina of the pterygoid, lateral lamina of the pterygoid.**

*** lateral lamina of the pterygoid** (Figure 21a–e)

In delphinids the lamina of the pterygoid is split by the development of the **pterygoid sinus** into a lateral lamina and a **medial lamina** (Fraser and Purves, 1960:19, 34, 35, 37–39, 43–45, 47–52, 54–57, 59, 61–66, 68, 76, 82, 83, 84, 85, 87, 89, 100, 102). Owen (1866a:37) referred to the lateral lamina as the outer or free lamellae, and Anderson (1879:507–509) referred to the lateral lamina as the external plate. Miller (1923:33) used the term "**external reduplication of the pterygoid**." Fraser and Purves (1960:60) referred to the lateral laminae as outer laminae and used **pterygoid plates** (1960:6, 22, 42, 53, 81–85, 87, 89, 102) to refer to the lateral lamina and medial lamina of the pterygoid bone.

medial flange of the pterygoid hamulus

Arnold and Heinsohn (1996:149, fig. 10) noted that in the delphinid *Orcaella*, a medial flange may extend from the **pterygoid hamulus** medially toward the contralateral element. *Tursiops* may develop a medial flange that becomes excavated by the **hamular fossa**. The medial flange of the **hamulus** should not be confused with the **medial lamina of the pterygoid**.

*** medial lamina of the pterygoid** (Figure 21a–e)

In *Tursiops* and other delphinids the **lamina of the pterygoid** is split by the development of the **pterygoid sinus** into lateral and medial laminae. The medial lamina forms the ventrolateral wall of the nasal passage and part of the attachment of the palatal sphincter and carries the **Eustachian notch**. Owen (1866a:28) referred to the medial lamina as the **inner plate of the pterygoid** and Anderson (1879:508, 509) referred to it as the internal plate. Miller (1923:34) used the term "internal reduplication of the pterygoid." See also Fraser and Purves (1960:31, 34, 39, 42, 43, 46, 47, 49–51, 53, 56, 57, 60, 65, 66, 68–70, 73, 82, 83, 85, 89, 102).

– middle pterygoid sinus = pterygoid sinus

Luo and Gingerich (1999:28, 38, 40) proposed the term "middle pterygoid sinus" for part of the **pterygoid sinus fossa** anteromedial to the path of the mandibular nerve in archaeocete whales.

In *Tursiops* the equivalent structure appears homologous with part of the **pterygoid sinus** (sensu stricto). The middle pterygoid sinus is presumed not to be homologous with the **basisphenoidal sinus** in *Phocoena* and other Phocoenidae.

We recommend that the name "middle pterygoid sinus" not be used for part of the pterygoid sinus (sensu stricto) because of confusion with the **middle sinus**, which is a lateral extension from the **tympanic cavity** via the **epitympanic hiatus** into the **tympanosquamosal recess** (Fraser and Purves, 1960).

*** nasopharyngeal surface of the pterygoid** (*facies nasopharyngea*) (Figure 21a,b,d,e)

In *Tursiops* the nasopharyngeal surface of the pterygoid is the smooth concave medial surface of the bone that forms part of the lateral wall of the nasopharynx.

See also **interpterygoid fossa.**

– orbital extension of the pterygoid (Fraser and Purves, 1960:45)

Fraser and Purves (1960:45, 49–51, 54, 56, 57, 59, 60) described the orbital extension of the pterygoid bone. An extension of the **dorsal lamina of the pterygoid** ventral to the **optic canal** partly covers the contents of the optic canal ventrally. This situation is best seen in some specimens of *Pseudorca* (Fraser and Purves, 1960:50, pl. 29). In that species the dorsolateral wall of the hamular lobe of the **pterygoid sinus** is formed by the **lateral lamina of the palatine**. The orbital extensions of the pterygoid emerge onto the orbital region from the dorsal border of the lateral lamina of the palatine, as can be seen in Fraser and Purves plate 29 and USNM 484982. The orbital extensions of the pterygoid extend anteriorly (preorbital extension, Fraser and Purves, 1960:51–53, 56, 58 or pre-orbital part of the pterygoid sinus, 1960:65) and posterior (postorbital extension Fraser and Purves, 1960:51, 52) to the optic canal. Some specimens of *Pseudorca* (USNM 208360) lack orbital extensions. The orbital extension should not be confused with the **posterior wing of the lateral lamina of the palatine** (q.v.) as seen in *Orcaella*.

– orbital lobes of the pterygoid sinus (Fraser and Purves, 1960:1, 64, 70)

Fraser and Purves mentioned the orbital lobes in their discussion of the **pterygoid sinus** in *Inia* (1960:64) and *Tursiops* (1960:70). They mentioned the orbital lobes in addition to the preorbital and postorbital lobes such that it is clear they were thinking of three separate structures, as can be seen in the following quotation: "The orbital, pre-orbital and post-orbital lobes are all well developed, the orbital lobe covering the orbito-sphenoid and forming a conspicuous laterally projecting ventral boundary to the **optic infundibulum**. The pre-orbital and post-orbital lobes are well extended and the latter spreads dorsally under the **postorbital process of the frontal**" (Fraser and Purves, 1960:70).

Fraser and Purves did not indicate the presence of orbital lobes in their plates of *Tursiops* (1960: pls. 43, 44), nor in their table of abbreviations (1960:137, 138), but they labeled orbital lobes in their illustration of *Inia* (1960:pls. 21, 22). It is clear that the structure labeled as orbital lobes in both plates 21 and 22 is the **preorbital lobe of the pterygoid sinus**.

In describing the situation in *Globicephala melas*, Fraser and Purves (1960:72) wrote: "This arrangement is well shown in Pl. 34 which figures the pterygoid sinus of *Globicephala*. The orbital portion is fairly prominent, covers the orbito-sphenoid and forms the ventral boundary of the optic infundibulum. The pre-orbital and post-orbital lobes are well extended laterally and unite above the optic infundibulum to form its dorsal boundary."

Here they are using the orbital portion (orbital lobes) as that portion of the pterygoid sinus that covers the **orbitosphenoids**.

In view of this confusion we recommend using the term "orbital lobes" with care, including a statement of the context of use.

– orbitosphenoidal portions of the external plate of the pterygoid (Anderson 1879:509)

The orbitosphenoidal portions of the **external plate of the pterygoid** are those portions of the lateral plate of the pterygoid that lie external to the **orbitosphenoid** (Anderson, 1879:509).

Delphinids do not develop their lateral plate such that it extends over the orbitosphenoids.

– orifice for the inferior maxillary (mandibular) nerve

Anderson (1879:514) described the orifice for the inferior maxillary (mandibular) nerve as bounded by the **pterygoperiotic plate** in *Platanista*. In the specimen of *Platanista* available to us (USNM 172409) the orifice is bounded by the pterygoid not the **falciform process** of the squamosal bone. The exposure of the pterygoid is thin and could easily by hidden by the squamosal. In USNM 23456 the orifice is bounded by the pterygoid. The mandibular nerve normally emerges from the skull via the ***foramen ovale***, but the modifications of the pterygoid and squamosal have hidden the *foramen ovale* in *Platanista*.

= palatine process of the pterygoid = lateral lamina of the pterygoid

Fraser and Purves (1960:13) paraphrased Boenninghaus (1904), who used palatine process of the pterygoid for the **lateral lamina.**

* **palatine surface of the pterygoid** (*facies palatina*) (Owen, 1866a:39) (Figures 2, 21b,c)

The palatine surface is the surface of the palatine bone that is exposed on the palate of the skull (Evans and Christensen, 1979:141, 143; Schaller, 1992:34.20, 36.17; Feneis, 1994:24.29). The expansion of the pterygoid in cetaceans (see general discussion under pterygoid bone) has resulted in exposure of the pterygoid on the palate.

The palatine surface of the pterygoid is formed by the ventral portion of the **medial laminae of the pterygoid** in odontocetes. Owen (1866a:39) referred to the palatine surface as the palatine plate of the inner portion (medial lamina). He also referred to the palatine portion of the pterygoid and made reference to plate 13, figure 2, item 24, which illustrates the **lateral lamina of the pterygoid.** We prefer to think of this discrepancy as just a lapsus calami on Owen's part and have interpreted the text as referring to the medial lamina.

* **pharyngeal crest** [new term under "Basioccipital Bone"] (Figure 2)

The pharyngeal crests in delphinids are the paired crests on the ventral surface of the skull that separate the pharyngeal region from the auditory region and optic regions. They consist of an anterior extension of the **basioccipital crests** onto the pterygoids.

See further discussion under "Basioccipital Bone."

– pharyngeal groove

Novacek (1986:45) described the pharyngeal grooves, or pharyngeal sulci (1986:6), as present, carrying nerves and vessels, along the internal base of the endopterygoid in leptictids.

Tursiops does not have recognizable pharyngeal grooves at the base (dorsal part) of the **medial lamina of the pterygoid.**

* **posterior lamina** (Owen, 1866a:39) (Figure 21a–c)

Owen, in his description of *Kogia sima* (1866a:39), referred to that portion of the pterygoid bone that forms the dorsolateral wall of the nasal passage as the posterior lamella. To keep our terms parallel, we have treated it as the posterior lamina. Delphinids have a similar conformation.

This structure is termed the medial **pterygoid plate** (*lamina medialis*) in humans (Gray, 1918:151; Feneis, 1994:3) and the **nasopharyngeal surface of the pterygoid** bone (*facies nasopharyngea*) in the dog (Evans and Christensen, 1979:145). It does not seem to have been recognized as a separate structure in most domestic animals since it is not found in Schaller (1992:20.25–29).

– postpalatine shelf

The postpalatine shelf extends along the inner edge of the descending laminae of the pterygoid, and is a feature in sloths that was mentioned by Gaudin (2004:267) in a list of cladistic characters without further amplification.

Tursiops and other cetaceans do not appear to have a structure that is homologous with the postpalatine shelf.

– pterygoid canal (*canalis pterygoideus*)

The pterygoid canal lies in the suture between the pterygoid and the **pterygoid process of the sphenoid**. It contains the autonomic nerve of the pterygoid canal (Gray, 1918:181; Evans and Christensen, 1979:145; Schaller, 1992:20.8; Feneis, 1994:12.12). Vesalius (1543:52; Vesalius et al., 1998:131) referred to the pterygoid canal (Vidian canal) as the *aliud foramen inchoatur, recta antrorsum ion narium usque amplitudinem, meatus olongi modo protensum, and arteriae ramo viam exhibens, qui a soporalis arteriae surculis pulsum edens sensibilem*.

Although we have not been able to visualize this canal in delphinids because the **basisphenoid** is not visible on the ventral portion of the skull, there is no reason to assume that the canal is not present in odontocetes in general.

– pterygoid crest

Andrews (1911:36, unnumbered tbl.) and Cowan (1944: tbl. 2), in accounts of Dall's porpoise (*Phocoenoides dalli*), used the term "pterygoid crest" in a way that suggests they were referring to the **pterygoid hamulus**. Pterygoid crest should not be used for cetaceans in this context.

Pterygoid crest has been used for features of the insectivore basicranium (McDowell, 1958:169) and the mandible in Mesozoic mammals (e.g., Wible and Rougier, 2000:62).

Tursiops and other delphinids lack a pterygoid crest in these senses.

– pterygoid fossa (*fossa pterygoidea*)

Pterygoid fossa, in the sense of McDowell (1958:128, a fossa for the origin of the pterygoid muscles on the skull base) and in the sense of Luo and Wible (2005, a fossa for insertion of pterygoid muscle on the mandible), should not be confused with the fossa for the **pterygoid sinus**. See further discussion under **ectopterygoid fossa** and **ectopterygoid crest**, above, and under **pterygoid fossa of the palatine**.

Tursiops and other delphinids do not have a pterygoid fossa in the sense of other mammals. For cetaceans, "pterygoid fossa" is an acceptable contraction for "**pterygoid sinus fossa**"; the term has had wide use in this context.

See also "Palatine Bone" and "Sphenoid Bone."

– pterygoid groove (*sulcus n. canalis pterygoidei*)

The pterygoid groove is a minute groove leading to the caudal opening of the **pterygoid canal** (Evans and Christensen, 1979:154; Schaller, 1992:20.9).

In delphinids the ventral surface of the **basisphenoid** is covered by the vomer, and the pterygoid canal continues posteriorly. The pterygoid groove is absent.

*** pterygoid hamulus** (*hamulus pterygoideus*) (Figures 2, 21b–e)

The pterygoid hamulus is the posteroventral angle of the pterygoid that is hook-shaped in most mammals (Fraser and Purves, 1960:4, 19, 22, 35, 37–40, 43, 45–62, 64–66, 68–71, 73, 82–85, 87, 89, 100, 102, 107). McDowell (1958:125, **hamular process**) described it as a hook-like process of the internal **pterygoid lamina**. The tendon of the *m. tensor veli palatini* wraps around this hook. Fraser and Purves also referred to the pterygoid hamulus as the hamular part (1960:41, 54), hamular portion (1960:20,89), hamular process (1960:10, 44, 82), or hamular region (1960:42, 51, 59).

The pterygoid hamulus is well developed in *Tursiops* and other delphinids (Fraser and Purves, 1960:41, 42, 46, 48, 52–60, 68, 73, 82–84, 89, 100, 102), albeit commonly modified through being expanded toward the midline and excavated by the hamular sinus. Each **hamulus** may develop a dorsoventrally flattened medial flange. Because of major changes in shape and proportion with development of the hamular sinus, the pterygoid hamulus in delphinids has become recognized more or less as that part of the pterygoid ventral to the level of the **Eustachian notch**. The primitive (relatively unmodified) state of the hamulus in odontocetes and mysticetes is probably represented by the structure in some balaenopterids (e.g., *Balaenoptera acutorostrata*) and certain fossil odontocetes (e.g., *Simocetus rayi* of Fordyce, 2002).

= pterygoid lamina = entopterygoid

The pterygoid lamina in insectivores is the "downwardly projecting plate of bone from the sphenoid continuous anteriorly with the vertical lamina of the palatine" (McDowell, 1958:128). McDowell indicated (1958:127) that "internal pterygoid lamina" and "pterygoid lamina" are the same.

– pterygoid notch (*incisura pterygoidea*)

The pterygoid notch lies between the lateral and medial **pterygoid plates** in humans. It is occupied by the **pyramidal process of the palatine** (Feneis, 1994:12.4). It is also called the pterygoid fissure (Gray, 1918:151). In some artiodactyls it occurs between the pterygoid bone and the **pterygoid process of the basisphenoid** (**alisphenoid**) (Schaller, 1992:20.26; not in Gray, 1918; Sisson, 1910; Evans and Christensen, 1979).

The cetacean pterygoid has been modified by the development of the **pterygoid sinus fossa** and the splitting of the pterygoid into the medial and **lateral laminae**. This has altered the relationship of the pterygoid and it no longer forms the pterygoid notch.

Fraser and Purves (1960:41, 43, 72) used "pterygoid notch" for the notch in the pterygoid through which the **Eustachian tube** enters the nasopharynx (see **Eustachian notch** of the pterygoid).

See also **ectopterygoid fossa**.

– pterygoid plexus (Fraser and Purves, 1960:120)

The pterygoid plexus is the fibro-venous plexus that surrounds the **accessory air sinuses** (**pterygoid sinus** system). Fraser and Purves (1960:120) proposed that the pterygoid plexus acts to compensate for the decrease in volume of the accessory air sinuses caused by changes in pressure with diving.

– pterygoid ridge

The pterygoid ridge is an oblique ridge beginning at or near the posteromedial margin of the pterygoid and extending anterolaterally for nearly the entire length of the pterygoid in *Mesoplodon europaeus*, but not in *M. mirus* (Moore, 1960:18).

There is no pterygoid ridge in *Tursiops*.

* **pterygoid sinus** (Figures 3, 29, 30)

The pterygoid sinus is a large air-filled diverticulum between the lateral lamina and **medial lamina of the pterygoid** and, in some cases, the palatine bones (Hanke, 1914; Fraser and Purves, 1960:8, 14, 68). The sinus is unique to cetaceans and is an extension of the middle ear cavity. The relationship of the pterygoid sinus to the guttural pouches of the horse has yet to be elucidated. The guttural pouches arise from the **Eustachian tube** (**auditory tube**) and lie ventral to the skull (Sisson, 1910:756). The pterygoid sinus arises from the auditory tube near the opening of the **tympanic bulla**. The sinus then runs anteriorly along the dorsal aspect of the pterygoid bone to enter the space between the **lateral lamina of the pterygoid** and medial lamina of the pterygoid (**pterygoid sinus fossa**). In many odontocetes, but not in mysticetes, the sinus extends dorsally onto the frontal and sphenoid. The pterygoid sinus develops preorbital and postorbital lobes (q.v.). In *Grampus* and *Tursiops* two posteriorly projecting extensions of the sphenoidal portion of the pterygoid sinus surround the ***foramen ovale*** (Fraser and Purves, 1960:100). Fraser and Purves also referred to the pterygoid sinus as the hamular cavity (1960:57, 59), hamular element (1960:89), **hamular fossa** (1960:22), hamular lobe (1960:64; but note the different sense of use by Fordyce et al., 2002), and hamular space (Fraser and Purves, 1960:22).

The entire complex of **accessory air sinuses** (q.v.) is sometimes referred to as the pterygoid sinus or the pterygoid sinus system. See Fraser and Purves (1960:1, 18, 22, 26, 30, 35, 37, 62–74, 76, 81, 85, 86, 88, 101, 102, 120, 133, 140).

More study is needed to resolve the exact relationships of the lobes of the pterygoid sinus complex around the tympanoperiotic.

* **pterygoid sinus fossa** (Figures 18b–c,e, 21c–d)

The pterygoid sinus fossa is the space occupied by the **pterygoid sinus** in the pterygoid and sometimes adjacent bones, including the palatine, maxilla, and frontal. It is the cavity between the **medial lamina** and **lateral lamina of the pterygoid**. Fraser and Purves referred to this feature as the inter-laminar space (1960:40, 44, 45, 48, 50, 57) or the inter-laminar air space (1960:76).

In *Tursiops*, as discussed elsewhere under the pterygoid bone, the pterygoid sinus is elaborated to produce distinct hamular, postorbital, preorbital, and **anterior sinuses** (or lobes, or sacs, in the terminology of Fraser and Purves). These changes have greatly modified the primitive state of the pterygoid sinus fossa as seen in the simple subspherical fossa of basal odontocetes and mysticetes and of basilosaurid archaeocetes.

– pterygopalatine ridge

The pterygopalatine ridge in the fossil mammal *Kryptobaatar* delimits a lateral and medial **pterygopalatine trough** or fossa (Wible and Rougier, 2000:30, 83, 84). The pterygopalatine ridge is apparently not homologous with the mammalian pterygoid lamina or entopterygoid.

Tursiops and other Cetacea lack a pterygopalatine ridge.

– pterygopalatine trough

In the fossil mammal *Kryptobaatar* the **pterygopalatine ridge** of the pterygoid delimits a lateral and a medial pterygopalatine trough or fossa (Wible and Rougier, 2000:30, 83, 84). The former is perhaps unrelated to the **Eustachian tube**, and the pterygopalatine ridge is apparently not homologous with the mammalian **pterygoid hamulus**.

Tursiops and other delphinids lack a lateral and medial pterygopalatine trough.

= tubal notch (Schulte, 1917:374, 394) = Eustachian notch

– tympanic process of the pterygoid (Wible and Gaudin, 2004:127)

Wible and Gaudin (2004:127) noted that in the yellow armadillo the **tympanic process** of the pterygoid is the feature that extends dorsolaterally from the posterodorsal corner of the pterygoid toward the ear region to contact the auditory bulla.

Tursiops and other Odontoceti lack a tympanic process of the pterygoid.

– ventral lamina of the pterygoid = inferior lamina (Fraser and Purves, 1960:37, 46, 138)

Fraser and Purves (1960:37, 46, 138) mentioned the ventral lamina as the inferior lamina but did not define it or give references to other anatomical works where it is defined. Fraser and Purves mentioned it in their discussion of the pterygoid of *Caperea* (1960:37) and *Inia* (1960:46; "fenestrated vestiges of the inferior lamina") and illustrated the feature in plates 5 and 6 (*Caperea*) and plate 21 (*Inia*).

We interpret the ventral lamina of the pterygoid as the portion of the bone that forms a ventral floor to the fossa between the medial and **lateral laminae of the pterygoid**. The ventral lamina is clear in balaenopterids such as *Balaenoptera acutorostrata*; there, the ventral lamina is a distinct area of bone that forms a floor to the **pterygoid sinus fossa**, lateral to the well-differentiated **pterygoid hamulus**, and ventrolateral to the **Eustachian notch**.

In *Tursiops* and other delphinids the pterygoid (including the **hamulus**) is heavily excavated by the **pterygoid sinus fossa**, with bone thinned or lost. Further, the pterygoid sinus fossa is laterally narrow, with the only major ventral surface being that of the excavated hamulus. It is debatable whether the ventral surface of the hamulus is homologous with the ventral lamina as seen in *Balaenoptera acutorostrata*; otherwise, *Tursiops* lacks a ventral lamina. The "fenestrated vestiges of the inferior lamina" in *Inia* (see Fraser and Purves, 1960:46, pl. 21) do not clearly represent the ventral lamina.

We have examined the USNM specimen of *Caperea* (550146) and compared it to Fraser and Purves (1960: pls. 5, 6). The bone labeled "inferior lamina" in plate 5 is clearly part of the squamosal in USNM 550146. Another specimen of *Caperea* (Otago Museum A81.2) has a prominent sulcus on the left squamosal where Fraser and Purves (pl. 5) indicated a suture. We think that they were working with an abnormal specimen. We feel that the ventral lamina in *Caperea* is the small thick shelf of the pterygoid that is immediately dorsal to the squamosal and exterior to the Eustachian notch. The notch is actually a groove prolonged anteromedially, associated with an indistinct hamulus at the medial end; the hamulus floors the **choanae** rather than flooring the **pterygoid sinus fossa**. Fraser and Purves differentiated the ventral lamina and the pterygoid hamulus in their figures of *Caperea* (1960: pl. 6) and *Inia* (1960: pl. 21). We agree with their interpretation of *Caperea* but, as above, question the interpretation of *Inia*.

= **ventral process** = pterygoid hamulus

= **Vidian canal** = pterygoid canal

SEPTOMAXILLA

Os Septomaxilla

The septomaxilla (Parker, 1871) is an ossification that occurs in monotremes and edentates posterior to the nasal aperture and extends inward as a plate overlying the vomeronasal organ. It has also been termed the intranasal (Ecker et al., 1904) and the intranarial (Wegner, 1922).

Cetaceans do not have a septomaxilla.

SPHENOID BONE

Os Sphenoidale

FIGURES 6B,F, 8, **22**, 28–32

The sphenoid bones form the middle part of the floor of the cranium (Schaller, 1992:18.9, 17, 20.12; Evans and Christensen, 1979:126–129; Feneis, 1994:10.1; Gray, 1918:147). Vesalius (1543:21–23, 25) referred to the sphenoid as the *cuneiform os*, the *os cuneo* (ibid., 21, 23, 25), and the *os cuneiforme* (ibid., 22, 23). Eustachius and Lancisius (1714:104, 112) referred to the sphenoid as *cuneiformia ossa*, but they also referred to it as the *osse sphaenoide* or the *sphaenoides os* (ibid., 112).

The sphenoid bones consist of a midline pair of bones and two lateral pairs of bones (Flower, 1885: fig. 47, 126, 127). The anterior midline ossification is termed the presphenoid and articulates anteriorly with the mesethmoid. The presphenoid articulates laterally with the first of the paired sphenoid ossifications, the orbitosphenoids. The presphenoid also articulates posteriorly with the basisphenoid, which in turn articulates with the basioccipital. The basisphenoid articulates laterally with the second pair of sphenoid ossifications, the alisphenoids or greater wings of the sphenoid. Because they form the base of the cranium, the sphenoid bones form the exits for cranial nerves II–VI (the optic, oculomotor, trochlear, trigeminal [ophthalmic, maxillary, mandibular], and the abducens nerves).

The base of the skull has been modified in cetaceans, principally in the posterior area where the tympanic and periotic parts of the temporal bone have been isolated from the rest of the skull. This, plus the elaboration of the air and vascular sinus systems (pterygoid, peribullary, etc.) has resulted in changes in detailed relationships of the sphenoid bones. The four elements of the sphenoid complex (basisphenoid, presphenoid, orbitosphenoid, alisphenoid) are still present.

= ***ala orbitalis*** = orbitosphenoid (Schulte, 1917:354, 394, under orbitosphenoid)

See "Ethmoid Bone."

= ***ala parva*** = orbitosphenoid

= **alar canal** (*canalis alaris*) = alisphenoid canal

The alar canal runs through the anteromedial part of the **alisphenoid.** The anterior opening of the alar canal is known as the **rostral alar foramen** and the posterior opening as the **caudal alar foramen** (Evans and Christensen, 1979:128; Schaller, 1992:20.2). The alar canal perforates the pterygoid process for passage of the maxillary artery in the dog and horse (Schaller, 1992:20.2). The alar canal communicates with the **foramen rotundum** and transmits the maxillary branch of the trigeminal nerve (maxillary nerve), which exits via the rostral alar foramen (Evans and Christensen, 1979:914).

The alar canals are not developed in Cetacea.

= ***ala temporalis*** = alisphenoid (Evans and Christensen, 1979:128)

– **alicochlear process** (*processus alicochlearis*) (Kernan, 1916:623)

Schulte (1917:374) referred to a process in the sphenoid of *Kogia* that he thought was "probably the *processus ali-cochlearis*." This structure was on the ventral part of the **alisphenoid** close to the tympanoperiotic, on the margin of the **posterior lacerate foramen** (1917:379) and included that part of the alisphenoid or **basisphenoid** that carries the narrow groove leading to the **carotid foramen of the sphenoid** and the groove leading from the ***foramen ovale***.

Kernan (1916:623, pl. 1, 3–6), in describing a 20 mm human embryo, used "*processus ali-cochlearis*" to mean a lateral part of the **temporal wing** of the sphenoid that continues posteriorly to contact the **cochlea**.

In mature *Tursiops* the region between the carotid foramen and *foramen ovale* is formed apparently by contributions of alisphenoid and basisphenoid. A discrete alicochlear process is not apparent.

* **alisphenoid** (temporal wing, greater wing) (*ala temporale*) (Figures 6b, 22a,b,d, 28, 29, 31b, 32)

The alisphenoids lie lateral to the **basisphenoid** (**body of the sphenoid**). They contain the ***foramen ovale***, ***foramen rotundum***, and ***foramen spinosum***. The alisphenoids are also known as the ***ala temporalis*** (Owen, 1866a:26; Flower, 1885:120, 211; Schulte, 1917:379, 392, 393; Ridewood, 1922; Fraser and Purves, 1960:35, 46, 47, 49, 51–53, 57, 59; Evans and Christensen, 1979:45, 128).

The alisphenoid is sometimes termed the **pterygoid process of the basisphenoid** (e.g., Schaller, 1992:20.1), or the **auditory plates of the basisphenoid** (Anderson, 1879:508), but we here follow literature on cetacean anatomy and mammalian phylogenetic anatomy in preferring use of "alisphenoid."

The alisphenoid of *Tursiops* is a well-defined shelf of bone that is present lateral to the basisphenoid. The alisphenoid and basisphenoid centers of ossification are fused at birth in *Tursiops*. Owen (1853:447) referred to the alisphenoids as the great alae. Fraser and Purves (1960:87) referred to the alisphenoids in *Monodon* as the alar process (not to be confused with the **alar process of the vomer**) or the lateral wing of the sphenoid (1960:61).

– alisphenoidal infundibulum (Fraser and Purves, 1960:100)

Fraser and Purves (1960:100) mentioned the alisphenoidal infundibulum in this sense: "The osseous **lateral lamina of the pterygoid** is wanting, as in *L. acutus*, and the alisphenoidal infundibulum of the 5th nerve is much shorter than in either of the previous species (text-fig. 20e')."

We presume that Fraser and Purves refer to the conical hollow formed in the **alisphenoid** by the passage of the mandibular branch of the trigeminal nerve and that it is the same feature referred to as the bony infundibulum of the ***foramen ovale*** (1960:30, 35–40, 46, 53, 61, 87, 100, 102). Fraser and Purves also referred to a bony tube (1960:44, 45, 47–60, 85, 87, 89) or a bony channel (1960:89), which we have equated with the alisphenoidal infundibulum.

Fraser and Purves (1960) seemed to correlate the alisphenoidal infundibulum, **falciform process**, and the inter-laminar space. They stated (1960:34): "The splitting of the pterygoid, and sometimes of the alisphenoid and squamosal also, into lateral and mesial laminae, connected to a greater or lesser extent by superior and inferior laminae."

We paraphrase that by saying that there existed a time when the pterygoid, alisphenoid, and squamosal had been split into lateral and medial laminae with the formation of an inter-laminar space. The mandibular branch of the trigeminal nerve traversed the inter-laminar space by sheathing itself in the alisphenoidal infundibulum. The falciform process is a remnant of this situation, being the residue of the lateral lamina of the squamosal bone.

– alisphenoidal region (Fraser and Purves, 1960:102)

The alisphenoidal region is that portion of the basicranium that lies ventral to the **alisphenoid** bone.

– alisphenoid canal (Flower, 1885:141)

The alisphenoid canal or **alar canal** in the dog (Evans and Christensen, 1979:128, 154) and other carnivores is a short horizontal canal that runs anteroposteriorly through the anteromedial part of the **alisphenoid** (*canalis alaris* of the **pterygoid process of the sphenoid** sensu Schaller, 1992:20.2, in dog and horse) on the ventral surface of the skull. The anterior opening of the alar canal is also known as the **rostral alar foramen**, and the posterior opening near the ***foramen ovale*** is the **caudal alar foramen**. The **foramen rotundum** opens into the dorsal part of the alisphenoid canal, and transmits the maxillary branch of the trigeminal nerve (maxillary nerve) into the canal; the maxillary nerve exits via the rostral alar foramen (Evans and Christensen, 1979:914). The canal also transmits the maxillary artery in the dog and horse (Schaller, 1992:20.2). Wible and Gaudin (2004:154) noted that the exit for the maxillary nerve may be separate from the alisphenoid canal, in which case the exit for the maxillary nerve is termed the foramen rotundum. The maxillary nerve may also exit via the **sphenorbital fissure** (q.v.). Wible (1987) discussed further details of the alisphenoid canal in Cetacea.

The **external carotid artery** does not penetrate the skull in Cetacea, and (Wible, 1987:130) there is no alisphenoid canal.

– alisphenoid portion of the lateral lamina (Fraser and Purves, 1960:48)

Fraser and Purves (1960:48) referred to the lateral lamina in this sense as a structure composed of the **lateral laminae of the palatine, of the pterygoid, and of the alisphenoid** in monodontids (see their plate 13).

= anterior carotid foramen (MacPhee, 1981:46) = internal carotid foramen

– anterior lacerate foramen (*foramen lacerum anterius*)

In the horse the anterior **lacerate foramen** is the large opening anterior and medial to the **periotic bone** (**petrosal**). It includes the following in its anterior border (Sisson and Grossman, 1953:72, fig. 49): ***foramen spinosum***, for passage of the middle meningeal artery; ***foramen ovale***, for passage of the mandibular branch of trigeminal nerve; and **internal carotid foramen** (*foramen lacerum medium*), for passage of the internal carotid artery into the cranial cavity (McFarland et al., 1979:7).

In *Tursiops* the anterior lacerate foramen is confluent with the cranial hiatus and does not exist as a separate entity.

= auditory plates of the basisphenoid (Anderson, 1879:508) = alisphenoid

See **alisphenoid.**

*** base of the alisphenoid** (Owen, 1866a:28; pl. 9: fig. 3(6)) (Figure 22a)

Owen referred to the midportion of the **alisphenoid** as the base of the alisphenoid.

= basioccipitosphenoid (Owen, 1866a:39)

Owen (1866a:39; pl. 13: fig. 2(5)), in his description of the holotype of *Kogia sima*, referred to the fused basioccipital and **basisphenoid** as the basioccipito-sphenoid.

*** basisphenoid** (*os basisphenoidale*) (Figures 6b, 22a,b,d, 31a)

The basisphenoid lies posterior to the **presphenoid** and anterior to the basioccipital in the floor of the cranium. In humans the basisphenoid is referred to as the corpus (not *corpus sphenoidale*) (Feneis, 1994:10.2). MacPhee (1981:49) summarized the ontogeny of the basisphenoid and its fusion with the **alisphenoid.**

The basisphenoid is connected with the **orbitosphenoids** anteriorly and the alisphenoids laterally (Schulte, 1917:374, 379, 383, 384, 386, 394; McFarland et al., 1979:8; Schaller, 1992:18.9).

– basisphenoidal sinus [new term]

Fraser and Purves (1960:49, 65, 92, 107) noted that, in *Phocoena*, the main part of the **pterygoid sinus** gives rise to a medially and posteriorly directed diverticulum in the **basisphenoid**. They referred to it as the "sphenoidal part of the sinus," (1960:107) and otherwise did not name it.

The term "basisphenoidal sinus" is used here for that lobe of the pterygoid sinus. **Sphenoidal sinus** has already been used for one of the **paranasal sinuses.**

Tursiops lacks a basisphenoidal sinus.

* **basisphenoid–presphenoid fissure** (Schulte, 1917:375, 386) (Figure 28)

The basisphenoid–presphenoid fissure is the space between the **basisphenoid** and the **presphenoid** that is occupied by the **intersphenoidal synchondrosis**. Schulte (1917:373, 378–380, 384, 392, 394, 400) also referred to this as the sphenoid fissure or basisphenoid–presphenoid cleft.

Not mentioned in Sisson, 1910; Gray, 1918; Evans and Christensen, 1979; Schaller, 1992; or Feneis, 1994.

= body of the sphenoid = basisphenoid

– caroticotympanic canals (*canaliculi caroticotympanici*)

The caroticotympanic canals are small canals in the wall of the **carotid canal of the sphenoid** for arterial branches and neural branches of the internal carotid artery and internal carotid plexus. The caroticotympanic canals connect the carotid canal and the **tympanic cavity** (Schaller, 1992:24.11; Feneis, 1994:12.27).

We are unable to demonstrate the existence of the caroticotympanic canals in cetaceans.

* **carotid canal of the sphenoid** (Figures 22a, 28)

The carotid canal transmits the internal carotid artery to the cranial cavity. In the dog the carotid canal begins at the **caudal carotid foramen of the sphenoid bone** in the medial wall of the osseous bulla. The carotid canal terminates at the **internal carotid foramen** (Gray, 1918:143, 181; Evans and Christensen, 1979:134, 156, 661, 676; McFarland et al., 1979; Schaller, 1992:24.10; Feneis, 1994:12.26). Vesalius (1543:52; Vesalius et al., 1998:131) referred to the carotid canal as the *insigne foramen maiori soporalis arteriae ramo calvaria ingredienti excavuatum*. Eustachius and Lancisius (1714:105) referred to the ventral opening of the carotid canal as the *foramen, per quod transit arteria carotis*.

In *Tursiops* the external (ventral) opening of the carotid canal is formed by the anterodorsal portion of the basioccipital and the posteroventral portion of the **basisphenoid**. The carotid canal courses through the basioccipital to issue in anteriorly directed openings in the cranial surface of the basisphenoid. In the adult *Tursiops* the cranial openings of the carotid canal are immediately lateral to the ***sella turcica*** (McFarland et al., 1979: fig. 55). Owen, in his discussion of the cetacean skull in general (1866b–1868(vol. 2):420), said that "the basisphenoid . . . is perforated or grooved by the **entocarotids**."

– carotid foramen of the sphenoid

The nomenclature associated with the extracranial course of the mammalian carotid artery (involving one or more foramina, canal, and sulci) is complicated and often confusing, as noted by Wible and Gaudin (2004:149). In contrast, the names applied to Cetacea seem reasonably straightforward and accordingly we discuss the cetacean situation first.

In *Tursiops*, as in other Cetacea, an osteological feature cited widely as the carotid foramen (here, **ventral carotid foramen**) opens medial to the **pterygoid sinus fossa** and tympanoperiotic, and transmits the usually vestigial internal carotid artery into the cranial cavity via the internal **carotid canal of the sphenoid**. No other bony pathway for a carotid vessel has been identified with any confidence in Cetacea.

In *Tursiops* the ventral carotid foramen is the ventral or external opening of the internal carotid canal, which is formed in the posteroventral portion of the **basisphenoid**.

The internal carotid canal courses through the basisphenoid to issue in an anteriorly directed **dorsal carotid foramen** in the cranial surface of the basisphenoid. The name "carotid canal" is not used for the cetacean structure because of possible confusion with the nonhomologous carotid canal of the dog and other carnivores, which is a structure associated with the medial margin of the **tympanic bulla**.

In the adult *Tursiops* the cranial openings of the internal carotid canal are immediately lateral to the ***sella turcica*** (McFarland et al., 1979: fig. 55). Owen (1866b–1868(vol. 2):420) said, in his discussion of the cetacean skull in general, that "the basisphenoid . . . is perforated or grooved by the **entocarotids**."

In spite of the persistent carotid foramina and internal carotid canal, it appears that, at the level of the carotid foramina, the internal carotid artery is generally nonpatent in adult cetaceans; it is functional in fetal specimens but the lumen closes ontogenetically (McFarland et al., 1979:20). Kernan (1918:357) stated that the **internal** (here, dorsal) **carotid foramen** is more apparent in young *Ziphius* specimens. Mead (pers. obs.) has dissected the contents of the dorsal carotid foramen in specimens of *Grampus* (USNM 572267) and *Mesoplodon europaeus* (USNM 571848) and found it to be traversed by a plexus of blood vessels. Walmsley (1938:141) summarized carotid circulation in some odontocetes and mysticetes. See McFarland et al. (1979) for a detailed discussion of cetacean endocranial circulation.

The situation may be more complicated in other Cetacea because in the archaeocete whale *Dorudon atrox* there appear to be no separate internal carotid canal or associated foramina (Uhen, 2004).

Wible and Gaudin (2004:149), in discussing carotid circulation, gave a useful interpretation of the account of Evans (1993), noting that the latter used two terms for the foramen in the braincase, internal carotid foramen, and ***foramen lacerum***. Wible and Gaudin (2004:149) also noted that Evans (1993) used internal carotid foramen in two senses: for the foramen in the braincase and also for the rostral opening of the carotid canal as seen in carnivores.

– carotid notch (*incisura carotica*)

In some mammals the carotid notch occurs in the posterior margin of the **alisphenoid** and forms, with the squamosal, the ***foramen lacerum*** [**jugular foramen**] (Evans and Christensen, 1979:129, S18.25). The carotid notch transmits the internal carotid artery (Evans and Christensen, 1979: S18.25). The carotid notch is also known as the **medial notch** (Evans and Christensen, 1979:129).

In *Tursiops* the carotid notch is more medially located with respect to the alisphenoid, and the **carotid canal of the sphenoid** transmits the internal carotid artery.

– carotid sulcus (*sulcus caroticus*)

The carotid sulcus lies on the cerebral surface of the **basisphenoid** posterior to the **caudal clinoid process**. The carotid sulcus contains the internal carotid artery (Evans and Christensen, 1979:127). The carotid sulcus, in the sense of an endocranial structure in noncetacean mammals, lies on the cerebral surface of the basisphenoid posterior to the caudal clinoid process. The carotid sulcus contains the internal carotid artery (Evans and Christensen, 1979:127). In some armadillos (Wible and Gaudin, 2004) a carotid sulcus is developed more externally in the basicranium, medial to the **tympanic bulla** and visible to ventral view. The carotid sulcus is also known as the carotid groove (McFarland et al., 1979:8). Vesalius (1543:51; Vesalius et al., 1998:131) referred to the carotid groove as the *ductus ucro* and *sinus non adeo commode*.

A carotid sulcus is not developed in *Tursiops* or other delphinids either within the braincase (due to the lack of a cerebral portion of the internal carotid artery) or without, in the basicranium.

– **caudal alar foramen** (*foramen alare caudale*)

The caudal alar foramen is the posterior opening of the **alar canal** (Evans and Christensen, 1979:128; Schaller, 1992:20.4). The alar canal transmits the maxillary artery (Schaller, 1992:20.2).

Alar canals are not developed in delphinids.

– **caudal carotid foramen of the sphenoid bone** (*foramen caroticum caudalis*)

In the dog the **carotid canal of the sphenoid** begins at the caudal carotid foramen in the medial wall of the osseous bulla (Evans and Christensen, 1979:134, 156, 661, 676; not in Schaller, 1992). The caudal carotid foramen is also known as the **posterior carotid foramen** (MacPhee, 1981:59, 60).

The nomenclature associated with the bony path of the carotid foramen in mammals is complex. See discussion under **carotid foramen of the sphenoid.**

In *Tursiops* we recognize the **ventral carotid foramen**, a synonym of the caudal carotid foramen. The ventral carotid foramen lies on the ventral surface of the **basisphenoid** just posteromedial to the oval foramen.

– **caudal clinoid process** (*processus clinoideus caudalis*)

The caudal clinoid process projects anteriorly from the ***dorsum sellae***. Also known as the posterior clinoid process or the middle clinoid process (McFarland et al., 1979:10).

The caudal clinoid process in *Tursiops* and other delphinids is not developed.

* **cerebral hollow** (Anderson, 1879:504) (Figure 22a)

Anderson (1879:504) referred to the smooth dorsal surface of the **alisphenoid** in *Platanista* that houses part of the ventral surface of the brain as the cerebral hollow.

* **cerebral surface of the sphenoid** (*facies cerebralis*) (Figure 22d)

The cerebral surface of the sphenoid is the surface that is part of the cranial cavity (Schaller, 1992:18.18, 24.34).

* **chiasmatic groove** (*sulcus chiasmaticus*) (Figures 22a, 28, 31b)

The chiasmatic groove lies on the cerebral surface of the **basisphenoid** between the anterior edge of the basisphenoid and the ***tuberculum sellae*** (Schaller, 1992:15; Evans and Christensen, 1979:128, 155). The chiasmatic groove is continuous laterally with the **optic foramen**, through which the optic nerve is transmitted to the orbit. The chiasmatic groove contains the optic chiasma (Gray, 1918:147). Feneis (1994:10.4) referred to the *sulcus chiasmaticus* as the *sulcus prechiasmaticus* and Gray (1918:147) referred to it as the chiasmatic groove or the **optic groove.** Vesalius (1543:50; Vesalius et al., 1998:131) referred to the *sulcus chiasmatis* as the *huic sinui cuneiformi ossi inciso, visoriorum nervorum coitus innititur*.

The chiasmatic groove is faintly developed in *Tursiops* and has come to lie on the anterior portion of the basisphenoid.

= **clinoid process** = rostral and caudal clinoid processes

– **craniopharyngeal canal** (*canalis craniopharyngeus*)

The craniopharyngeal canal is the remnant in adults of the pharyngeal diverticulum from which the *pars glandularis* of the hypophysis develops (Evans and Christensen, 1979:128).

There is no record of a craniopharyngeal canal being present in delphinids.

* **dorsal carotid foramen** (Figures 22a, 28, 31b)

The nomenclature associated with the bony path of the **carotid foramen of the sphenoid** in mammals is complex. Here, we recognize the dorsal carotid foramen in *Tursiops* as the internal opening of the internal **carotid canal of the sphenoid**, which marks the entry of the mostly vestigial internal carotid artery into the braincase.

The term "**internal carotid foramen**" should be avoided for Cetacea because of confusion between the general concept of foramina for the internal carotid artery and the foramen opening within the braincase.

See **carotid foramen of the sphenoid.**

= **dorsal optic process**

See **metoptic process.**

* ***dorsum sellae*** (Figures 22a,c, 28)

The *dorsum sellae* is a flattened expanded process on the dorsal surface of the **basisphenoid.** It lies at the posterior border of the ***sella turcica*** (Evans and Christensen, 1979:128, 157).

The *dorsum sellae* in *Tursiops* is reduced to a low transverse ridge of bone that lies medial to the **foramen rotundum.** The *dorsum sellae* is a small conical tubercle in *Kogia* (Schulte, 1917:383).

= **entocarotids** = internal carotid artery

– **epitympanic wing**

MacPhee (1981:53) identified an epitympanic wing as a general term for any outgrowth of a basicranial bone that contributes to the roof of the **tympanic cavity**, such as the epitympanic wing of the sphenoid or the epitympanic wing of the squamosal.

In *Tursiops* and other Cetacea the tympanic cavity is roofed by the periotic so that other skull bones do not have an epitympanic wing.

= **ethmoidal foramen**

See under "Frontal Bone."

– **ethmoidal spine**

The anterior surface of the **basisphenoid** bone, in humans, presents a prominent spine, the ethmoidal spine, for articulation with the **cribriform plate** of the ethmoid (Gray, 1918:147).

The ethmoidal spine is not developed in *Tursiops* and is probably lacking in other Cetacea.

– external carotid artery (Schaller, 1992:246.12)

In the dog the external carotid artery branches off the common carotid artery at the level of the **occipital condyles** (Evans and Christensen, 1979:656, figs. 11–16). The external carotid artery then follows a circuitous path along the basicranium and the **tympanic bulla**. The external carotid artery then bifurcates into the mandibular artery and the maxillary artery. The maxillary artery gives off the middle meningeal artery, which enters the cranial cavity via the ***foramen spinosum*** (Evans and Christensen, 1979:666). The maxillary artery then enters the **alar canal** in the **alisphenoid** bone through the **caudal alar foramen** (Evans and Christensen, 1979:128, 665). No branches are given off from the maxillary artery while it is in the alar canal. The maxillary artery exits the alar canal through the **rostral alar foramen**.

Fraser and Purves (1960:14, 15, 23–26) described in detail the course of the external carotid artery and its branches. The maxillary artery does not enter the alisphenoid in Cetacea (Fraser and Purves, 1960:26) and no alar canals are present.

– false posterior clinoid process

The false posterior clinoid process lies on the dorsal surface of the **basisphenoid** and forms the posterior margin of the **hypophyseal fossa** in *Platanista* (Anderson, 1879:503). The process does not appear to occur in any odontocete other than *Platanista*, although further work is necessary to define what Anderson really meant by this term.

– foramen for the inferior petrosal sinus

The foramen for the inferior (ventral) petrosal sinus in the yellow armadillo lies in the medial portion of a gap between the promontory of the periotic, the **alisphenoid** and **basisphenoid** anteriorly, and the basioccipital medially (McDowell, 1958:125; Wible and Gaudin, 2004:131).

This region has been incorporated into the cranial hiatus (q.v.) in odontocetes and the respective foramina are no longer visible.

– foramen for the lesser petrosal nerve

MacPhee (1981:54) identified the foramen for the lesser petrosal nerve as an aperture in the **tympanic process of the alisphenoid** of some mammals.

The foramen for the lesser petrosal nerve has not been identified in *Tursiops*.

– foramen for the *ramus inferior* of the stapedial artery

MacPhee (1981:54) identified the foramen for the ramus inferior of the stapedial artery as an aperture in the **tympanic process of the alisphenoid** next to the ***foramen ovale***. Sometimes the feature may be an incisure rather than a foramen. The stapedial artery is vestigial in *Tursiops*, and a foramen for the ramus inferior has not been identified.

– foramen for the *ramus superior* of the stapedial artery

See "Periotic Bone."

= foramen for zygomatic nerve = zygomatic foramen

– foramen of Vesalius (*foramen Vesalii*)

The foramen of Vesalius is a variable structure that sometimes occurs in humans medial to the ***foramen ovale***, opposite the root of the pterygoid process, opening near the **scaphoid fossa** and transmitting a small vein from the cavernous sinus (Gray, 1918:150, 192). It is not mentioned in Evans and Christensen, 1979; Schaller, 1992; or Feneis, 1994.

Vesalius (1543:52; Vesalius et al., 1998:131) referred to the *foramen Vesalii* (emissary sphenoidal foramen) as the *verum id in uno calvariae latere raro uisitur, atque adhuc multo rarius in utroque*.

There does not appear to be a structure homologous with the foramen of Vesalius in the cetaceans.

* ***foramen ovale*** (oval foramen) (Figures 22a,b,d, 30, 31a,b)

In humans (Gray, 1918:150, 180, 192; Feneis, 1994:10.34) the *foramen ovale* opens in the wing of the sphenoid (**alisphenoid**) and transmits the mandibular nerve (mandibular branch of the trigeminal nerve) (McFarland et al., 1979:10), the accessory meningeal artery, and the lesser superficial petrosal nerve. In the dog (Evans and Christensen, 1979:128, 914; Schaller, 1992:18.27) the *foramen ovale* is a large opening in the alisphenoid that leads directly through the cranial wall, posterior to the ***foramen rotundum***. Vesalius (1543:51; Vesalius et al., 1998:131) referred to the *foramen ovale* as the *non ad amussim orbiculare, sed circulo respondet utringue modice in longum compresso*.

Many cetaceans, including *Tursiops*, have a single bony foramen that has been called the *foramen ovale*, but in some Cetacea the mandibular nerve is associated with two foramina in the skull. Ridewood (1922) and Fraser and Purves (1960:35) noted that when the mandibular nerve leaves the braincase in living Cetacea, the nerve passes through a notch or foramen in the posterior edge of the alisphenoid, forming the *foramen ovale* as commonly recognized in *Tursiops*. From the notch or foramen in the posterior edge of the alisphenoid, the mandibular nerve may run externally in a groove or canal or "bony infundibulum" (sensu Fraser and Purves, 1960:35), which may be visible ventrally (e.g., *Tursiops*) or may be hidden from ventral view by development of adjacent bones, especially the pterygoid. In those cetaceans with a continuous bony lateral lamina to the **pterygoid sinus fossa** (namely, living Mysticeti, some Odontoceti, and basilosaurid Archaeoceti), the mandibular nerve exits toward the mandible through a second, external, foramen. Ridewood (1922) noted that, for mysticetes, the latter foramen is a "cleft between the squamosal and the pterygoid." Fraser and Purves (1960) termed the latter cleft the "external opening of the *foramen ovale*," and used the term "cranial aperture" (of the infundibulum) for the notch in the alisphenoid.

Fordyce (1994:175) used *foramen ovale* in the sense of Fraser and Purves for the internal notch or foramen in the posterior edge of the alisphenoid, and used the term "foramen 'pseudo-ovale'" for what Fraser and Purves named the "external opening of the *foramen ovale*." Luo and Gingerich (1999:49), conversely, identified the "external opening of the *foramen ovale*" as homologous with the *foramen ovale* in terrestrial mammals, and stated that "the *foramen ovale* of odontocetes has no equivalent in non-cetacean mammals."

For *Tursiops* and other delphinoids, and for other odontocetes that lack a continuous bony lateral lamina to the pterygoid sinus fossa, we use the term "*foramen ovale*" for the structure located along the posteromedial margin of the alisphenoid. The *foramen ovale* is a notch in juveniles but is an enclosed foramen within the alisphenoid in adults; the adult foramen is commonly associated with a laterally directed groove on the ventral surface of the alisphenoid.

For cetaceans that have two foramina, as discussed above, a modification of the terminology of Fraser and Purves (1960) seems best: "cranial *foramen ovale*" for the notch or foramen in the alisphenoid that marks the exit of the mandibular nerve from the braincase, and "external opening of the *foramen ovale*" or "external *foramen ovale*" for the exit of the mandibular nerve toward the mandible.

See Schulte (1917:373, 374, 379, 400) and Fraser and Purves (1960:4, 30, 35, 37, 38, 40–54, 56, 65, 66, 68–71, 73, 85, 87, 89, 100, 132) for a description of the *foramen ovale* in other species of cetaceans.

* ***foramen rotundum*** (round foramen) (Figures 8a, 22a, 28, 30, 31b, 32)

The *foramen rotundum* lies in the lateral portion of the **basisphenoid**, just anterior to the ***foramen ovale*** (Gray, 1918:150, 192; Schulte, 1917:373, 379, 384, 400; Evans and Christensen, 1979:127; Feneis, 1994:10.33). The *foramen rotundum* transmits the maxillary nerve (maxillary branch of the trigeminal nerve) (Flower, 1885:123; Evans and Christensen, 1979:914; McFarland et al., 1979:11; Schaller, 1992:18.24). Vesalius (1543:50; Vesalius et al., 1998:131) referred to the *foramen rotundum* as the *foramen orbiculare*.

The *foramen rotundum* in *Tursiops* lies along the anteromedial border of the **alisphenoid**, in the suture between the alisphenoid and **presphenoid**, and is confluent with the sphenorbital fissure.

There is some confusion about the identity of the *foramen rotundum*. Fraser and Purves (1960:59) implied incorrectly that the *foramen rotundum* is confluent with the **optic foramen**; and Kellogg (1936:110) noted that, in the archaeocete *Zygorhiza kochii*, the maxillary nerve exited the sphenorbital fissure. See **sphenorbital fissure** for more comment.

* ***foramen spinosum*** (spinose foramen) (Figures 22b, 28)

The *foramen spinosum* is a variable structure that sometimes opens into the posterolateral border of the ***foramen ovale***. The *foramen spinosum* serves to transmit the middle meningeal artery (Gray, 1918:150, 180, 192; Evans and Christensen, 1979:128; Schaller, 1992:18.29; Feneis, 1994:10.36). Vesalius (1543:52; Vesalius et al., 1998:131) referred to the *foramen spinosum* as the *rursus ad externum foraminis Q indicati latus, aliud multo minus hoc, and exacte orbiculaltum, in cuneiforme osse cernitur, quo internae jugularis venae portio a soporali abscedens arteria, calvarium subintrat*. Schulte (1917:374) identified a presumed *foramen spinosum* in *Kogia*, and Fordyce (1994) reported a possible *foramen spinosum* in the extinct odontocete *Waipatia*; see comments by Luo and Gingerich (1999:65, char. 54).

What could be the *foramen spinosum* in *Tursiops* lies in the **sphenoparietal suture**, just lateral to the *foramen ovale*. In old adults it lies lateral to the bony prominence that develops in the anteroventral edge of the bony ***tentorium***. The identity of this feature has yet to be confirmed by dissection.

See also **anterior lacerate foramen**, **vascular foramen (associated with the periotic)**, and **foramen for the *ramus superior* of the stapedial artery**.

* **fossa for the postorbital lobe of the pterygoid sinus** (Figures 22b, 30)

The **pterygoid sinus** system is peculiar to cetaceans. The **postorbital lobe of the pterygoid sinus** is a lateral diverticula of the pterygoid sinus that arises between the **falciform process** and the **orbital fissure** (Beauregard, 1894; Fraser and Purves, 1960:8, 25: fig. 8, 70, pl. 44). The fossa for the postorbital lobe of the pterygoid sinus lies over most of the anteroventral surface of the **alisphenoid**, anterior to the ***foramen ovale*** and a bony ridge that extends laterally from the foramen. The fossa passes over the anteroventral surface of the parietal near the suture between the parietal, frontal, and alisphenoid. The fossa for the postorbital lobe of the pterygoid sinus then extends anterolaterally onto the frontal, occupying a fossa that lies between the base of the **postorbital process of the frontal bone** and the crest that extends anterolaterally from the posterior margin of the orbital fissure.

In adult *Tursiops* the anterolateral portion of the fossa can approach a centimeter in depth. This has been referred to as the postorbital smoothed area or recess (Fraser and Purves, 1960:53,54ff.,60) or the post-orbital depression (Fraser and Purves, 1960:54), or the post-orbital recess (Fraser and Purves, 1960:54).

* **frontal border of the sphenoid** (*margo frontalis*) (Figure 22a)

The frontal border of the sphenoid consists of that portion of the sphenoid that borders on (articulates with) the frontal.

In delphinids it is the anterior and lateral surfaces on which the frontal border occurs.

* **frontal groove** (Schulte, 1917:384) (Figure 30)

Schulte (1917:384) used the term "frontal groove" in *Kogia* to indicate a sulcus that was just posterior to a ridge (unnamed) that leads to the **sphenoidal fissure** (**orbital fissure**). That would make the frontal groove the lateral continuation of the **optic canal**.

In *Tursiops* the frontal groove is a major sulcus leading laterally from the optic canal on the **orbitosphenoid**.

* **Glaserian process of the basisphenoid** (Anderson, 1879:510) (Figure 30)

Anderson (1879:510) spoke of the Glaserian process in *Platanista* in this fashion:

> By its inward growth it also contributes to the division of this fissure in the cranial walls into two parts; one the ***foramen lacerum anterius*** . . . the other the *foramen lacerum posterius*, behind the two last-mentioned processes which define its anterior border, its inner margin being formed by a deep concavity lying between the Glaserian process of the basisphenoid and the strong, outward projection of the basioccipital which constitutes the anterior border of the **precondyloid foramen** [**jugular foramen**] of the occipital.

The Glaserian process of the basisphenoid is the projection on the posterolateral part of the basisphenoid that forms the posteromedial border of the **endocranial sulcus / foramen for the vestibulocochlear nerve**.

= greater wing (*ala major*) = alisphenoid

* **groove for mandibular nerve** (*sulcus n. maxillaris*) (Figure 22b)

The mandibular nerve lies in a sulcus on the cranial surface of the sphenoid, leading anteriorly toward the ***foramen ovale***. The mandibular nerve is synonymous with the inferior maxillary nerve (Gray, 1918:893).

* **groove for middle meningeal artery** (*sulcus arteriae meningea mediae*) (Figures 22a, 31a)

The groove for the middle meningeal artery runs obliquely dorsolaterally from the aperture of the oval foramen on the cerebral surface of the **alisphenoid**. The groove continues on the cerebral surface of the squamosal and the cerebral surface of the parietal bones and carries branches of the middle meningeal artery (Evans and Christensen, 1979:129).

In *Tursiops* the groove for the middle meningeal artery runs from a fissure in the ventromedial cerebral surface of the parietal bone laterally along the cerebral surface of the alisphenoid. Branches of the groove for the middle meningeal artery continue dorsolaterally onto the cerebral surface of the parietal and cerebral surface of the frontal bones.

= groove for optic chiasm = chiasmatic groove

* **hypophyseal fossa** (*fossa hypophysialis*) (Figures 22a, 28)

The hypophyseal fossa lies in the center of ***sella turcica*** in the dorsal surface of the **basisphenoid**. The hypophyseal fossa is delimited anteriorly by the ***tuberculum sellae*** and posteriorly by the ***dorsum sellae***. The hypophyseal fossa contains the hypophysis or pituitary gland (Evans and Christensen, 1979:128; Schaller, 1992:18.12; Feneis, 1994:10.8). Gray (1918:147, 190) referred to the hypophyseal fossa as the *fossa hypophyseos*. Vesalius (1543:51; Vesalius et al., 1998:131) referred to the hypophyseal fossa as the *sinus in cuneiforme osse incisus, ac glandulam cotinens, cui ex cerebro defluens pituita instillat*.

The hypophyseal fossa in *Tursiops* and other delphinids is very weakly developed. There exist two **transverse ridges** on the dorsal surface of the basisphenoid in adults, just medial to the ***foramen rotundum***, that represent the *tuberculum sellae* and *dorsum sellae*. The hypophysis is contained within a pocket in the thick dura mater. The position of the hypophysis is immediately posterior to the optic chiasma (McFarland et al., 1979: fig. 44).

* **inferior orbital fissure** (*fissura orbitalis inferior*) (Figures 6f, 28, 30, 31a,b, 32)

The inferior orbital fissure in humans is a cleft between the **greater wing** of the sphenoid (**alisphenoid**) and the **orbital surface of the maxilla**. The inferior orbital fissure transmits the zygomatic nerve plus the infraorbital nerve and infraorbital vessels (Gray, 1918:184; Feneis, 1994:32.24; not in Schaller, 1992). Vesalius (1543:50; Vesalius et al., 1998:131) referred to the inferior orbital fissure as the *praesens foramen omnium quae in oculi sede conspiciuntur*.

In *Tursiops* the inferior orbital fissure lies in the alisphenoid / **orbitosphenoid** suture, just lateral to the **optic canal** and medial to the **superior orbital fissure**. The contents of the inferior orbital fissure in Cetacea have not been positively determined. See comments on **orbital fissure**.

* **infratemporal crest / subtemporal crest** (*crista infratemporalis*) (Figures 2, 10b)

The infratemporal crest in humans is a transverse ridge on the temporal surface of the **alisphenoid** that forms the ventral boundary of the **temporal crest**. The infratemporal crest divides the lateral surface into two portions, the vertically oriented superior portion or temporal portion and the horizontally oriented inferior portion or infratemporal portion (Feneis, 1994:10.32). The superior portion forms a part of the **temporal fossa** and gives rise to the *m. temporalis*. The inferior, together with the infratemporal crest, gives rise to the *m. external pterygoideus* (Gray, 1918:150). The infratemporal crest is also known as the superior orbital ridge (*crista orbitalis superior* Davis, 1964:48).

The infratemporal crest is weakly developed in delphinids. The crest starts out posteriorly as the **sphenoparietal suture**, then deviates dorsally from that suture to follow the posterodorsal margin of the **fossa for the postorbital lobe of the pterygoid sinus**. The crest continues anteriorly and ends at the **postorbital process of the frontal bone**. Schulte (1917:384, 392, 393) described this crest similarly in *Kogia*.

= internal carotid foramen (*foramen caroticum internum*) = dorsal carotid foramen

See **carotid foramen of the sphenoid**.

* **intersphenoidal synchondrosis** (*synchondrosis intersphenoidalis*) (Figure 28)

The **basisphenoid** articulates with the **presphenoid** anteriorly forming the intersphenoidal synchondrosis (*synchondrosis intersphenoidalis*) (Evans and Christensen, 1979:129; Schaller, 1992:78.19). The presphenoid is united to the basisphenoid (postsphenoid) one month before birth in humans (Gray, 1918:153).

Owen (1866a:37) called the intersphenoidal synchondrosis the posterior fissure *Kogia sima*. In *Tursiops* it is open at birth (Figure 28) but is covered externally by the vomer and closes near the time that cranial maturity happens (Dailey and Perrin, 1973:465; Walker, 1981:5).

– lateral lamina of the alisphenoid (Fraser and Purves, 1960:34, 47–49, 51, 52, 56)

Fraser and Purves (1960:47, 48) described the most lateral extent of the **alisphenoid** as the lateral lamina of the alisphenoid in *Monodon*: "The lateral laminae of the alisphenoid, pterygoid and palatine on each side, form a bony bridge extending posteriorly from the anterior border of the **orbital process of the frontal** to the squamosal. The greater part of the ventral portions of these laminae has disappeared leaving a wide, gaping, irregular concavity on the ventrolateral aspect of the skull." Fraser and Purves (1960) illustrated that situation in plate 13 in which they labeled the **lateral laminae of the palatine and pterygoid**. Fraser and Purves (1960:35, 63) also referred to the lateral lamina of the alisphenoid and the lateral wings of the alisphenoid. The lateral part of the alisphenoid is continuous with the lateral laminae of the pterygoid and palatine but is not labeled as such.

Fraser and Purves (1960:56), in their description of the skull of *Lagenorhynchus obscurus*, state that "no part of the lateral lamina of the pterygoid and alisphenoid remains, and of the superior lamina (PT(SL)) only a small plate extends under the orbito-sphenoid." Fraser and Purves illustrated that in plate 40, which shows the same relationship of those bones as their illustration of *Tursiops* (their plates 43 and 44).

In conclusion *Monodon* has a lateral lamina of the alisphenoid but delphinids do not. The increased development of the **orbitosphenoid** has taken the place of the lateral lamina of the alisphenoid in delphinids.

= lateral notch

See **musculotubal canal of the sphenoid bone**.

= lesser wing of the sphenoid (*ala minor*) = orbitosphenoid (Feneis, 1994:10.19; not in Schaller, 1992)

See "Ethmoid Bone."

– *lingula* (*lingula sphenoidalis*)

The *lingula* is a low ridge of bone separating the openings of the **medial notch** and the **musculotubal canal of the sphenoid bone** (Evans and Christensen, 1979:129).

The *lingula* is not developed in delphinids due to the lack of the musculotubal canal.

= mesial lamina of the alisphenoid = alisphenoid

Fraser and Purves (1960:34, 47, 48, 56) defined and illustrated (pl. 13) a **lateral lamina of the alisphenoid** (q.v.) in *Monodon*. They mention a mesial lamina in contradistinction to the lateral lamina only once on page 34. We assume that they meant the rest of the **alisphenoid**. This could conceivably be called the "body of the alisphenoid," but that could generate confusion with the **body of the sphenoid** (**basisphenoid**).

Delphinids do not seem to have developed a lateral lamina of the alisphenoid. The alisphenoid in delphinids is entirely composed of what Fraser and Purves called the "mesial lamina."

– metoptic foramen

According to Wible and Rougier (2000:33), the metoptic foramen is the foramen for the oculomotor nerve.

Tursiops does not have a separate foramen for the oculomotor nerve; the latter issues from the **sphenorbital fissure**.

*** metoptic process** (Figure 31b)

Schulte (1917:378) stated, for *Kogia*: "The **optic foramen** is confluent with the **sphenoidal fissure** in the skull of the calf. In the adult it is on both sides separated by a very tenuous osseous lamella. In view of its late ossification the metoptic process would seem to be on the verge of disappearance." Schulte here appeared to equate the metoptic process with the "tenuous osseous lamella" separating the optic foramen from the **sphenorbital fissure**. Metoptic process sensu Schulte seems to be equivalent to the embryological feature of mammals known as the ***pila metoptica*** (see Wible and Rougier, 2000:49): a bar separating the optic foramen from the **metoptic foramen** or exit for the oculomotor nerve. The term "metoptic process" seems useful for the bony equivalent of the embryological *pila metoptica*. The metoptic process is also known as the superoptic process (Owen, 1866a:40).

Tursiops does have a metoptic process.

– musculotubal canal of the sphenoid bone (*canalis musculotubarius*)

The musculotubal canal is formed by the **lateral notch** of the sphenoid bone with its counterpart on the squamosal bone. This is a short canal that transmits the *m. tensor veli palatini* and the **auditory tube** (**Eustachian tube**) (Evans and Christensen, 1979:129). This squamosal portion in terrestrial mammals has been transferred to the **tympanic bulla** in cetaceans.

See **musculotubal canal of the tympanic bulla**.

– nasopharyngeal surface of the sphenoid (*facies nasopharyngea*)

The nasopharyngeal surface of the sphenoid is the surface that is in contact with the nasopharyngeal cavity.

The vomer and the pterygoid have expanded posteroventrally in delphinids and have covered the ventral surface (nasopharyngeal surface) of the sphenoid.

*** optic canal** (*canalis opticus*) (Figures 28, 30, 31a,b, 32)

The optic canals occur in the **presphenoid** bone and convey the optic nerves (Owen, 1866a:36; Evans and Christensen, 1979:127; Schaller, 1992:20.20; Feneis, 1994:10.20;). Owen (1866a:36) also referred to the optic canal and the optic channel. Gray (1918:147) did not recognize the optic canal, merely the **optic foramen.** Vesalius (1543:50; Vesalius et al., 1998:131) referred to the optic canal as the *qui venulae cum visorio nervo hac excidente paratur*.

In *Tursiops* the anterior portion of the optic canals is formed by the **orbital wings** of the presphenoid (**orbitosphenoid**). The posterior portion of the optic canals is formed by the **metoptic process** (= optic process of the presphenoid) (Fraser and Purves, 1960:51).

*** optic foramen** (*foramen opticum*) (Figure 31a)

The optic foramen lies on the lateral portion of the cranial surface of the **presphenoid.** It is continuous with the **optic canal** and serves to transmit the optic nerve (Owen, 1866a:27, 30, 36; Gray, 1918:147, 151, 190; McFarland et al., 1979:10). Evans and Christensen (1979:128, 150), Schaller (1992:20.20), and Feneis (1994:10.20) did not recognize the optic foramen but referred instead to the optic canal without naming the entrance and exit foramina. Eustachius and Lancisius (1714:93) referred to the optic foramen as the *foramen nervorum opticorum*.

The optic foramen is usually distinct in adult delphinids, separated from the combined **sphenorbital fissure** and ***foramen rotundum*** by a fine **metoptic process**, and is well developed in cetaceans (Schulte, 1917:373, 378, 380, 384, 400; Fraser and Purves, 1960:29, 50, 57, 59, 85, 87).

Fraser and Purves (1960, e.g., many of plates 9–47) used optic foramen in a broader sense for the large bony opening that they elsewhere recognized as a "confluent aperture of the optic foramen, foramen rotundum and **sphenoidal fissure**" (Fraser and Purves, 1960:59, for *Delphinus delphis*). "Optic foramen" should not be used in this broader sense but should be restricted to the bony foramen for the optic nerve.

= optic groove = chiasmatic groove

– optic infundibulum

Fraser and Purves (1960:30, 61, 68–70, 72, 73, 99, 100, 102) used optic infundibulum without definition in text and illustrations. They stated that . . .

> "the paths of the nerves concerned [on the skull base] are restricted [by soft tissues of the **pterygoid sinus** system] to three exits, that associated with the optic infundibulum, that of the infundibulum of the ***foramen ovale*** and that of the 'cranial hiatus' in the vicinity of the periotic" (Fraser and Purves, 1960:30).

In reference to *Delphinus delphis* (1960:59), Fraser and Purves mentioned a "confluent aperture of the **optic foramen**, **foramen rotundum** and **sphenoidal fissure**," but they did not use the name optic infundibulum for any of these bony features. On skulls shown among plates 9–47, Fraser and Purves identified the large bony opening at the **orbit** as the optic foramen (in our terminology, optic foramen separate from confluent **sphenorbital fissure** and foramen rotundum), whereas for specimens shown on plates 9–47 in which air sacs are preserved on the skulls, the exit for orbital soft tissues was identified as optic infundibulum. In summary, optic infundibulum in the sense of Fraser and Purves (1960) apparently comprises the soft-tissue pathway, as constrained by the adjacent pterygoid sinus lobes, for nerves and vessels exiting the optic foramen, foramen rotundum, and orbital (sphenorbital) fissure. Contrary to past uses (e.g., Fordyce, 1994, 2002), the term is not applicable to a bony feature.

* **orbital fissure** (*fissura orbitalis*) (Figure 6f)

The orbital fissure is located lateral to the **body of the sphenoid** in the sutures between the **orbitosphenoid** and **alisphenoids**. The orbital fissure is situated slightly posterolateral to the **optic canals** (Evans and Christensen, 1979:128; Schaller, 1992:14.30; Feneis, 1994:32.23). The orbital fissure contains the ophthalmic nerve (ophthalmic branch of the trigeminal nerve), the oculomotor nerve, the trochlear nerve, and the anastomotic artery. The orbital fissure has also been called the intersphenal fissure (Owen, 1866a:30, 36, 40), the intersphenal fossa (Owen, 1866a:36), or the sphenofrontal fissure (Owen, 1866a:30). Owen (1866a:27) used the term "***foramen lacerum anterius***" as a lapsus calami for "*fissura lacera anterior*." Schulte, 1917:384) referred to this structure as the orbital fissure.

The orbital fissure is only applicable in very young delphinids. The contents of the orbital fissure divide in adults into the **superior orbital fissure** and the **inferior orbital fissure** (q.v.). The exact contents of the superior orbital fissure and the inferior orbital fissure in Cetacea are not well known and it may be that the fissures are not homologous with other species.

The orbital fissure is also known as the **sphenoidal fissure** (Whitney, 1889–1910:[vol. 3]2239; Fraser and Purves, 1960:59) and the **sphenorbital fissure** (Fraser and Purves, 1960:59).

Kellogg (1936:110) stated that, in the archaeocete *Zygorhiza kochii*, "the maxillary division of the trigeminal nerve leaves the cranial cavity through the sphenorbital fissure [orbital fissure]." We interpret Kellogg's statement to mean not that the **foramen rotundum** is synonymous with the sphenorbital fissure [orbital fissure], but that the foramen rotundum, which in other mammals marks the exit for the maxillary nerve, is confluent with the sphenorbital fissure [orbital fissure].

= **orbital infundibulum** (Fordyce, 1994) = optic infundibulum

* **orbital surface of the sphenoid** (*facies orbitalis*) (Figure 8b)

The orbital surface of the sphenoid bone is that part of the sphenoid that borders the **orbit**. We have decided to use the definition of the **orbital part of the frontal** to define the orbit: the orbital part is a segment of a cone with the apex located at the **optic canal** and the base forming the medial border of the infraorbital margin of the frontal bone (Evans and Christensen, 1979:125).

Thus defined, the orbital surface of the sphenoid bone in delphinids is confined to the lateral portion of the optic canals in the **presphenoid** (Schulte, 1917:384).

= **orbital wing**

See **orbitosphenoid of the presphenoid**.

* **orbitosphenoid of the presphenoid** (*ala orbitalis*) (Figures 6b, 8a–e, 28, 31b)

The orbitosphenoids of the presphenoid lie anterior to the **optic canal** (Evans and Christensen, 1979:127).

The **orbitosphenoids** are strongly developed in *Tursiops* and other cetaceans (Schulte, 1917:373, 379, 384, 391, 392, 400). They form the anterior portion of the optic canal. Owen used the terms "orbitosphenoid" (1866a:26, 30, 36, 37, 39) and "orbito-sphenoid" (1866a:27, 28, 30) interchangeably.

– **orbitosphenoidal crest** (*crista orbitosphenoidalis*)

The orbitosphenoidal crest lies dorsal to the **optic canals** on the **presphenoid**. It is formed by the **sphenoidal yoke** (Evans and Christensen, 1979:128).

The orbitosphenoidal crest is not developed in *Tursiops* due to the absence of the sphenoidal yoke.

* **parafalciform fossa [new term]** (Figure 30)

The parafalciform fossa lies on the posterolateral surface of the ventral aspect of the **alisphenoid**, directly dorsal to the **falciform process** in delphinids. The fossa extends posterolaterally from the ***foramen ovale***, from which it is separated by a crest. The fossa terminates on the squamosal immediately dorsal to the attachment of the falciform process. The parafalciform fossa communicates laterally with the squamosal cleft.

* **parietal border of the sphenoid** (*margo parietalis*) (Figure 22a)

The parietal border of the sphenoid consists of that portion of the sphenoid that borders on (articulates with) the parietal.

In delphinids it is the posterior portion of the lateral surface on which the parietal border occurs.

– **petrosal foramen** (*foramen petrosum*)

In humans the petrosal foramen is a variable structure that lies between the ***foramen ovale*** and the ***foramen spinosum***. The petrosal foramen transmits the lesser petrosal nerve (Feneis, 1994:10.37).

There is no evidence of the existence of a petrosal foramen in delphinids.

= ***pila metoptica***

See **metoptic process** (Wible and Rougier, 2000:49).

= **posterior carotid foramen** = caudal carotid foramen of the sphenoid bone

– **posteroexternal process of the alisphenoid**

In the fossil platanistoid *Zarhachis*, a posteroexternal process of the alisphenoid projects back to contact the squamosal near the periotic (Kellogg, 1926:16).

The homology of the posteroexternal process in *Tursiops* is not clear.

* **presphenoid** (*os presphenoidale* [*prae-*]) (Figures 8a,b,d,e, 31b)

The presphenoid lies just posterior to the ethmoid and anterior to the **basisphenoid.** It houses the **optic canals** (Evans and Christensen, 1979:128).

In *Tursiops* the presphenoid is fused to the ethmoid at birth. The presphenoid forms the anterior half of the optic canal. It also consists of the body of the bone immediately posterior to the ***crista galli.*** The **rostral clinoid process** is developed faintly in adults. It is present in all cetaceans (Schulte, 1917:374, 378, 384–386, 390, 392, 394).

= ***processus clinoideus medius*** (McFarland et al., 1979:10) = caudal clinoid process (Gray, 1918:147)

– **pterygoid canal** (*canalis pterygoideus*)

The pterygoid canal leads from the **pterygoid groove** through the pterygosphenoid suture and ends in the posterior part of the **pterygopalatine fossa** (**antorbital fossa**) (Evans and Christensen, 1979:129, 127). The pterygoid canal carries the nerve of the pterygoid canal, which is a parasympathetic branch of the facial nerve destined for the pterygopalatine ganglion, and a variably developed Vidian artery (Evans and Christensen, 1979:145; MacPhee, 1981:61, 47).

The existence of the pterygoid canal does not appear to have been demonstrated in *Tursiops*, but we have seen what may be the pterygoid canal in a fossil cetacean.

– **pterygoid crest** (*crista pterygoidea*)

The pterygoid crest is a dorsal continuation of the **pterygoid process of the sphenoid** and borders the **pterygopalatine fossa** (**antorbital fossa**) (Schaller, 1992:20.6). It is present in horses and pigs and absent in carnivores (Schaller, 1992:20.6). The pterygoid crest serves as the origin of the lateral pterygoid muscle (*m. pterygoideus lateralis*; Schaller, 1992:102.21; Feneis, 1994:80.16). The lateral pterygoid muscle is also known as the external pterygoid muscle (*m. pterygoideus externus*) (Gray, 1918:386; Fraser and Purves, 1960:6, 14, 17–19, 22, 24, 26, 29, 31, 76, 82).

The pterygoid process has been reduced in delphinids to the extent that it is just a small protuberance on the ventral surface of the **basisphenoid.** As a consequence the pterygoid crest has disappeared as a functional element.

– **pterygoid fossa of the sphenoid** (*fossa pterygoidea*)

The pterygoid fossa in humans lies in the lateral surface of the **pterygoid processes of the sphenoid** and contains the origins of the medial pterygoid muscle (*m. pterygoideus medialis*) and *m. tensor veli palatini* (McFarland et al., 1979:11; Feneis, 1994:12.5).

In *Tursiops* the pterygoid process is not differentiated into separate fossae (pterygoid fossa and **scaphoid fossa**).

– **pterygoid groove** (*sulcus n. pterygoidei*)

The pterygoid groove is located in the pterygosphenoid suture. The pterygoid groove begins anterior to the small muscular process of the squamosal bone, leads into the **pterygoid canal,** which ends in the posterior part of the **pterygopalatine fossa** (**antorbital fossa**) (Evans and Christensen, 1979:129, 127). This groove carries the nerve of the pterygoid canal, which is a parasympathetic branch of the facial nerve destined for the pterygopalatine ganglion.

The existence of the pterygoid groove has not been demonstrated in delphinids.

– **pterygoid plate**

The pterygoid plates (lateral pterygoid plate and medial pterygoid plate) in humans consist of ventral projections of the **basisphenoid** that form the **pterygoid process of the sphenoid.**

In *Tursiops* the pterygoid process is not differentiated into lateral and medial pterygoid plates. Fraser and Purves (1960:6, 22, 42, 53, 81–85, 87, 89, 102) used “pterygoid plates” to refer to the **lateral lamina** and **medial lamina of the pterygoid** bone.

= **pterygoid process of the basisphenoid** (e.g., Schaller, 1992:20.1) = alisphenoid

See **alisphenoid.**

* **pterygoid process of the sphenoid** (*processus pterygoideus*) (Figure 22b–d)

The pterygoid process of the sphenoid bone is a ventrolateral process of the **basisphenoid**, consisting of a pair of lateral **pterygoid plates** and medial pterygoid plates, serving as attachments for the pterygoid bones (Evans and Christensen, 1979:129; McFarland et al., 1979:11; Schaller, 1992:20.1; Feneis, 1994:12.1). Vesalius (1543:21, 23, 25) compared the pterygoid process of the sphenoid to the wings of bats (*quos vespertilionum alis comparabimus*, *vespertilionum alarum*, and *processus vespertilionum alis*, respectively).

In *Tursiops* the pterygoid processes of the sphenoid are much reduced and are situated on the ventral surface of the basisphenoid just anterior to the **caudal carotid foramen of the sphenoid bone.**

– **rostral alar foramen** (*foramen alare rostrale*)

The rostral alar foramen is the anterior opening of the **alar canal** (Evans and Christensen, 1979:128) and transmits the maxillary nerve (maxillary branch of the trigeminal nerve) (Evans and Christensen, 1979:914).

Alar canals are not developed in *Tursiops.*

– **rostral clinoid process** (*processus clinoideus rostralis*)

The rostral clinoid process projects posteriorly from the posterolateral margin of the **presphenoid,** over the **orbital fissure** (Evans and Christensen, 1979:128, 157). The rostral clinoid process is also known as the anterior clinoid process (McFarland et al., 1979:7).

Tursiops does not develop a rostral clinoid process.

– **scaphoid fossa** (*fossa scaphoidea*)

The scaphoid fossa is a small oval depression that lies above the **pterygoid fossa of the sphenoid** on the **basisphenoid.** It is the origin of the *m. tensor veli palatini.*

Neither the pterygoid fossa nor the scaphoid fossa are developed in *Tursiops.*

* ***sella turcica*** (Figures 22a, 28)

The *sella turcica* lies on the dorsal part of the **basisphenoid** and consists of the ***tuberculum sellae***, the **hypophyseal fossa,** and the ***dorsum sellae*** (Gray, 1918:147, 190; Evans and Christensen, 1979:128, 155, 605; Schaller, 1992:18.11; Feneis, 1994:10.5.). The *sella turcica* is also known as the Turk's saddle. Eustachius and Lancisius (1714:112) referred to it as the *sella turcica*.

Delphinids have a poorly developed *sella turcica*.

= **small alar foramen** (*foramen alare parvum*) = zygomatic foramen

= **small wing** = orbitosphenoid

– **sphenoethmoidal suture** (*sutura sphenoethmoidalis*)

The sphenoethmoidal suture lies between the **presphenoid** and the **cribriform plate** of the ethmoid (Gray, 1918:190; Evans and Christensen, 1979:129, 138; Schaller, 1992:76.10; Feneis, 1994:54.7). Vesalius (1543:51; Vesalius et al., 1998:131) referred to the sphenoethmoidal suture of the anterior cranial fossa as the *quae durae cerebri membranae hic firmadae extruitur*.

The sphenoethmoidal suture closes in utero and no trace of it is evident in *Tursiops* neonates.

* **sphenofrontal suture** (*sutura sphenofrontalis*) (Figures 28, 30, 31b)

The sphenofrontal suture is formed by the joining of the frontal to the sphenoid (**alisphenoid**) (Gray, 1918:182, 190; Evans and Christensen, 1979:126, 129; Schaller, 1992:76.9; Feneis, 1994:54.6). Vesalius (1543:23) referred to the sphenofrontal suture as merely the *sutura*.

In delphinids the sphenofrontal suture is formed on the frontal border of the alisphenoid (Figure 22a).

– **sphenoidal concha** (*concha sphenoidalis*)

The sphenoidal conchae are located at the anteroventral portion of the sphenoid bone. The **sphenoidal sinus** communicates with the nasal cavity via an aperture in the anterior wall of the conchae.

Sphenoidal conchae and the paranasal sinus system are not developed in cetaceans (Fraser and Purves, 1960:5, 75).

– **sphenoidal crest** (*crista sphenoidalis*)

The sphenoidal crest lies in the midline of the anterior surface of the sphenoid (**presphenoid**) in humans and articulates with the **perpendicular plate** of the ethmoid bone and forms part of the **nasal septum** (Gray, 1918:149).

The appearance of the sphenoidal crest in delphinids is moot. The presphenoid is already fused with the ethmoid in neonatal *Tursiops*, thereby obliterating any trace of the sphenoidal crest.

= **sphenoidal fissure** = sphenorbital fissure

Fraser and Purves (1960:59) said that in *Delphinus delphis*, "the confluent aperture of the **optic foramen, foramen rotundum,** and sphenoidal fissure was very much enlarged by resorption of the boundary margins of the **orbitosphenoid** and **alisphenoid**." This use of sphenoidal fissure is equivalent to sphenorbital fissure or **orbital fissure** sensu Wible and Gaudin (2004:165).

– **sphenoidal fossae**

The sphenoidal fossa lies on the anteroventral surface of the **presphenoid** at the junction of the **orbitosphenoids** and the body of the presphenoid. It houses the posteroventral portions of the **ethmoturbinates** (Evans and Christensen, 1979:128, 158). The sphenoidal fossae are formed by a longitudinal septum that divides the hollow anterior portion of the presphenoid (Evans and Christensen, 1979:128).

The sphenoidal fossa is not developed in odontocetes due to the reduction in structures associated with olfaction.

= **sphenoidal incisure**

See "Vomer."

– **sphenoidal rostrum** (*rostrum sphenoidale*)

The sphenoidal rostrum is a small median tubercle that projects from the anterior border of the **sphenoidal yoke** (Evans and Christensen, 1979:128).

The sphenoidal rostrum is not developed in *Tursiops* due to the absence of the sphenoidal yoke.

– **sphenoidal sinus** (*sinus sphenoidalis*)

The sphenoidal sinus lies within the **presphenoid** bone in dogs and is largely occupied by the fourth endoturbinate (Evans and Christensen, 1979:159; Schaller, 1992:20.10, 180.24). The extent of the sphenoidal sinus is variable in other animals. It also occupies the **basisphenoid** in pigs (Schaller, 1992:20.10).

The sphenoidal sinus is a paranasal sinus and as such is not developed in cetaceans (Fraser and Purves, 1960:5, 75).

– **sphenoidal sinus septum** (*septum sinuum sphenoidalium*)

The sphenoidal sinus septum separates the right and left paired sphenoidal sinuses (Schaller, 1992:20.11, 20.23, 180.25; Feneis, 1994:10.6).

The **sphenoidal sinus** is not developed in cetaceans.

* **sphenoidal spine** (*spina angularis*) (Figure 22b–d)

The sphenoidal spine in humans is a projection off the posterolateral part of the **alisphenoids** that fits into the angle between the squamosal and **petrosal** (Gray, 1918:150).

In *Tursiops* the sphenoidal spine has been modified into a rather blunt process that articulates with the squamosal and lies dorsal to the **falciform process** of the squamosal bone and ventral to the parietal bone.

– **sphenoidal yoke** (*jugum sphenoidale*)

The sphenoidal yoke is formed by the fusion of the **orbital wings** and forms the base of the anterior cranial fossae (Evans and Christensen, 1979:128). The sphenoidal yoke in delphinids is not developed due to the lack of fusion of the orbital wings.

– **sphenoid sinus aperture** (*apertura sinus sphenoidalis*)

The sphenoid sinus aperture is the opening into the **sphenoidal sinus** (Schaller, 1992:20.24, 20.22, 180.26).

The sphenoidal sinus is a paranasal sinus and is not developed in cetaceans (Fraser and Purves, 1960:5, 75).

= **sphenomaxillary fissure** = alar canal (Gray, 1918:184)

= **sphenomaxillary fossa** = pterygopalatine fossa = antorbital fossa

See "Maxilla."

– **sphenomaxillary suture** (*sutura sphenomaxillaris*)

The sphenomaxillary suture lies between the **pterygoid process of the basisphenoid** (**alisphenoid**) and the maxilla in some mammals (e.g., the pig; Schaller, 1992:76.34) but in other mammals (e.g., the dog; Evans and Christensen, 1979:129) the basisphenoid does not contact the maxilla. In humans it is variable (Gray, 1918:183; Feneis, 1994:54.24), depending on the development of the basisphenoid and maxilla around the **sphenomaxillary fissure**. Vesalius (1543:23) referred to the sphenomaxillary suture merely as the *sutura*.

In delphinids, including *Tursiops*, the maxilla does not contact the sphenoid.

* **sphenooccipital synchondrosis** (*synchondrosis spenooccipitalis*) (Figures 6f, 28)

The sphenooccipital synchondrosis is the cartilaginous joint (synchondrosis) between the **basisphenoid** and the basioccipital bones (Evans and Christensen, 1979:45, 51, 129; Schaller, 1992:78.16; Feneis, 1994:56.2). The sphenooccipital synchondrosis is also known as the occipitosphenoid synchondrosis (Gray, 1918:284). Vesalius (1543:23) referred to the sphenooccipital synchondrosis as the *transversam lineam* or merely the *linea*.

Cetacea have a normal sphenooccipital synchondrosis, which fuses with age. In external views of adult *Tursiops* the sphenooccipital synchondrosis is hidden by the posterior part of the vomer.

– **sphenoparietal suture** (*sutura sphenoparietalis*) (Gray, 1918: 182)

The sphenoparietal suture is the suture between the **greater wing** of the sphenoid (**alisphenoid**) and the parietal bone (Feneis, 1994:54.9). The point corresponding with the posterior end of the sphenoparietal suture is named the *pterion*. (Evans and Christensen, 1979:129; Schaller, 1992:76.12).

In *Tursiops* the sphenoparietal suture lies at the medial surface of the **temporal fossa**, where the alisphenoid meets the parietal (Fraser and Purves, 1960:61, 63).

= **sphenorbital fissure** (Kellogg, 1936) = *foramen rotundum*

* **sphenosquamosal suture** (*sutura sphenosquamosa*) (Figure 31b)

The sphenosquamosal suture lies between the **alisphenoid** (or **presphenoid**) and the squamosal in mammals (Gray, 1918:182; Evans and Christensen, 1979:129; Schaller, 1992:76.11; Feneis, 1994:54.8). Vesalius (1543:23) referred to the sphenosquamosal suture as merely the *sutura*. Fraser and Purves (1960:39) referred to the sphenosquamosal suture as the alisphenoid–**squamosal suture** in reference to the pterygoid in *Caperea*.

In delphinids the alisphenoid contacts the squamosal and forms a sphenosquamosal suture just anterior to the **falciform process**. This suture lies on the sphenoidal margin of the squamosal (Figures 30, 31b).

– **sphenozygomatic suture** (*sutura sphenozygomatica*)

The sphenoid does not contact the zygomatic in most mammals, including the dog, cow, horse and pig (Evans and Christensen, 1979:129; Schaller, 1992:76). In humans the zygomatic (jugal) has expanded and contacts the **alisphenoid** in the **orbit** (Gray, 1918:182; Feneis, 1994:54.23). Vesalius (1543:23) referred to the sphenozygomatic suture as merely the *sutura*.

In delphinids the zygomatic (jugal) does not contact the alisphenoid.

= ***spina ossis sphenoidalis*** = sphenoidal spine

– **squamosal border of the sphenoid** (*margo squamosus*)

The squamosal border of the sphenoid consists of that portion of the **alisphenoid** that borders on (articulates with) the squamosal.

Tursiops has a normal mammalian squamosal border.

– **sulci for intracranial extensions of spinal meningeal arteries**

See "Exoccipital Bone."

= ***sulcus n. canalis pterygoidei*** = pterygoid groove

– ***sulcus tubae auditivae***

The *sulcus tubae auditivae* is a groove in the lateral portion of the **alisphenoid** where it articulates by a synchondrosis with the **petrosal**. The *sulcus tubae auditivae* holds the cartilaginous part of the **auditory tube** (**Eustachian tube**) (Gray, 1918: 150).

The auditory tube has moved ventrally with the auditory bulla and does not contact the alisphenoid in delphinids, hence the *sulcus tubae auditivae* is not developed.

* **superior orbital fissure** (*fissura orbitalis superior*) (Figures 28, 30, 31a,b, 32)

The superior orbital fissure in humans is located in the posterior part of the lateral wall of the **orbit** between the greater and lesser **wings of the sphenoid**. It transmits the ophthalmic, oculomotor, trochlear, and abducens nerves as well as the superior ophthalmic vein (McFarland et al., 1979:11; Feneis, 1994:32.23). Vesalius (1543:50; Vesalius et al., 1998:131) referred to the superior orbital fissure as the *praesens foramen caelatur gratia secundi* [sic; third] *paris nervorum cerebri*.

In *Tursiops* the superior orbital fissure is located in the lateral part of the **presphenoid–basisphenoid** suture just lateral to the **inferior orbital fissure**. It is separated from the **optic canal** by the **metoptic process**. The contents of the superior orbital fissure in Cetacea have not been positively determined. See comments on **orbital fissure**.

– **temporal surface of the sphenoid** (*facies temporalis*)

The temporal surface of the sphenoid bone is that surface in contact with the temporal bone.

The temporal surface is not present in delphinids because the tympanic and periotic no longer contact the sphenoid.

= **temporal wing** = alisphenoid

– **transverse canal foramen**

Wible and Gaudin (2004:153, 166) identified the transverse canal foramen of the **basisphenoid** or alisphenoid basicranium as associated with the ***foramen ovale*** in a common depression on the **alisphenoid** of the [yellow] armadillo. In marsupials (e.g., Wible, 2003, *Monodelphis*), the transverse canal foramen opens laterally in the basisphenoid, anterior to the **carotid foramen of the sphenoid**.

Tursiops does not appear to have a transverse canal foramen in the alisphenoid or adjacent basisphenoid.

The transverse canal foramen of the basisphenoid or alisphenoid should not be confused with the **transverse canal** (q.v.) at the **internal occipital protuberance** in mature *Tursiops*, or with the transverse canal of the vertebrae.

* ***tuberculum sellae*** (Figures 22a, 28)

The *tuberculum sellae* is a ridge of bone formed at the juncture of the **presphenoid** and **basisphenoid**. It serves as the anterior limit for the **hypophyseal fossa** (Evans and Christensen, 1979:128).

In *Tursiops* the *tuberculum sellae* has moved posteriorly and occupies a position about 1 cm posterior to the presphenoid–basisphenoid suture (McFarland et al., 1979: fig. 44, related the pituitary to the optic chiasma).

– **tympanic process of the alisphenoid** (Wible and Gaudin, 2004: 131)

Wible and Gaudin (2004:131) noted that in the yellow armadillo, the tympanic process of the alisphenoid is a low posterior ridge on the **alisphenoid**, which, as it runs from the posterolateral base of the **entopterygoid crest** to the **entoglenoid process** of the squamosal, abuts the **tympanic bulla**.

In *Tursiops* the alisphenoid does not abut the tympanic **bulla**, and a **tympanic process** is absent.

– **vaginal process** (*processus vaginalis*)

The vaginal process in humans consists of a thin lamina of the medial **pterygoid plate** that articulates with the sphenoid process of the palatine and the ala of the vomer.

The **pterygoid process of the sphenoid** of *Tursiops* is not differentiated into medial and lateral pterygoid plates, and, as such, a vaginal process is not developed.

* **ventral carotid foramen** (Figures 22b,c, 30)

The nomenclature associated with the bony path of the carotid foramen in mammals is complex (see discussion under **carotid foramen of the sphenoid**). Here, we recognize the ventral carotid foramen in *Tursiops* as the external or ventral opening of the **carotid canal of the sphenoid**, which marks the path of the mostly vestigial internal carotid of Cetacea into the braincase.

The term "external carotid foramen" should be avoided for Cetacea because of possible confusion with the **external carotid artery** of other mammals.

= **wings of the sphenoid** = alisphenoid

– **zygomatic border of the sphenoid** (*margo zygomaticus*)

The zygomatic border of the sphenoid consists of that portion of the sphenoid that borders on (articulates with) the zygomatic (Gray, 1918:148).

In delphinids the zygomatic border does not occur because the sphenoid does not contact the zygomatic (jugal).

– **zygomatic foramen**

The zygomatic foramen is a variable feature that lies on the anterodorsal surface of the **basisphenoid**. The zygomatic foramen lies on a ridge of bone between the **orbital fissure** and the **rostral alar foramen**. The zygomatic nerve passes through the zygomatic foramen on its route to the **orbit** (Evans and Christensen, 1979:127, 129, 914). The zygomatic foramen is also known as the *foramen alare parvum* (Evans and Christensen, 1979:128).

The zygomatic foramen has not been reported in delphinids. Evidently the zygomatic branch of the maxillary nerve leaves the main root of the nerve in the orbit. The zygomatic nerve supplies the eyelid and some of the surrounding skin in most mammals (Evans and Christensen, 1979:916).

SQUAMOSAL BONE

Os Temporale / Pars Squamosa

FIGURES 1, 3–5, 6B,C, **23**, 29–32

There is no single temporal bone in Cetacea. See discussions of the temporal bone in other mammals (Gray, 1918:138; Evans and Christensen, 1979:129; Schaller, 1992:22.1; Feneis, 1994:12.14). Vesalius (1543:21–23) referred to the temporal as the *temporis os*. Temporal elements occur separately as ossified squamosal, periotic, tympanic bulla, and associated middle ear ossicles. Accordingly, we treat these elements separately. Some conventions follow widespread previous use in the cetacean literature; we use the terms "tympanic bulla" to refer to the ectotympanic bulla, and "periotic" for the periotic (or petrosal) bone. See ectotympanic part, below.

The squamosal bone consists of the squamosal plate, which extends dorsally over the parietal (Evans and Christensen, 1979:134), and the glenoid process, which includes the zygomatic process, mandibular fossa (glenoid fossa), retroarticular or postglenoid process, and ear region.

The squamosal (squamous part of the temporal) in delphinids has, in addition to the anatomical relationships in terrestrial mammals, developed a large ventral process, the falciform process. See Schulte (1917:373, 375, 380–384, 392, 394) and Fraser and Purves (1960:9, 19, 34, 35, 37–39, 41–45, 47, 48, 55, 57, 62, 77, 79, 80, 85, 115, 132, 135, 136).

– **anterior angle of the tympanosquamosal recess** (Fraser and Purves, 1960:45, 46)

Fraser and Purves (1960:45, 46) mentioned the anterior angle in the context of the anterior extremity of the **tympanosquamosal recess**, which they viewed as a triangular structure.

* **anterior meatal crest** (Figure 23c)

The anterior meatal crest lies posteromedial to the **postglenoid** or **retroarticular process** (Fordyce, 1994:156) and forms the anterior boundary of the **external acoustic meatus** sensu lato. Owen, when describing *Orcaella* (1866a:28, pl. 9: fig. 3(8), stated that the "mastoid part terminates below in a rough, flattened, triangular surface (figs. 3, 8), 5", 7''' [5 inches, 7 lines] in diameter, which is divided from the zygomatic or articular process of the squamosal (g) by a deep fissure." (The lines symbol, ''', is an obsolete shorthand for measurement in lines—as in feet, inches, and lines; one line (1''') represents one-tenth or one-twelfth of an inch.) We feel that the "mastoid part" of Owen is synonymous with the anterior meatal crest. Owen (1866a:40, pl. 13: fig. 2, #8) reiterated this in his description of *Kogia sima*.

– **anterior process of the tympanosquamosal recess** (Fraser and Purves, 1960:47)

Fraser and Purves (1960:47) mentioned the anterior process of the **tympanosquamosal recess** in passing in their discussion of *Inia*: "The development of the tympano-squamosal recess (TSQR) shows a considerable advance on *Inia*, its anterior process projecting halfway along the mesial border of the **zygomatic process of the squamosal** (SQ)." We interpret "anterior" as a general orientation term, not a specific term of a process.

See **anterior angle of the tympanosquamosal recess.**

The **tympanosquamosal recess** of delphinids does not have an anterior process.

= **articular surface of the squamosal** (*facies articularis*)

See **mandibular fossa.**

– **articular tubercle** (*tuberculum articulare*)

The articular tubercle is a rounded eminence anterior to the **mandibular fossa** on the **zygomatic process of the squamosal** (Schaller, 1992:24.29; Feneis, 1994:16.20).

Delphinids do not develop an articular tubercle.

= **dactyloid process** (Kellogg, 1928:62) = falciform process

– **entoglenoid process**

MacPhee (1981:52) followed McDowell (1958) in recognizing this feature in eutherians as a descending process of the squamosal that may anterolaterally bound the tympanic region, but is distinct from the **postglenoid** or **retroarticular process.**

Luo (1998:287) mentioned the presence of an entoglenoid process on the squamosal of archaeocetes, and Luo and Gingerich (1999: fig. 1) indicated that the posterior **falciform process** forms part of the entoglenoid region in archaeocetes. Geisler and Sanders (2003:48, 54) equated falciform process with entoglenoid process, and used both terms.

If the entoglenoid process and falciform process are homologous, then *Tursiops* has an entoglenoid process. The term "falciform process" (q.v.) has been used widely by cetologists for the feature that Luo and Gingerich (1999) termed the entoglenoid process, and we continue to use falciform process here.

* **falciform process** (*processus falciformis*) (Figures 6f, 23a–e, 29, 30)

The falciform process of the squamosal bone (van Kampen, 1905, cited by Ridewood, 1922:262, fig. 15) is a unique development in Cetacea. It was first recognized by Beauregard in 1894 (Fraser and Purves, 1960:8). In delphinids it arises from the median dorsal border of the **tympanosquamosal recess** (which houses the **middle sinus**; Fraser and Purves, 1960:8, 9, 13, 14, 33–35, 37–41, 43–61, 65–71, 73, 85, 87, 89) and extends medially to lie just ventral to the ***foramen ovale***. The falciform process is crescentic, concave posteriorly. The distal (medial) end of the falciform process abuts the anterior end of the **tympanic bulla** at the **anterodorsal crest** anterior to the **accessory ossicle** (viz., with the dorsal lateral edge of the **semicanal for the auditory tube** of the tympanic **bulla**). The falciform process fits into the semicanal for the **auditory tube** (confirmed on USNM 504420).

Luo (1998:287) and Luo and Gingerich (1999:32; tbl. 3, #16a) noted that in some archaeocetes the anterior process (= ***processus tubarius* of the bulla**) of the tympanic bulla contacts the **squamosal bullar process**. We presume that the squamosal bullar process is the falciform process.

The falciform process in the ziphiids becomes long and thick and has been termed the **dactyloid process** by Kellogg (1928:62).

See also **entoglenoid process.**

Schulte (1917:369) described the falciform process of the frontal in *Kogia*. It is a long slender process that lies dorsally between the maxilla and the **supraoccipital.** It is homologous with the **external surface of the frontal** bone that lies between the maxilla and the parietal in *Tursiops*.

– **foramina for *rami temporales***

Wible and Gaudin (2004:154) used the term "foramina for *rami temporales*" for openings in the squamosal or parietal of armadillos that transmit the *rami temporales* of the stapedial artery and accompanying veins. They reported that such foramina are absent in the dog.

Tursiops has no significant supply from a stapedial artery (see **sulcus for the internal carotid artery**), and foramina for *rami temporales* are not identifiable.

– ***foveola suprameatica*** [*suprameatalis*]

In *Nomina Anatomica* (IANC, 1883:A14), under *processus zygomaticus* of *pars squamosa* of *os temporale*, there is an entry for *foveola suprameatica* [*suprameatalis*]. It is not in Whitney (1889–1910), Gray (1918), Sisson and Grossman (1953), Evans and Christensen (1979), Schaller (1992), or Feneis (1994). *Foveola suprameatica* translates as "small depressions above the (auditory) meatus."

See **suprameatal fossa.**

= **glenoid cavity** (Fraser and Purves, 1960:23,60)

See **mandibular fossa.**

= **glenoid fossa** = glenoid surface

See **mandibular fossa.**

– **glenoid plate**

The glenoid plate extends from the **postglenoid process** of the squamosal bone to the **falciform process** of the squamosal in *Platanista* (Anderson, 1879:513). It forms the lateral border of the **tympanosquamosal recess.**

The glenoid plate occurs in delphinids.

* **glenoid process** (Figures 23a–e, 29)

The glenoid process is a strong quadrilateral mass of bone attached medially to the **squamosal plate** (Kernan, 1918:377). The glenoid process bears the **zygomatic process, mandibular fossa,** and the **postglenoid** or **retroarticular process.**

Delphinids have a well developed glenoid process (Fraser and Purves, 1960:38, 39, 44).

= **glenoid surface** = glenoid fossa

See **mandibular fossa.**

– **groove for middle temporal artery** (*sulcus a. temporalis mediae*)

The groove for the middle temporal artery lies on the dorsomedial portion of the external surface of the squamosal in humans (Feneis, 1994:16.16). The groove for the middle temporal artery does not seem to appear in other animals (equids, bovids, caprids, suids, and canids) (Sisson and Grossman, 1953).

The groove for the middle temporal artery is not present in delphinids.

* **mandibular fossa** (*fossa mandibularis*) (Figures 2, 23b–d, 29)

The mandibular fossa lies on the ventrolateral portion of the squamous part of the temporal and receives the **condyloid process** of the mandible (Gray, 1918:140, 180, 183; Evans and Christensen, 1979:134; Schaller, 1992:24.27; Feneis, 1994:16.20). The mandibular fossa is also known as the **glenoid fossa** (Schulte, 1917:393) or the **glenoid cavity**, **glenoid surface**, mandibulo-articular surface, **articular surface of the squamosal**, articular cavity, or articular process of the squamosal (Owen, 1866a:26, 29, 40, 43; pl. 9: fig. 3(g); Fraser and Purves, 1960:9, 23, 41–43, 45, 49, 54, 56, 60, 67, 69, 71, 73, 77). Eustachius and Lancisius (1714:105) referred to the mandibular fossa as the *sinus ossis ad excipiendum posterius caput madibulae inferioris*.

The mandibular fossa in delphinids lies on the ventrolateral portion of the squamosal and receives the condyloid process of the mandible, forming the **temporomandibular joint.**

– **mastoid diapophyses** (Fraser and Purves, 1960)

Owen (1866b–1868(vol. 2):420) described the parietal in a skull of a fetal *Physeter*, using terms that implied serial homology of skull components with vertebrae: “the lower angles are confluent with the diapophyses, called ‘mastoids,’ which here, as in other Cetacea, are distinct from the **petrosals**, and chiefly support the squamosals . . . .”

It is not clear what Owen meant by this use of the name mastoid. We cannot apply it in a useful way to *Tursiops*.

– **mastoid portion of the squamosal** (Fraser and Purves, 1960)

Owen (1866a:29), in his description of the skull of *Orcaella*, stated:

> The rough posterior tract articulating with the parietal (7) and exoccipital (2), and contributing to the outer wall of the **otocrane** (fig. 3, *or*), I consider to be the “mastoid” confluent with the squamosal, together forming the bone which should be termed “*squamo-mastoid*.” The mastoid part terminates below in a rough, flattened, triangular surface (fig. 3, 8), 5" 7‴ [5 inches, 7 lines] in diameter, which is divided from the zygomatic or articular process of the squamosal (g) by a deep fissure. On the inner side of the base or back part of the mastoid, in the line of its suture with the parietal, is the (stylomastoid?) fossa.

Fraser and Purves (1960:77) identified in *Caperea* a “portion of the squamosal immediately anterior to the ***pars mastoidea***, of a rugose and laminated appearance . . .”, which they interpreted as a mastoid component of tympanoperiotic fused to the squamosal posterodorsal to the **external auditory meatus**. This led to the suggestion that part of the mastoid process or **posterior process of the periotic bone** has lost its usual connection with the periotic, and has become fused to the squamosal (Fraser and Purves, 1960:5, 9, 34, 35, 37, 40–44, 47, 58, 77, 78: fig. 13, 79, 80; Purves, 1966:340, Kasuya, 1973: fig. x). Oelschläger (1986a: fig. 6) provided a possible interpretation of mastoid–squamosal fusion in *Tursiops*.

Our studies of fetal and neonate skulls of modern species of Odontoceti and Mysticeti, and of skulls of fossil archaic Cetacea (Archaeoceti, Odontoceti, Mysticeti), provide no evidence that any mastoid component of the periotic fuses with the squamosal. The mastoid process of the periotic does fuse with the **posterior process of the tympanic bulla** (q.v.) in mysticetes but not in *Tursiops*. The mastoid portion of the squamosal bone in the sense of Fraser and Purves (1960:77) is identified here as the **posttympanic process** of the squamosal (q.v.).

See **posterior process of the tympanic bulla** for further discussion.

= **medial sac** (Beauregard, 1894; Fraser and Purves, 1960:8–10)
= middle sinus

= **medial sinus** (Beauregard, 1894; Fraser and Purves, 1960:14)
= middle sinus

– **middle sinus** (Fraser and Purves, 1960:63–65)

The middle sinus is located in the **tympanosquamosal recess.** The middle sinus originates as a lateral projection from the **tympanic cavity** via the **epitympanic hiatus** (Fraser and Purves, 1960:1, 63–65, 67–69, 71–74, 76).

= **notch for external auditory meatus** = groove for external auditory meatus (Kernan, 1918:359) = retroarticular notch

– **occipital groove**

The occipital groove in humans is medial to the origin of the digastric muscle (Gray 1918:179), on the posteroventral aspect of the external surface of the temporal. In the yellow armadillo (Wible and Gaudin, 2004:138) the groove is on the mastoid surface near the **paroccipital process**.

Due to the separation of the periotic from the skull in odontocetes, the mastoid process no longer contacts the squamosal and the occipital groove is absent.

* **occipital margin of the temporal** (*margo occipitalis*) (Figure 23c)

The occipital margin of the temporal bone is that portion of the squamosal that abuts the occipital.

The occipital margin in delphinids consists of the posterolateral portion of the squamous part of the temporal.

* **occipital process** (*processus occipitalis*) (Figure 23c)

The occipital process is the most posterior extension of the squamosal that fits between the parietal and the occipital (Schaller, 1992:24.21; not in Feneis, 1994).

The occipital process on the delphinid squamosal is the most posterior projection of that part of the temporal that overrides the parietal in a squamose suture.

– **occipitosquamosal suture** (*sutura occiptosquamosa*) (Schaller, 1992:76.6)

The occipitosquamosal suture lies between the occipital and the squamosal bone (Feneis, 1994:76.6). In adult delphinids it runs from the ventral portion of the **temporal crest** anteriorly and then turns ventrally to follow the **retroarticular notch**. Fraser and Purves (1960:77) have named the portion of the occipitosquamosal suture that lies between the **paroccipital process** and the squamosal the "squamoparoccipital suture."

* **parietal margin of the temporal** (*margo parietalis*) (Figure 23a,c)

The parietal margin of the temporal bone is that portion of the temporal that abuts the parietal.

The parietal margin in delphinids consists of the dorsal portion of the squamous part of the temporal.

* **parietal notch** (*incisura parietalis*) (Figures 3, 23c)

The parietal notch lies on the dorsal margin of the external surface of the squamosal in the posteroventral part of the **temporal fossa** in humans where the squamosal, **petrosal**, and parietal bones meet (Feneis, 1994:16.12; not in Schaller, 1992).

In delphinids the periotic no longer contacts the parietal. Instead its place has been taken by the exoccipital. The parietal notch, as a feature of the external surface of the cranium in delphinids, consists of that place in the posteroventral part of the temporal fossa where the margins of the squamosal, parietal, and exoccipital meet.

= **parietal plate** (Anderson, 1879:514) = *pars squamosa*

* **periotic fossa** (Figure 2, 28, 30)

The periotic fossa is that area on the squamosal, exoccipital, and parietal that lies dorsal to the periotic and provides a fossa into which the periotic fits (Fordyce, 1994:156).

In delphinids the anterior part of the periotic fossa bounds the **alisphenoid** and is largely occupied by the **posterior lacerate foramen** and the **jugular foramen**.

= **petro-pterygo-tympanic plate** = falciform process

The petro-pterygo-tympanic plate was used by Anderson (1879:513) for the medial process of the squamosal that contacted the **anterior process of the periotic bone** and the reduced lateral wall of the pterygoid. This is an extremely modified **falciform process**.

* **posterior meatal crest** (Figure 9b)

The posterior meatal crest lies at the posterior margin of the **external acoustic meatus** (Fordyce, 1994:158, 156).

In *Tursiops* the posterior meatal crest is no longer identifiable because of changes around the external acoustic **meatus**.

= **postglenoid border** (Anderson, 1879:513) = retroarticular or postglenoid process

– **postglenoid foramen**

The postglenoid or retroarticular foramen in the dog lies on the lateral surface of the squamous part of the temporal just posterior to the **retroarticular process** (Evans and Christensen, 1979:134, 152, 153; Schaller, 1992:24.31). The retroarticular foramen contains the retroarticular vein, which originates from the temporal sinus and drains into the maxillary vein (Evans and Christensen, 1979:793; Schaller, 1992:362.3). The canal that opens as the retroarticular foramen is the temporal meatus (*meatus temporalis*) (Schaller, 1992:24.31, 10.12).

In the literature on mammalian phylogenetic anatomy, the term "postglenoid" is used widely; thus, postglenoid foramen.

Wible et al. (2004), in their review of cranial drainage in the Cretaceous mammal *Zalambdalestes*, stated that an emissary vein exited the postglenoid foramen. They noted that elsewhere the vein was known as the capsuloparietal emissary vein.

Geisler and Luo (1998:188–191) gave detailed discussion of the postglenoid foramen and capsuloparietal emissary vein. They argued that in cetacean history the postglenoid foramen has moved from within the squamosal to the squamosal–**petrosal** (periotic) suture; such a homology implies that the capsuloparietal emissary vein might traverse the lateral face of the periotic, perhaps associated with the **anteroexternal sulcus** of some Cetacea. However, the archaeocete *Zygorhiza* may have a nonpatent postglenoid foramen within the squamosal and also show a well-developed anteroexternal sulcus between the squamosal and **periotic bones**, suggesting that the postglenoid foramen (and capsuloparietal emissary vein) are not related to the anteroexternal sulcus.

Tursiops lacks a patent postglenoid foramen within the squamosal. Dissection is needed to determine whether *Tursiops* lacks an emissary vein (capsuloparietal emissary vein); similarly, the postglenoid foramen is absent in archaic odontocetes (Fordyce, 1994:157), archaic mysticetes, and some archaeocetes.

= **postglenoid fossa** = tympanosquamosal recess (Anderson, 1879:512)

= **postglenoid notch** (Anderson, 1879:428) = retroarticular notch

= **postglenoid process** = retroarticular process

MacPhee (1981:60) identified the postglenoid process as any process receiving the **mandibular condyle**, noting that in some mammals the structure may be replaced by an analogue, the **entoglenoid process** (q.v.). Postglenoid process and **retroarticular process** (q.v.) are equally applicable in Cetacea.

= **postmeatal process** or **postmeatal apophysis** = posttympanic process (de Muizon, 1987:3, 4)

= **posttemporal fossa** = temporal fossa (Fraser and Purves, 1960:100, 108; Perrin, 1975:9)

– **posttympanic process** (Figure 23b,c)

MacPhee (1981:60) cited van Kampen (1905:353) that the posttympanic (or **retrotympanic**) process in mammals is a feature of the squamosal that lies next to or on the posterior margin of the **external acoustic meatus**. See also Wible and Gaudin (2004:133,176). In Cetacea, the posttympanic process (sensu Fordyce, 1994, following Pompeckj, 1922: pl. 2) is the posterolateral portion of the squamosal, just lateral to the suture for the **tympanic bulla**. Flower (1878:423) employed posttympanic process for both "mastoid and squamosal" in ziphiids, while de Muizon (1987:3, 4) used the terms "**postmeatal process**" or "**postmeatal apophysis**" for posttympanic process.

– preglenoid process

The preglenoid process in some mammals is a transverse ventrally-directed ridge anterior to the glenoid fossa (e.g., Geisler, 2001). Kernan (1918:356) used preglenoid process for the anterior of the zygomatic process of the squamosal in *Ziphius*.

– pterygoid process of the squamosal (Ridewood, 1923:224–226, 237, 259, 260)

The pterygoid process of the squamosal is that anterior part of the squamosal bone that lies dorsal to the ***foramen ovale*** (Ridewood, 1923:224, fig. 15; Fraser and Purves, 1960:34, 35, 37–39). The pterygoid process is developed in mysticetes, typically contacting the pterygoid (e.g., fin whale, *Balaenoptera physalus*), but sometimes reaching the palatine (e.g., blue whale, *B. musculus*, and bowhead, *Balaena mysticetus*).

= pterygoperiotic plate = petro-pterygo-tympanic plate = falciform process

The pterygoperiotic plate was apparently a slip-of-the-pen for the **petro-pterygo-tympanic plate** (Anderson, 1879:514).

= pterygotympanic process (Anderson, 1879:508) = falciform process

Anderson, in his description of the basicranium of *Platanista*, assigned several terms to what we consider the **falciform process** of the squamosal bone. One of these is the pterygotympanic process (1879:508).

* **retroarticular notch** (Figures 3, 23c)

The retroarticular or **postglenoid notch** marks the lateral end of the **external auditory meatus** (or external acoustic meatus) in the broad sense. A notch develops because the cetacean tympanic has become isolated from the squamosal bone and has moved medially away from the lateral end of the external auditory meatus, so that the meatus is not fully floored by bone.

The retroarticular notch in delphinids lies immediately posterior to the **retroarticular** or **postglenoid process**. The anterior border of the notch consists of the postglenoid process of the squamosal, and the posterior border consists of the **posttympanic process** of the squamosal. The cartilaginous **external acoustic meatus** sensu stricto lies ventral to the retroarticular notch.

* **retroarticular process** (*processus retroarticularis*) = postglenoid process (Figures 2, 23c)

The retroarticular process in mammals is a ventral extension of the squamous part of the temporal immediately posterior to the **mandibular fossa** (Evans and Christensen, 1979:134). This is not to be confused with the **entoglenoid process** (q.v.).

In Cetacea, the retroarticular or **postglenoid process** is a transverse crest immediately posterior to the mandibular fossa (Schulte, 1917:393; Fordyce, 1994:156, 157).

* **retrotympanic process** (*processus retrotympanicus*) (Figures 3, 23c)

The retrotympanic process is a posterolateral process of the squamosal that passes posteriorly over the tympanic and articulates with the **mastoid process of the petrosal** (Schaller, 1992:24.33; not in Feneis, 1994). **Posttympanic process** is an equally applicable synonym.

The retrotympanic process or posttympanic process (q.v.) in odontocetes is lateral to the bulla and posterolateral to the **external auditory meatus**, sensu lato. The process typically articulates with the bulla and exoccipital.

= ***sac moyen*** (Beauregard, 1894; Fraser and Purves, 1960:114) = middle sinus

* **sphenoidal margin of the temporal** (*margo sphenoidalis*) (Figures 23d, 30, 31b)

The sphenoidal margin of the temporal bone is that portion of the temporal that abuts the **alisphenoid**.

The sphenoidal margin in delphinids consists of the anteromedial portion of the squamous part of the temporal.

* **spiny process** (Figure 25v)

The spiny process (de Muizon, 1987; Fordyce, 1994:156, 158) lies on the posteromedial corner of the squamosal bone, just posterior to the medial edge of the **tympanosquamosal recess**. In *Platanista*, the spiny process is a distinct medial projection of the squamosal that carries a transversely oriented groove (part of the **external acoustic meatus** in the broad sense) on its ventral surface, and that articulates with the ***hiatus epitympanicus*** of the **periotic bone** and with the **posterior process of the tympanic bulla**.

In *Tursiops* and other delphinids, the spiny process is generally indistinct or not developed in the adult. Occasional specimens have the spiny process articulated with the periotic.

– squamocranial notch (Fraser and Purves, 1960:46)

The squamocranial notch is the broad anterior notch formed by the **glenoid process** of the squamosal bone and the cranium (Fraser and Purves, 1960:46).

– squamosal bullar process

Luo and Gingerich (1999:32) equated the **anterior process of the tympanic bulla** with the ***processus tubarius***, and noted that in some archaeocetes the latter structure contacts the squamosal bullar process.

See **anterior process of the tympanic bulla**.

* **squamosal plate** (Figure 23a–e)

The squamosal plate of the squamosal bone in odontocetes consists of that part of the bone that lies immediately medial to the **glenoid process** and that forms a squamous suture (**squamosal suture**) with the parietal (Kernan, 1918:377).

* **squamosal suture** (*sutura squamosa*) (Figure 32)

The squamosal suture is a squamose suture formed by overriding of the parietal by the squamosal part of the squamosal bone (Gray, 1918:183; Evans and Christensen, 1979:135; Schaller, 1992:76.16; Feneis, 1994:54.10). Vesalius (1543) referred to the squamous suture as the *conglutinationem squamaeformem* (ibid., 21), the *glutinatio squamaeformis* (ibid., 21), the *squamaeformis conglutinatio* (ibid., 23), the s*quamaeformis est conglutinataio* (ibid., 21), and the *squamosa conglutinatio* (ibid., 21, 25).

Cetaceans have a normal squamosal suture.

– squamous part of the temporal bone (*pars squamosa*)

The squamous part of the temporal bone consists of the portion of the temporal that forms the lateral part of the cranium. The squamous part comprises the **glenoid process**, the **zygomatic process of the squamosal**, and the **squamosal plate** (Gray, 1918:139; Evans and Christensen, 1979:134; Schaller, 1992:24.19; Feneis, 1994:16.10). The squamous part is also known as the squama (*squama temporalis*) (Gray, 1918:139). The squamous part is differentiated from the petrous part, the mastoid part, the tympanic part, and the **styloid process** (Gray, 1918:138).

We have chosen to recognize the squamous part of the temporal bone in Cetacea as a separate ossification known as the squamosal bone (q.v.).

= subsquamosal foramina = foramina for *rami temporales*

The term "subsquamosal foramen" has been used in armadillos (Wible, 2003:183) for vascular apertures in the squamosal dorsal to the **suprameatal bridge**. Later, Wible and Gaudin (2004:154) used **foramina for *rami temporales*** as an alternative.

*** subtemporal crest** (Figures 3, 23c)

The subtemporal crest of the squamosal bone lies on the ventromedial surface of the **zygomatic process of the squamosal**, where it forms "the abrupt ventrointernal margin of the **temporal fossa** (here mainly formed by **alisphenoid**) which extends from near the **choanae** towards the squamosal, to separate the basicranium from the temporal fossa and **orbit**" (Fordyce, 1994:154, 155). The subtemporal crest limits the temporal fossa anteroventrally.

In *Tursiops* the curve of the crest is continuous with the anterior curve of the **falciform process**.

= supramastoid crest (*crista supramastoidea*)

The supramastoid crest is on the dorsal part of the **zygomatic process** of the **squamous part of the temporal bone**. It is attached to the temporal fascia (Schaller, 1992:24.25; not in Feneis, 1994). It is continuous with the **nuchal crest** (Evans and Christensen, 1979:131). This is also known as the **temporal crest** (Evans and Christensen, 1979:134). Fordyce (1994:157) used the terms "crest of the zygomatic process" (of the squamosal) for a more-anterior structure, and "**lambdoid crest**" for the more-posterior structure.

= suprameatal bridge = supramastoid crest (Wible, 2003:183; Wible and Gaudin, 2004:132)

In the yellow armadillo the suprameatal bridge (Wible, 2003:183; Wible and Gaudin, 2004:132) is a well-developed crest developed posterior to the dorsal margin of the **zygomatic process of the squamosal**; it presumably marks the lateral limit of the origin of the temporalis muscle.

See discussion under **supramastoid crest**.

– suprameatal foramen

Some mammals have a suprameatal foramen dorsal or anterodorsal to the **external acoustic meatus** (e.g., Ross and Covert, 2000; Gabbert, 2004). In *Monodelphis* (see Wible, 2003:156) the foramen is associated with the **postglenoid foramen**. The relationship is not clear with the ***foveola suprameatica***.

Tursiops lacks a suprameatal foramen.

– suprameatal fossa (Wang et al., 2004, 2005; Wesley-Hunt and Flynn, 2005:5)

The suprameatal fossa of some Carnivora is a depression immediately posterior to the bony **external auditory meatus** on the lateral wall of the skull (Wang et al., 2004, 2005; Wesley-Hunt and Flynn, 2005:5). See also ***foveola suprameatica* [*suprameatalis*]**.

Tursiops lacks a suprameatal fossa in the sense of the structure in carnivores.

Suprameatal fossa in the sense of a feature on the lateral face of the squamosal should not be confused with the suprameatal fossa as recognized on the cetacean periotic (see **suprameatal fossa of the periotic**).

– suprameatal pit (Geisler and Sanders, 2003:50)

Geisler and Sanders (2003:50) named the suprameatal pit of the squamosal bone for the feature described by de Muizon (1987) as the fossa that receives the hook-like **articular process** of the periotic in *Platanista*. Geisler and Sanders considered the pit likely to house part of the **peribullary sinus** as well as the hook-like articular process of the periotic.

In *Tursiops* the periotic lacks a hook-like articular process, and there is no corresponding pit in the squamosal. The exact relationship between bone and soft tissue in *Tursiops* is uncertain for the fossae, pits, and ridges in the squamosal adjacent to the periotic.

– suprameatal spine (*spina suprameatica* [*suprameatalis*])

The suprameatal spine is a variable spinous process located at the root of the **zygomatic process of the squamosal**, posterodorsal to the **external auditory meatus** in humans (Feneis, 1994:16.5). It is located on the anterior border of the suprameatal triangle.

The suprameatal spine is not known in delphinids.

– supratubercular ridge (Fordyce, 1994:158)

The supratubercular ridge divides the **periotic fossa** into an anterior and a posterior portion in *Waipatia* (fossil platanistoid; Fordyce, 1994:158). The supratubercular ridge lies lateral to the ***foramen spinosum*** and posteromedial to the **falciform process**. Geisler and Sanders (2003:48) commented further on this feature, associating it with the **suprameatal pit**.

The supratubercular ridge is not developed in delphinids.

*** temporal arch** (Figure 3)

The temporal arch in odontocetes is formed by the **zygomatic process of the squamosal** and the **postorbital process of the frontal bone** (Kernan, 1918:356). The temporal arch forms the anterior limit of the **temporal fossa**.

*** temporal crest** (Figures 3, 5)

The temporal crest lies on the dorsal surface of the **zygomatic process** of the squamous part of the temporal. The temporal crest is a continuation anteriorly of the **nuchal crest** (Evans and Christensen, 1979:134; Feneis, 1994:28.10a). Gray (1918:139) and Schaller (1992:24.25) referred to this as the **supramastoid crest**. Vesalius (1543:22) referred to the temporal crest as asperitas (slight roughness).

The temporal crest in adult delphinids is a well-defined crest that defines the lateral extent of the **temporal fossa**. The temporal crest lies on the dorsal surface of the **zygomatic process of the squamosal**, where it is also known as the supramastoid crest. Posteriorly and dorsally the temporal crest is formed by the parietal. Anterodorsally it is formed by the frontal. Anderson (1879:428, 501) referred to the temporal crest as the lambdoidal ridge.

See also **supramastoid crest**.

* **temporal fossa** (Figures 3, 32)

The temporal fossa is the origin of the temporal muscle and consists of the lateral areas of the parietal, squamosal, frontal, and **alisphenoid** bones (Gray, 1918:183; Evans and Christensen, 1979:124; Schaller, 1992:10.22; Feneis, 1994:30.11). Vesalius (1543:25) referred to the temporal fossa as the *temporis*. The temporal fossa is bounded by the **temporal crest, orbitotemporal crest, infratemporal crest**, and **subtemporal crest**.

Tursiops has a normal temporal fossa that is representative for delphinids; the fossa is subcircular in lateral view, formed mainly in squamosal and parietal, and bounded by distinct nuchal and associated crests. In dorsal view, each fossa is formed by the laterally convex wall of the braincase. In contrast to archaeocetes and most other mammals, the temporal fossae do not meet medially, to separate the facial region from the supraoccipital region.

The temporal fossa was mistakenly referred to as the posttemporal fossa (Fraser and Purves, 1960:100, 108; Perrin, 1975:9). See Schulte (1917:369, 370, 375, 376, 381, 391–393, 401), Fraser and Purves (1960:19, 22, 35, 100, 102, 106). Schulte also inadvertently referred to it as the zygomatic fossa (1917:373).

* **temporal surface of the squamosal** (*facies temporalis*) (Figures 23c, 32)

The temporal surface of the squamosal bone is that portion of the external surface of the squamous portion that borders the **temporal fossa** (Schaller, 1992:24.24; not in Feneis, 1994).

The temporal surface of the squamosal lies dorsal to the **zygomatic process of the squamosal**.

– **temporomandibular joint** (*articulatio temporomandibularis*)

The temporomandibular joint is formed by the **mandibular fossa** of the squamous part of the temporal and the articular condyle of the mandible (Evans and Christensen, 1979:134). It is also known as the "jaw joint" and frequently abbreviated "TMJ."

The temporomandibular joint in delphinids consists of the same elements as it does in terrestrial mammals. However, the temporomandibular joint in delphinids is a fibrous joint and the boundaries and surfaces of it are not as well defined as they are in terrestrial mammals, where it is a synovial joint. In mysticetes the fibrous joint has been called the interarticular fibro-cartilage (Fraser and Purves, 1960:22).

* **temporozygomatic suture** (*sutura temporozygomatica*) (Figure 32)

The temporozygomatic suture lies between the jugal and the **zygomatic process of the squamosal** (Evans and Christensen, 1979:135, 143; Schaller, 1992:76.35; Feneis, 1994:54.25). Gray (1918:182) referred to the temporozygomatic suture as the zygomaticotemporal suture. Vesalius (1543:23) referred to the temporozygomatic suture as the *sutura ossi iugalis*.

Most living cetaceans have a temporozygomatic suture that remains open throughout life.

* **tympanosquamosal recess** (Figures 23d, 30)

The tympanosquamosal recess (Fraser and Purves, 1960:9, 19, 35, 38, 39, 41–61, 63–65, 67, 69, 71–74) is the smooth fossa just medial to the **mandibular fossa** of the squamosal bone. It contains the **middle sinus**.

* **zygomatic process of the squamosal** (*processus zygomaticus*) (Figures 23a–d, 29)

The zygomatic process of the squamous part of the temporal is a long, curved process that overlaps the posterior portion of the jugal bone and makes up the zygomatic arch. The zygomatic process comes laterally off the middle portion of the squamous part and is directed anteriorly (Gray, 1918:139; Evans and Christensen, 1979:134, 131; Schaller, 1992:24.26; Feneis, 1994:16.16;). Vesalius (1543:22, 23) referred to the zygomatic process of squamosal as the *temporis ossis processus*, jutting out like a stylus for writing *sciptorii stili*.

The zygomatic process in delphinids is a triangular process that lies on the anteroventral portion of the **glenoid process** of the squamosal bone (Schulte, 1917:373, 375, 382, 390, 393, 398, 401; Fraser and Purves, 1960:9, 13, 19, 26, 34, 37, 38, 41–47, 50–57, 60, 61, 70, 77, 84). The base is immediately anterior to the **mandibular fossa**. The apex is directed anteromedially and articulates with the jugal. Owen (1866a:36) referred to this process at one point as just the *zygoma*, at others as the zygomatic part (1866a:29, 36), and at others as the zygomatic process (1866a:28, 39, 40).

SUPRAOCCIPITAL BONE

Os Supraoccipitalis

FIGURES 3–5, 6A,C,E, 12A–C,E, **24**, 31A

The supraoccipital is one of the three bones that surround the *foramen magnum* and that form the occipital region of the cranium. The supraoccipital is the most dorsal of the three and forms the dorsal border of the *foramen magnum* and part of the roof of the cranium (Schulte, 1917:369–371, 375, 376, 382, 383, 401).

In cetaceans the occipital region has been evolutionarily modified by the process that has become known as "telescoping" (q.v.). In adult cetaceans the supraoccipital, together with the interparietal, forms the occipital shield. Schulte (1917:370) referred to the occipital shield as the occipital complex.

Owen (1866a) consistently referred to this bone as the superoccipital.

* **cerebral fossa** (*fossa cerebralis*) (Figure 31a)

Feneis (1994:8.34a) defines the cerebral fossa in humans as the depression for the occipital lobes of the cerebrum. Some authorities take a more general view, such as Whitney (1889–1910:[vol. 3]2347): "cerebral fossae, one of three depressions, anterior, middle, and posterior, on each side of the floor of the cranial cavity, lodging respectively the frontal and temporal lobes of the cerebrum and the cerebellum." It does not appear to have been used in describing nonhuman animals because no mention of it is found in Schaller (1992) or Evans and Christensen (1979).

Anderson (1879:511) used cerebral fossa to refer to that part of the cranial cavity that contains the cerebrum. In delphinids it is comprises portions of the exoccipital, **supraoccipital**, parietal, interparietal, frontal, ethmoid, and squamosal. The cerebral fossa is bounded posteroventrally by the ***tentorium*** and anteromedially by the basicranium.

* **cruciform eminence** (*eminentia cruciformis*) (Figure 24b)

The cruciform eminence is formed on the internal surface of the **supraoccipital** by the confluence of the **sulci for the transverse sinus**, **sagittal sinus**, and occipital sinus. The cruciform eminence centers on the **internal occipital protuberance** (Gray, 1918:130; Schaller, 1992:10.11; Feneis, 1994:8.28).

The cruciform eminence is developed in *Tursiops* but the lower limb of it (groove for the occipital sinus) is weakly developed. Owen (1866a:26) and Anderson (1879:501, 502) used the term "lateral sinus" instead of **transverse sinus**.

* **dorsal sagittal sinus sulcus** (*sulcus sinus sagittalis dorsalis*)

See "Interparietal Bone."

* **external occipital crest** (*crista occipitalis externa*) (Figures 5, 24a,c)

The external occipital crest is a smooth **median ridge** extending from the **external occipital protuberance** to the ***foramen magnum*** (Evans and Christensen, 1979:122; Schaller, 1992:16.27; Feneis, 1994:8.24).

The external occipital crest is weakly developed in *Tursiops* and most odontocetes (e.g., Anderson, 1879:501). It is more evident in the larger delphinids such as *Globicephala* and *Orcinus*.

– **external sagittal crest** (*crista sagittalis externa*)

The external **sagittal crest** is a median crest immediately anterior to the **external occipital protuberance** (Evans and Christensen, 1979:121; Schaller, 1992:16.30). It is not developed in humans (Feneis, 1994).

The external sagittal crest has become incorporated into the **vertex** in all living odontocetes and is not present as a recognizable feature. It is present in a number of fossil groups of cetaceans.

= **foramen for the dorsal sagittal sinus** (*foramen sinus sagittalis dorsalis*)

See ***foramen impar***.

– ***foramen impar***

The *foramen impar* lies on the dorsal surface of the **internal occipital protuberance**. It contains the posterior end of the **sagittal sinus** as it joins with the **transverse sinuses**. It is also known as the **foramen for the dorsal sagittal sinus** (Evans and Christensen, 1979:122, 157).

The *foramen impar* is present in odontocetes that have developed the internal **occipital protuberance** (i.e., older animals and large species).

= **great occipital crest** = external occipital crest

* **groove for dorsal sagittal sinus** (*sulcus sinus sagittalis dorsalis*) (Figures 12b, 24b)

The **sagittal sinus** drains the dorsal surface of the cranial cavity. It begins at the confluence of the rhinal veins, continues posteriorly in the attached edge of the *falx cerebri*. It terminates posteriorly in the **transverse sinus** (Evans and Christensen, 1979:791; Schaller, 1992:10.9, 26.21, 28.6). In humans this feature is known as the groove for superior sagittal sinus (*sulcus sinus sagittalis superior* (Feneis, 1994:8.31, 16.26a, 18.16, 28.26).

In most mammals this sulcus lies along the **sagittal suture** of the parietals, but in cetaceans it lies along the median portion of the **supraoccipital**, interparietal, and may extend a bit onto the frontals. In *Tursiops* it does not occur on the frontals.

* **groove for occipital sinus** (*sulcus sinus occipitalis*) (Figure 24b)

The occipital sinus in humans is situated in the attached margin of the *falx cerebelli*. It commences around the margin of the ***foramen magnum*** and ends in the confluence of the sinuses. It runs dorsally from the *foramen magnum* to its termination in the **internal occipital protuberance**. The groove for occipital sinus forms the ventral limb of the **cruciform eminence** on the internal side of the **supraoccipital** bone. It is the smallest of the cerebral venous sinuses (Gray, 1918:658; Feneis, 1994:8.33a). It also occurs in the horse (Sisson, 1910:591) and the camel (Smuts et al., 1987:170) but not in the dog (Evans and Christensen, 1979:791).

The occipital sinus occurs in delphinids and the groove for the occipital sinus is on the ventral side of the cruciate eminence.

= **groove for sagittal sinus**

See **groove for dorsal sagittal sinus**.

* **groove for transverse sinus** (*sulcus sinus transversi*) (Figures 24b, 31a)

The **transverse sinus** is a paired structure. It begins on the midline of the **supraoccipital** bone at the confluence of the sinuses (*confluens sinuum*). There, the **sagittal sinus**, transverse sinus, and sometimes straight sinuses (*sinus rectus*) (Schaller, 1992:238.17) converge. The transverse sinus then runs laterally and anteriorly to terminate in the temporal sinus and sigmoid sinuses on the squamosal bone (Evans and Christensen, 1979:122; Schaller, 1992:16.37, 18.6; Feneis, 1994:8.32).

In *Tursiops* and other odontocetes the **groove for transverse sinus** begins medially at the **internal occipital protuberance** on the supraoccipital, and extends laterally across the dorsal portion of the exoccipital bone to the posteroventral part of the parietal bone.

– **highest nuchal line** (*linea nuchae suprema*)

The highest nuchal line in humans occurs on the dorsal portion of the **supraoccipital** bone in humans and is formed by the attachment of the *galea aponeurotica* to the skull (Gray, 1918:129, 379). This thin broad sheet of connective tissue serves as the tendon of insertion for the occipital and frontal parts of the epicranius muscle. The *galea aponeurotica* serves as attachment to the scalp, permitting considerable movement.

This specialization does not occur in cetaceans, and the *galea aponeurotica* is absent.

– inferior nuchal line (*linea nuchae inferior*)

The inferior nuchal line is the line on the **supraoccipital** between the insertions of the *m. semispinalis capitis* dorsally and the *m. rectus capitis posterior* and *m. obliquus capitis superior* (Gray, 1918:129; Feneis, 1994:8.27).

The inferior nuchal line may be identifiable in cetaceans as the line on the supraoccipital bone ventral to the insertion of the *m. semispinalis capitis*.

– internal occipital crest (*crista occipitalis interna*)

The internal occipital crest sometimes consists of a pair of crests that bound the **vermiform impression** in the dog (Evans and Christensen, 1979:122) on the **supraoccipital**. The internal occipital crest extends posteroventrally from the **internal occipital protuberance** (Schaller, 1992:16.33; Feneis, 1994:8.30). In humans the internal occipital crest runs from the internal **occipital protuberance** to the ***foramen magnum*** (Gray, 1918:131, 193). The internal occipital crest separates the inferior occipital fossae, which house the hemispheres of the cerebellum.

Anderson (1879:502) could find no trace of the internal occipital crest in *Platanista*, nor have we been able to find it in *Tursiops* or other delphinids.

* **internal occipital protuberance** (*protuberantia occipitalis interna*) (Figures 24b, 31a)

The internal **occipital protuberance** develops on the dorsal midline of the internal surface of the **supraoccipital**. It is closely associated with the posterior termination of the *falx cerebri* (Evans and Christensen, 1979:122; Schaller, 1992:16.32; Feneis, 1994:8.29).

In *Tursiops* and other odontocetes the internal occipital protuberance develops as the animal matures. It comes to contain the **transverse canal** and the posterior portion of the **sagittal sinus**. It forms the medial portion of the ossified ***tentorium***.

= internal vertical ridge (Anderson, 1879) = internal sagittal crest

* **keyhole notch** (Figure 24e)

The keyhole notch (Evans and Christensen, 1979:121, 123) is a variable feature that lies dorsal to the ***foramen magnum***. The ventral limits of the keyhole notch are the **nuchal tubercles** (Evans and Christensen, 1979:123; Schaller, 1992:16.4). The keyhole notch is formed by the supraoccipital ossification not extending ventrally to fill the gap between the exoccipital ossifications.

The keyhole notch is common in cetaceans.

* **nuchal tubercles** (*tubercula nuchalia*) (Figure 24a,e)

The nuchal tubercles are paired projections of the posterior limbs of the **supraoccipital** into the dorsal surface of the ***foramen magnum***. The nuchal tubercles are developmental features that tend to be more apparent in young animals (Evans and Christensen, 1979:123; Schaller, 1992:16.4).

Nuchal tubercles are variable in Cetacea.

= occipital protuberance

See **internal occipital protuberance** or **external occipital protuberance**.

= occipital shield = occiput

– occipital tuberosity (Barnes and McLeod, 1984:9, 17, fig. 2)

In the gray whale, bilateral occipital tuberosities occur on the **supraoccipital**, presumably forming the origin for some of the neck musculature (Barnes and McLeod, 1984:9, 17, fig. 2).

Occipital tuberosities are not developed in *Tursiops*.

* **occiput** (Figure 24c)

The occiput is the lower back of the head in newborn humans (Dox et al., 1979:341). The occiput lies between the ***foramen magnum*** and the **vertex** (Fraser and Purves, 1960:5). Vesalius (1543:21,23,25) referred to the occiput as the *occipitis os*; Eustachius and Lancisius (1714:28,111) as the *occiput*.

The occiput consists of the occipital ossification, which in cetaceans is the **supraoccipital** plus interparietal bones. In adult cetaceans, where the supraoccipital and interparietal are fused, the occiput has been referred to as the **occipital shield**.

* ***opisthion*** (Figures 5, 24d)

The *opisthion* is a craniometric point that occurs on the midpoint of the dorsal border of the ***foramen magnum*** (Gray, 1918:181).

* **parietal margin of the supraoccipital** (*margo parietalis*) (Figure 24a,c)

In noncetacean mammals the parietal margin of the **supraoccipital** bone is the entire anterior margin of that bone. Because of the inability in most mammals to differentiate the interparietal, it is assumed that the parietals make up 100% of the parietal ossification.

In delphinids the parietal is excluded from the midline by the extensive interparietal ossification. The parietal margin of the supraoccipital bone is therefore the anterolateral border of the supraoccipital.

= sagittal crest

See **external sagittal crest, internal sagittal crest**.

= supraoccipital (*squama occipitalis*) = supraoccipital bone

= supraoccipital crest (Kernan 1918:383) = internal sagittal crest

– supraoccipital foramina

Wible and Gaudin (2004:166) mentioned the presence of small supraoccipital foramina in the dog and some armadillos, associated with the **transverse sinus** and occipital emissary vein.

Tursiops may have scattered small foramina on the **supraoccipital** bone but none is identifiable as supraoccipital foramina.

= supraoccipital shield (occipital shield) (Miller, 1923:5) = supraoccipital plus interparietal

* ***tentorium*** **/ bony tentorial ossification** (*tentorium osseum* / *processus tentoricus* / *tentorium cerebelli osseum*) (Figure 31a,b)

The bony *tentorium* is an ossification that develops as a shelf in the cerebellar *tentorium* (*tentorium cerebelli membranaceum*). It spreads laterally from the **internal occipital protuberance** to the posterior edge of the parietal. The *tentorium* is formed by a leaf of bone that projects anteromedially from the dorsal part of the posterior border of the parietal and the internal **occipital protuberance** (Evans and Christensen, 1979:124; Schaller, 1992:10.10; Feneis, 1994:268.25).

The anterolateral margin of the tentorial ossification in odontocetes ends on the most medial aspect of the **internal surface of the parietal**. The primary portion of the *tentorium* is on the **supraoccipital** and exoccipital bones. The *tentorium* is well developed in odontocetes, increasingly so in older animals. The development of the *tentorium* also seems to be correlated with overall size, that is, the *tentorium* is more developed in large species of delphinids than in small species.

* **transverse canal** (*canalis sinus transversis*) (Figure 31a)

The transverse canal lies on dorsal portion of the internal surface of the **supraoccipital** bone and penetrates the **internal occipital protuberance**. It is continuous laterally with the **groove for transverse sinus** (Evans and Christensen, 1979:122; Schaller, 1992:10.13). The ***foramen impar*** opens dorsally into the transverse canal.

The transverse canal is not present in newborn *Tursiops* but appears upon development of the internal occipital protuberance.

– vermiform impression / vermiform fossa (*impressio verminalis*)

The vermiform impression lies between the **internal occipital protuberance** and the ***foramen magnum***. It is bounded laterally by the paired **internal occipital crests**. The vermiform impression accommodates the vermis of the cerebellum (Evans and Christensen, 1979:154; Schaller, 1992:16.36).

The vermiform impression is very faintly developed in odontocetes because of the increased size of the *foramen magnum* to accommodate the vertebral vascular plexus. Most of the vermis abuts the vascular plexus instead of the **supraoccipital** bone.

The vermiform impression is not expressed in Delphinids.

TYMPANOPERIOTIC COMPLEX

PERIOTIC BONE

Os Temporale / Pars Petrosa

FIGURES **25**, 28

The mammalian temporal bone (e.g., Evans and Christensen, 1979; Novacek, 1986) can be separated into petrosal, tympanic, and squamosal centers of ossification. The petrosal (*pars petrosa*, *petrous temporal*, or pyramid) contains the inner ear (cochlea and semicircular canals). The petrosal is bounded by the other elements of the temporal bone (tympanic and squamosal) and the basioccipital, exoccipital, basisphenoid, and parietal (Gray, 1918:142; Evans and Christensen, 1979:129; Schaller, 1992:22.2; Feneis, 1994:12.15). Vesalius (1543:23) did not differentiate the petrosal, merely labeled it as *temporis ossis*, but Eustachius and Lancisius (1714:104, 107, 109, 112) referred to it as the *os petrosum*. Craigie (1831:46) referred to the periotic in cetaceans as the lithoid.

The cetacean ear is one of the most divergent regions of the skull. The tympanoperiotic in *Tursiops* is highly modified from the condition in many other mammals, and homologies are not always clear. Many of the identifications offered here should be investigated by detailed dissections and by embryological study. A complex anatomical terminology applies to the auditory region in mammalian embryos (e.g., Boenninghaus, 1904; MacPhee, 1981). We have found it difficult to identify many embryonic features in adults, and generally have not included anatomical terms for those features that are apparent only in embryos.

In *Tursiops* the petrosal has been isolated from the rest of the skull; as in other Neoceti, it is now called the periotic. The periotic has most contact with the tympanic bulla, which lies ventral to it. It also is joined by delicate bony process to the squamosal just posterior to the retroarticular or postglenoid process. It lies on the ventral surface of the posterolateral margin of the skull, ventral to the jugular foramen and the bones that border it (alisphenoid, parietal, exoccipital, basioccipital) and dorsal to the tympanic bulla. Kellogg (1928:203, fig. 23) did a splendid figure of the tympanoperiotic of the narwhal.

= acoustic pore of the internal acoustic meatus

See **internal acoustic pore** and **internal acoustic meatus**.

– anterior bullar facet

In Neoceti the anterior bullar facet of the **periotic bone** lies on the ventral surface of the **anterior process of the periotic bone**. The anterior bullar facet is delimited posteriorly by the ***fovea epitubaria*** for the **accessory ossicle** (Fordyce, 1994:160) and, in many Odontoceti, it also receives the **periotic facet** on the convex elongate dorsal surface of the **outer lip** of the **tympanic bulla**. In *Tursiops* and other delphinids, the anterior bullar facet is lost because the accessory ossicle of the tympanic **bulla** is expanded to cover the ventral surface of the anterior process of the periotic bone.

Luo and Gingerich (1999: tbl. 2, #6b) stated that the bullar facet for the anterior process of the [ecto] tympanic (= anterior bullar facet of our use) is distinct from the *fovea epitubaria*, but it is only present in Odontoceti with a very elongate anterior process.

– anterior fissure of the facial foramen

Geisler and Luo (1996: fig. 3) used this term for the slit-like anterior opening of the **petrosal canal** in some Mysticeti.

See **petrosal canal**.

* **anterior incisure [new term]** (Figure 25d,m,v,x)

In Odontoceti, the cochlear process of the periotic is separated from the **anterior process of the periotic bone** by a "notch at the anterior border of the **cochlea** [sic; ***pars cochlearis***]" (Anderson, 1879:514). This notch, although prominent, has escaped attention; it may be the feature identified in older literature as the **groove for the tensor tympani muscle**. We have named it the anterior incisure.

Tursiops has an anterior incisure.

* **anterior keel** (Figure 25c,d,n)

In Neoceti, the anterior keel is a crest located on the **anterior process of the periotic bone** and lies between the **anteroventral** and **anterodorsal angles** (Fordyce, 1994:160). The anterior keel is a continuation of the **dorsal crest**. It is present in various archaic Odontoceti and in many Mysticeti.

The anterior keel in *Tursiops* is transversely rounded and indistinct.

– anterior lamina

In some archaic terrestrial mammals the **petrosal** may have a three parts: a ***pars cochlearis***, a ***pars canalicularis***, and a prominent anterior lamina that forms part of the lateral wall of the braincase (Wible and Rougier, 2000:36).

Adult *Tursiops* and other delphinids lack an anterior lamina.

*** anterior meatal pit [new term]** (Figure 25c–u)

The anterior meatal pit in *Tursiops* is a small but distinct depression within the **internal acoustic meatus**, located on or near the transverse crest and posterior to the proximal opening of the **facial canal**. It is not obviously associated with a foramen, and does not occur in all specimens. The pit should not be confused with the ***foramen singulare*** or **dorsal vestibular area**.

*** anterior process of the periotic bone** (Figure 25a,m,n,p,t,w,x)

The anterior process of the **periotic bone** is the anterior eminence of the element that, in its elongate state, is a neomorph in Neoceti and many Archaeoceti; it is prominent in *Tursiops*. Studies of fossils, of embryos and of other mammals indicate that the anterior process is an anterior extension of the mammalian ***tegmen tympani*** (Luo, 1998:276).

The anterior process in the broad sense consists of everything anterior to a transverse line through the anterior margin of the **cochlear portion / *pars cochlearis*** (Kellogg, 1936; Yamada, 1953; Kasuya, 1973); strictly, the anterior process should not include the **superior process** that is a development of the *tegmen tympani* (Luo, pers. comm.). For the ventral surface, Fordyce (1994) regarded the anterior process as that part of the periotic anterior to the **mallear fossa**, that is, anterior to the ***hiatus epitympanicus*** but including the ***fovea epitubaria***. Dorsally, the anterior process in *Tursiops* merges posteriorly into the **body of the periotic** without any distinct boundary.

Synonyms include **tuberosity of the *tegmen tympani*** in the sense of Schulte (1917:397), **prootic portion of the periotic bone** (Fraser and Purves, 1960:34), and **tegmental process** (Yamada, 1953:20).

*** anterodorsal angle** (Figure 25c,d,m,n,p)

The anterodorsal angle of the **periotic bone** is the anterior curvature of the **dorsal crest** (Fordyce, 1994:160), as seen in many archaic Odontoceti and Mysticeti. The dorsal angle on the **anterior process of the periotic bone** in *Tursiops* is probably homologous with the anterodorsal angle of other Neoceti, although the **anterior process of the periotic bone** in delphinids is too modified to be sure.

– anteroexternal sulcus

The anteroexternal sulcus of the **periotic bone** lies on the lateral surface of the **anterior process of the periotic bone**, just lateral to the **anterior bullar facet** (Fordyce, 1983; 1994:149, 160) in many Odontoceti, Mysticeti, and (but see below) Archaeoceti. It originates just anterior to the level of the **mallear fossa**, and rises toward the **anterodorsal angle**.

For some Archaeoceti, Luo and Gingerich (1999:45) named a comparable feature the transverse (or dorsoventral) vascular channel or vascular groove, and noted that when enclosed by the squamosal (e.g., in *Dorudon atrox*; their fig. 17) this structure forms a vascular foramen.

For the archaeocete *Basilosaurus cetoides*, Kellogg (1936:27, fig. 5) identified the ventral part of the anteroexternal sulcus (in our sense) as the ***fovea epitubaria***, and described the sulcus on the periotic as “a deep dorso-ventrally curved furrow” (p. 27). We have examined this specimen and also isolated periotics of Basilosauridae and conclude that the structure discussed by Kellogg is what we term the “anteroexternal sulcus” of the periotic bone. We presume, therefore, that the feature in *Basilosaurus cetoides* is homologous with the structure in *Dorudon atrox*, namely the transverse (or dorsoventral) vascular channel or vascular groove of Luo and Gingerich (1999).

For some Mysticeti, Geisler and Luo (1996, 1998) identified a large depression here as the **squamosal fossa** (q.v.).

The anteroexternal sulcus probably marks the path of an artery across the lateral surface of the **anterior process of the periotic bone**; Fordyce (1994) suggested the middle meningeal artery. Alternatively, it could be associated with the retroarticular or postglenoid vein, although we consider this less likely. Dissection is needed to clarify the identity of the sulcus.

The anteroexternal sulcus is not present in *Tursiops*.

– anterointernal sulcus (Fordyce, 1994:158, 160)

The anterointernal sulci lie on the ventromedial surface of the **anterior process of the periotic bone**, medial to the **anterior bullar facet** and ***fovea epitubaria*** in some Odontoceti. One of the sulci may carry the lesser petrosal nerve.

Tursiops does not have anterointernal sulci, but the sulci occur sporadically in other delphinids.

*** anteroventral angle** (Figure 25c,d,n–p,v)

In Neoceti, the anteroventral angle of the **periotic bone** is the angle that is made on the anteroventral surface of the **anterior process of the periotic bone** by a continuation of the **anterior keel**. The anteroventral angle lies anterior to the **anterior bullar facet** (Fordyce, 1983:30, 1994:160) or to the ***fovea epitubaria***.

An anteroventral angle is very pronounced in *Tursiops*.

= antrum of the *fenestra rotunda* (Novacek, 1986:55)

See **cochlear window** (or **round window**).

*** aperture for the cochlear aqueduct** (Figure 25a,b,e,l,m,o,q,u–w)

In the dog, the aperture or external opening for the **cochlear aqueduct** lies on the medial wall of the **petrosal**, posteroventral to the **internal acoustic meatus** in the dorsolateral border of the **jugular foramen**, and just dorsal to the **jugular incisure** (Evans and Christensen, 1979:130, 133). The aperture is in the anterior edge of the jugular foramen (**posterior lacerate foramen**) (Evans and Christensen, 1979).

In *Tursiops* and other delphinids the aperture for the cochlear aqueduct (or **cochlear canaliculus**) lies posteriorly on the dorsomedial surface of the **cochlear portion** (process) of the periotic. The aperture for the cochlear aqueduct is posteromedial to the **internal auditory meatus**.

= aperture of the facial canal

See **epitympanic foramen of the facial canal**.

= aperture for the endolymphatic duct (Kellogg, 1936; Fordyce, 1994: fig. 11)

See **aperture for the vestibular aqueduct**.

*** aperture for the vestibular aqueduct** (Figures 25a–l,o,t,u, 28)

In the dog, the aperture for the vestibular aqueduct lies posterodorsal to the opening of the **cochlear canaliculus** on the **medial surface of the petrosal** bone (Evans and Christensen, 1979:132). The **vestibular aqueduct** runs from the posterior medial side of the **vestibule** (Whitmore, 1953) posteroventrally to the posterior part of the cerebral surface of the **petrosal**. The vestibular aqueduct carries the **endolymphatic duct**.

The aperture is also known as the external aperture or foramen for the vestibular or endolymphatic duct or aqueduct, or the ***aquaeductus endolymphaticus*** (e.g., Kellogg, 1928: fig. 23; 1936). Kellogg emphasized that in some Cetacea, the aperture is quite voluminous.

In *Tursiops* the opening of the vestibular aqueduct lies on the dorsal surface of the periotic just posterior to the **internal acoustic meatus**.

– *apex pyramidalis* (apex of pyramid) (*apex partis petrosae*)

The *apex pyramidalis* lies on the medial side of the petrous portion of the mammalian temporal. The apex forms the anterior termination of the **petrosal crest** in the dog (Evans and Christensen, 1979:132) or the anteroventral tip of the **petrosal** in cattle (Schaller, 1992:22.9).

The *apex pyramidalis* cannot be identified with certainty in *Tursiops*.

See **pyramid**.

= aqueduct of Fallopius (*aqueductus Fallopii*) = Fallopian aqueduct

See **facial canal**.

= aqueduct of the cochlea (*aqueductus cochlearis*)

See **aperture for the cochlear aqueduct**.

= *aqueductus cochleae*

See **cochlear aqueduct**.

= *aqueductus endolymphaticus*

See **aperture for the vestibular aqueduct**.

– arcuate eminence (*eminentia arcuata*)

The arcuate eminence is an arched elevation on the anterior surface of the **pyramid** (**petrosal**) above the anterior semicircular canal in mammals (Feneis, 1994:14.3; not in Schaller, 1992).

The **semicircular canals** are greatly reduced in size in the Odontoceti and do not present external signs of their presence.

– *area cochleae* (Figure 25u)

The *area cochleae* is the ventral or posterior part of the **internal acoustic meatus** into which opens the canal for the vestibulocochlear nerve in archaic artiodactyls (Whitmore, 1953: 131).

In *Tursiops* the *area cochleae* merges without obvious boundary into the ***area nervus facialis***.

*** *area cribrosa media*** (Figure 25a,u)

In the human **petrosal**, the portion of the **internal acoustic meatus** beneath (medial to) the ***crista falciformis*** has three sets of foramina: "one group, just below the posterior part of the crest, situated in the *area cribrosa media*, consists of several small openings for the nerves to the **saccule**" (Gray, 1918:143). Gray (1918:1058, 1059) also stated that the filaments of the inferior branch of the vestibular nerve traverse the foramina in the ***area vestibularis inferior***, and end in the macula of the saccule; thus, the *area cribrosa media* and the *area vestibularis inferior* appear to be the same.

Some specimens of *Tursiops* show what may be an *area cribrosa media* separate from the **spiral cribriform tract**, but in other specimens the distinction is not clear. Kellogg (1928: fig. 23) showed the *area vestibularis inferior* for *Monodon*. Schulte (1917:396) identified the *area cribrosa media* in *Kogia* as a small foramen.

Further dissection is needed to confirm the identity of features discussed here.

– *area nervus facialis* (Figure 25u)

The *area nervus facialis* is the dorsal or anterior part of the **internal acoustic meatus** into which opens the dorsal foramen of the **facial canal** (**Fallopian aqueduct**) in archaic artiodactyls (Whitmore, 1953:131).

In *Tursiops* the *area nervus facialis* merges without obvious boundary into the ***area cochleae***.

= *area vestibularis inferior* = *area cribrosa media*

Gray (1918:1058–1059) used *area vestibularis inferior* in a manner suggesting synonymy with the ***area cribrosa media*** (q.v.).

– articular peg

De Muizon (1987:8) identified the articular peg as the projection found on the posterolateral face of the periotic in extinct eurhinodelphinid dolphins (formerly = rhabdosteid dolphins). De Muizon (1987:8) suggested that the articular peg may not be homologous with the **articular process** (q.v.).

The articular peg is absent in *Tursiops*.

– articular process

The articular process is one of an intergrading series of apparently homologous projections among a range of archaic platanistoids (de Muizon, 1987:8; Fordyce, 1994:149). The feature on some specimens was described by de Muizon as an **articular rim**, or small apophysis, or hook-like articular apophysis.

The articular process does not occur in *Tursiops* and appears to be restricted to the platanistoids (de Muizon, 1987:8).

– articular rim

In some Odontoceti, the articular rim of the periotic (de Muizon, 1987:7, 8) is the expanded margin immediately anterior, and dorsal-dorsolateral, to the base of the posterior process (Fordyce, 1994:160); in Platanistidae the articular rim is developed into the **articular process**.

The articular rim is not present in *Tursiops*.

= attic = epitympanic recess (Gray, 1918:142; Schulte, 1917:396)

– auditory tube (*tuba auditiva*)

The auditory (Eustachian) tube communicates between the mammalian middle ear cavity and the nasopharyngeal cavity (MacPhee, 1981:48; Schaller, 1992:538.19). The auditory tube comprises part of the musculotubal canal of the tympanic (not a tympanic bulla; see Schaller, 1992:24.12) and is commonly known as the **Eustachian tube.**

The auditory tube in *Tursiops* runs from the **tympanic opening of the auditory tube** through the **Eustachian notch** in the pterygoid bone.

See **Eustachian tube** and **musculotubal canal of the tympanic bulla** in "Tympanic Bulla."

= basicapsular fissure = basicochlear fissure

– basicochlear fissure

MacPhee (1981:48, 49) stated that the basicochlear fissure or **basicapsular fissure,** which is a feature of embryonic mammals, may persist into some adult mammals as a space between the ventromedial edge of the auditory region and the basioccipital.

The cranial hiatus in *Tursiops* probably includes the basicochlear fissure.

See **cranial hiatus** and **jugular foramen**.

– body of the periotic

The body of the periotic in Neoceti (e.g., Kellogg, 1931; Fordyce, 1994:161) is that part of the **periotic bone** other than the **anterior process,** posterior process, and ***pars cochlearis***. It is thus roughly equivalent to the ***tegmen tympani*** (q.v.) of other mammals. Schulte (1917:396) used the term "***pars vestibularis***" for that part of the periotic in *Kogia* other than the *pars cochlearis*. Fraser and Purves (1960:34) used the term "**otic portion**" for this part of the periotic in *Balaenoptera*.

The body of the periotic is present in *Tursiops*.

= canal for the acoustic nerve

See **internal auditory meatus**.

– canal for the auricular ramus of the vagus

For the armadillos *Euphractus* and *Dasypus*, Wible and Gaudin (2004:149) reported that a canal or small foramen for the auricular ramus of the vagus is associated with the **facial canal** or **stylomastoid foramen** in the **petrosal** (**periotic bone**).

We cannot identify in *Tursiops* a canal or foramen for the auricular ramus of the vagus.

= canal for the *chorda tympani* (*canaliculus chordae tympani*)

In mammals the canal for the *chorda tympani* arises from the peripheral turn of the **facial canal** (sensu lato) (q.v.) and passes through the wall of the facial canal to exit posterolateral to the **vestibular window** (Evans and Christensen, 1979:133, 931).

The canal for the *chorda tympani* is not developed in *Tursiops*, the *chorda tympani* leaving the facial nerve external to the facial canal. This is a result of the wall of the facial canal being absent distally (i.e., absent before the **stylomastoid foramen**), where a **facial sulcus** is present instead.

= canal for the facial nerve

See **facial sulcus**.

– canal for the lesser petrosal nerve (*canalis n. petrosi minoris*)

In mammals the lesser petrosal nerve in humans emerges from the tympanic plexus, pierces the anterior wall of the **petrosal** and exits the middle cranial fossa through the sphenopalatine fissure below the ***foramen ovale*** and joins the otic ganglion (Schaller, 1992:472.2, 474.21; Feneis, 1994:290.16). The lessor petrosal nerve bears parasympathetic fibers from the tympanic plexus to the otic ganglion (Feneis, 1994:294.15).

Dissection is needed to confirm that *Tursiops* has a lesser petrosal nerve and tympanic plexus. Fordyce (1994:158) implied that some Odontoceti have this nerve.

= canal for the major superficial petrosal nerve (*canalis n. petrosi majoris*) = petrosal canal

= canal for the stapedial muscle

See **fossa for the stapedius muscle**.

– canal for the trigeminal nerve (*canalis n. trigemini*)

In the dog the short canal for the trigeminal nerve is located anterior to the **internal acoustic meatus** in the **petrosal** (Evans and Christensen, 1979:132). The trigeminal nerve passes through this canal, then forms the semilunar ganglion and separates into the ophthalmic nerve, maxillary nerve, and mandibular nerve (Evans and Christensen, 1979:912).

The canal for the trigeminal nerve is not developed in cetaceans due to the ventral movement of the periotic. This movement has resulted in further separation of the periotic from the central nervous system.

*** caudal tympanic process** (Figure 25o,q,w)

MacPhee (1981:50) identified the mammalian caudal tympanic process as arising primarily from the anteroventral part of the ***pars canalicularis*** (= **tympanic process** of Wible et al., 2004:75).

Geisler and Luo (1996: fig. 3; see also Geisler and Sanders, 2003: char. 225) used caudal tympanic process for a plate-like process that extends posteriorly off the ***pars cochlearis*** lateral to the ***fenestra rotunda*** and medial to the fossa for the stapedial muscle. Fordyce (2002) used the term "**posterior cochlear crest**" for this feature in the fossil dolphin *Simocetus*.

The caudal or posterior tympanic process is well developed in *Tursiops*.

– cerebellar fossa (*fossa cerebellaris*)

In the dog, the cerebellar fossa lies on the posteromedial surface of the **petrosal** and houses the paraflocculus of the cerebellum (Evans and Christensen, 1979:132).

In the horse, there is no **subarcuate fossa**; the cerebellar fossa houses the cerebellum (Schaller, 1992:22.21).

There is no cerebellar fossa in *Tursiops*. The cerebellar fossa is represented by the region medial to the **superior process** of the **periotic bone** in Archaeoceti and some basal Neoceti.

See also **subarcuate fossa**.

– cerebellar surface of the petrosal

The cerebellar surface of the **petrosal** in the dog consists of that portion of the petrosal that borders on the cerebellum (Evans and Christensen, 1979:132).

The periotic in delphinids has moved ventrally and no longer directly contacts the cerebellum. We use the term "**cranial surface of the periotic**" to refer to the surfaces that are known as cerebral surface and cerebellar surface in other mammals.

– cochlea

The mammalian cochlea is a part of the **osseous labyrinth** and is a spiral structure located in the periotic. The basal turn of the cochlea lies lateral to the ventral portion of the **internal acoustic meatus**, and it produces the bulk of the promontory of the petrosal (Gray, 1918:1050; Evans and Christensen, 1979:132, 1069, 1070; Schaller, 1992:532.20; Feneis, 1994:376.18). Eustachius and Lancisius (1714:109) referred to this as the *cochlea*.

In *Tursiops* and other delphinids, the cochlea, **spiral lamina**, and associated structures bear the same anatomical relationships as they do in the dog. The apical turn of the cochlea lies just dorsal to the **vestibular window** and the basal turn of the cochlea lies next to the **internal acoustic pore** (Ketten and Wartzok, 1990). The basal turn makes up the bulk of the promontory of the **periotic bone**.

– cochlear aqueduct (*aqueductus cochleae*)

The cochlear aqueduct in the dog runs ventrally from the ventral wall of the *scala tympani* near its origin to the external opening of the cochlear aqueduct. This canal contains the perilymphatic duct and provides communication between the subarachnoid space and the **vestibule**, **cochlea**, and **semicircular canals** (Evans and Christensen, 1979:1070, 1063). This canal is also known as the **cochlear canaliculus** (*canaliculus cochleae*) (Evans and Christensen, 1979:1063, fig. 19–3; MacPhee, 1981:47, 51).

In *Tursiops* the opening or external **aperture for the cochlear aqueduct** lies on the dorsal surface of the **periotic bone** on the posteromedial aspect of the cochlear process / ***pars cochlearis***.

= cochlear canaliculus (*canaliculus cochleae*)

See **cochlear aqueduct**.

– cochlear fossula

The cochlear fossula is a depression that, in some mammals, contains the **cochlear window** (**round window**, ***fenestra rotunda***) (MacPhee, 1981:51).

The cochlear window in *Tursiops* may open in a slight depression in the profile of the ***pars cochlearis***, forming an indistinct cochlear fossula. It is not known whether, as in some terrestrial mammals (Wible et al., 2004:75), the cochlear fossula in *Tursiops* contains a diverticulum of the **tympanic cavity**.

*** cochlear portion**

See ***pars cochlearis***.

– cochlear posterior pole

The cochlear posterior pole in mammals is the posterior part of the **cochlear portion** that contains the region of the **cochlear fossula** (MacPhee, 1981:51).

Tursiops lacks a cochlear fossula and does not have a distinct cochlear posterior pole.

= cochlear window = *fenestra rotunda* (Figure 25b,e,m,q,v–x)

*** cranial surface of the periotic** (Figure 25l)

The cranial surface of the **periotic bone** in delphinids is that surface that borders the cranial cavity and **posterior lacerate foramen**. The cranial surface is the dorsal surface of the periotic that bears the **internal acoustic meatus**.

= *crista falciformis* (Gray, 1918:143)

See **transverse crest of the internal acoustic meatus**.

– *crista interfenestralis*

The *crista interfenestralis* in many mammals (Wible and Gaudin, 2004) is a bridge or strut of bone separating the *fenestra ovalis* and ***fenestra rotunda***. The fossa for the stapedial muscle may develop onto the *crista interfenestralis*.

In *Tursiops* the *crista interfenestralis* is a broad raised surface that is not particularly distinct from other parts of the ***pars cochlearis***; it merges back into the indistinct **caudal tympanic process**.

= *crista parotica* = facial crest of the periotic bone (Wible and Gaudin, 2004:136, 174)

– *crista vestibuli* (Whitmore, 1953:132)

In archaic artiodactyls, a horizontal crest that separates the ***fenestra cochleae*** (= **round window**) from the **vestibule**.

We could not determine this internal feature in *Tursiops*.

– distal opening of the facial canal (Figure 25m)

See **facial canal**.

*** dorsal crest** (Fordyce, 1994:158,161) (Figure 25u)

In the sense of Whitmore (1953:131) the mammalian dorsal crest is synonymous with the **petrosal crest** of Evans and Christensen (1979:130) and the *crista partis petrosae* of Schaller (1992:22.16).

In the sense of Fordyce (1994:158,161), the dorsal crest of the periotic in archaic Odontoceti is the median dorsal elevation that extends from the **anterodorsal angle** posteriorly to a point lateral to the **aperture for the endolymphatic duct**. This crest is presumed to be the vestigial homologue of the **superior process** in the sense of Kellogg (1936) (Fordyce, 1994:158,160,161). Geisler and Luo (1996:1055) used the name **dorsolateral ridge of the *tegmen tympani***, while Luo and Gingerich (1999:41) discussed it under the term "dorsal edge of the *tegmen tympani*." It is not clearly homologous with the petrosal crest of the dog or deer.

In *Tursiops* and other delphinids, the dorsal crest is vestigial and indistinct, or absent. In some Archaeoceti and archaic Neoceti it is elevated into a plate-like process, the superior process of Pompeckj (1922) and others.

= dorsal ridge (Fordyce, 1994:149) = dorsal crest

*** dorsal tuberosity** (Figure 25t)

The dorsal tuberosity is a rounded eminence on the dorsolateral surface of the periotic in some Odontoceti. The dorsal tuberosity lies between the **cochlear portion** and the **posterior process of the periotic bone** (Fordyce, 1994:160, fig. 11b).

A moderately developed dorsal tuberosity is present in some *Tursiops*.

* **dorsal vestibular area** (*area vestibularis utriculo-ampullaris / foramen acusticum superius*) (Figure 25u)

The dorsal **vestibular area** in mammals is located dorsal to the **transverse crest of the internal acoustic meatus** and contains the *utriculus* and the *ampullae*. Nerve fibers that come from the dorsal vestibular area leave in the vestibular nerve (Evans and Christensen, 1979:132).

In the extinct mammal *Prokennalestes* (see Wible et al., 2001:8), the dorsal vestibular area [*foramen acusticum superius* of their use] is a blind pit with tiny perforations for the vestibular nerve, lying posterior to the proximal opening of the **facial canal** within the superior or dorsal acoustic foramen / *foramen acusticum superius*.

The vestibular nerve in *Tursiops* exits via the ***foramen singulare***, rather than by the pit-like feature noted by Wible et al. (2001). The **anterior meatal pit** (q.v.) of *Tursiops* should not be confused with the dorsal vestibular area in the sense of Wible et al.

= **dorsolateral ridge of the *tegmen tympani*** (Geisler and Luo, 1996:1055)

See **dorsal crest**.

= **dorsoventral vascular channel** (Luo and Gingerich, 1999:45)

See **anteroexternal sulcus**.

– **elliptical recess for the utricle**

In mammals, the elliptical recess for the **utricle** lies in the posterodorsal part of the **vestibule** (Evans and Christensen, 1979:1070). It is separated from the **spherical recess** (for the **saccule**) by the vestibular crus.

We could not confirm this feature for *Tursiops*.

= **endolymphatic duct**

See **aperture for the vestibular aqueduct**.

* **epitympanic foramen of the facial canal** = aperture of the facial canal (*apertura tympanica canalis facialis*) (Figure 25x)

Kellogg (1936) used this term for the ventral or **distal opening of the facial canal** (q.v.) in the middle ear cavity of Archaeoceti. ***Foramen faciale*** (q.v.) is a synonym. All odontocetes have an epitympanic foramen.

See **facial canal** for further discussion of this matter.

* **epitympanic hiatus** (*hiatus epitympanicus*) (Figure 25n,t,v–x)

Evans and Christensen (1979:1063) summarized structures in this region of the dog as including the *membrana shrapnelli* or *pars flaccida* of the **tympanic membrane**, which partly bounds the upper tympanic pouch, also known as Prussak's pouch. All these are soft tissue structures.

In *Tursiops* the bony epitympanic hiatus is a transverse depression in the **epitympanic recess**, laterally on the ventral surface of the periotic. In the isolated periotic, it lies between the **lateral tuberosity** (q.v.; which in delphinids is integral with the **parabullary ridge**) and **posterior process of the periotic bone**. In the isolated periotic, the hiatus has two parts: an anterior smooth surface immediately posterior to the **parabullary ridge** marks the exit of the **middle sinus**, while, more posteriorly, a rough surface that extends onto the base of the posterior process marks a contact for the **spiny process** of the squamosal bone.

When the periotic is articulated, the hiatus is delimited ventrally by the **sigmoid process** and the **tympanic notch** (or **tympanic incisure**) of the **bulla**. Posteriorly, at least in the articulated periotic of young animals, the hiatus is limited by the spiny process, which is a medial extension of the squamosal; the spiny process is variably developed in adults. (See, e.g., Boenninghaus, 1904; Kellogg, 1936:118; Yamada, 1953:20; Kasuya, 1973; Fordyce, 1994:160; Geisler and Luo, 1996:1053).

A crest is developed on the posterior surface of the sigmoid process and a corresponding crest on the posterior process of the periotic bone. These crests serve to limit the epitympanic hiatus ventrally; they also mark the tympanic notch.

Among living species this ventrally restricted aperture is peculiar to Odontoceti (Yamada, 1953:20), in which it is the site of exit of the middle sinus into the **tympanosquamosal recess**.

This feature was called the *ductus petro-tympanicus* by Beauregard (1893), the *apertura petrotympanicus* by Reysenbach de Haan (1957), the ***hiatus epitympanicus*** by Boenninghaus (1904), and the **upper tympanic aperture** by Kasuya (1973) and Yamada (1953).

In the dissected periotic of *Delphinus delphis*, the middle sinus arises at the epitympanic hiatus.

* **epitympanic recess** (*recessus epitympanicus*) (Figure 25v)

In mammals, the epitympanic recess forms the dorsal part of the **tympanic cavity** (Whitmore, 1953:133; Evans and Christensen, 1979:132, 134; MacPhee, 1981:52). In the dog the epitympanic recess has also been called the **fossa for the head of the malleus** (Evans and Christensen, 1979:1068) (but see **mallear fossa**). The incus, part of the stapes, and the head of the malleus lie in the epitympanic recess.

In humans, the **tympanic antrum** opens into the epitympanic recess (Gray, 1918:142).

In *Tursiops* this region is modified to form a distinct mallear fossa (q.v.) or *fossa capitis mallei*, and ***fossa incudis*** (q.v.). Laterally, the epitympanic recess passes into the ***hiatus epitympanicus***. The **fossa for the tensor tympani muscle** (q.v.) is reduced and is no longer a useful landmark. The epitympanic recess is bounded ventrally by structures of the **bulla** at the tympanic notch (or incisure), specifically the posterior face of the apex of the **sigmoid process** and the bony shelf that projects anteriorly from the posterior process.

Luo and Gingerich (1999:30) indicated that in Archaeoceti the epitympanic recess may include part of the squamosal as well as periotic, but in *Tursiops* the epitympanic recess includes only the periotic.

Kellogg appeared to use ***recessus epitympanicus*** (e.g., 1936 :27) in the sense of ***tegmen tympani*** (q.v.) of other authors, implying that it lies posterolateral to the fossa for the *m. tensor tympani.*

– **epitympanic sinus**

The epitympanic sinus (sensu van der Klaauw, 1931; as elaborated by Wible and Gaudin, 2004 for armadillos) is a diverticulum dorsal to the **epitympanic recess**, developed into the squamosal and the ***pars mastoidea*** of the **petrosal.**

The periotic in *Tursiops* lacks a distinct fossa for the epitympanic sinus. The soft tissues of the **middle sinus**, which issue dorsal to the epitympanic recess, are not clearly homologous with the epitympanic sinus of other mammals.

= Eustachian tube = auditory tube

= external aperture for the cochlear canaliculus (*apertura externa canaliculus cochleae*)
See **aperture for the cochlear aqueduct**.

= external aperture for the vestibular aqueduct (*apertura externa aqueductus vestibuli*)
See **aperture for the vestibular aqueduct**.

– external opening of the facial canal (Figure 25m)
See **facial canal** for further discussion.

= facet for the malleus = mallear fossa (Schulte, 1917:397)

*** facial canal** (*canalis facialis*) (Figure 25a,m,q,v)

The facial canal lies in the mammalian **petrosal** bone and transmits the facial nerve. In the dog and other mammals (Evans and Christensen, 1979:133,922; Schaller, 1992:22.6), the facial canal of the petrosal bone comprises the full route of the facial nerve from the **internal acoustic meatus** (proximally) to the **stylomastoid foramen** (distally) of the temporal on the skull surface. The more-distal path of the facial nerve is sometimes described as within the **stylomastoid canal** (q.v.). The facial canal is also known as the **Fallopian aqueduct** (Kellogg, 1936). The facial nerve at this point in the ear has also been termed the hyomandibular branch of the facial nerve (Wible et al., 2001:6, 14; Wesley-Hunt and Flynn, 2005:5). The **distal opening** or **aperture of the facial canal** is known as the **facial sulcus**.

The situation is modified in *Tursiops* and other Cetacea. The proximal (or cerebral, or internal, or dorsal) opening of the facial canal is in the ***area nervus facialis*** of the internal acoustic meatus, just dorsal to the transverse crest.

In Archaeoceti the opening has also been termed the internal **facial foramen** (Luo and Gingerich, 1999:45). For Cretaceous placental mammals, Ekdale et al. (2004:170) termed the opening the *foramen acusticum superius*. In *Tursiops* the distal opening is in the middle ear, lateral and slightly anterior to the ***fenestra ovalis***.

Synonyms for this foramen include epitympanic orifice (of Kellogg, 1936), ***foramen faciale***, **secondary facial foramen** (e.g., Ross and Covert, 2000:243), or ventral or **distal or external opening of the facial canal**. This is not to be confused with the stylomastoid foramen of other mammals.

See also **stylomastoid notch**.

= facial canal within the *tegmen tympani* (Novacek, 1986:59)
See **petrosal canal**.

*** facial crest of the periotic** (*crista facialis petrosi*) (Figure 25m,o,v)

According to van der Klaauw (1931:239) the mammalian *crista facialis petrosi* is the crest to which fuses the **tympanohyal**. Wible and Gaudin (2004:136,174) indicated that the *crista facialis* is synonymous with ***crista parotica*** and stated: "the lateral wall of the **facial sulcus** [has] a lambdoidal bifurcation into medial and lateral arms . . . . The more anteroventrally projecting lateral arm borders the aperture connecting the **tympanic cavity** proper and the **epitympanic sinus**; the medial arm is the *crista parotica*. Between these two arms is a small ovoid depression, the ***fossa incudis*** for the ***crus breve*** of the incus." The *fossa incudis* in *Tursiops* is bounded medially by a facial crest that continues posteriorly toward the position of the variably developed tympanohyal.

See discussion under **tympanohyal**; see also ***processus cristae facialis***.

= facial foramen (*foramen faciale*)
See ***foramen faciale*** and **facial canal**.

= **facial groove** = facial sulcus

* **facial sulcus** (Figure 25e,m,o,q,r,u–w)

The mammalian facial sulcus (Whitmore, 1953:131) occurs on the ventral surface of the periotic posterior (distal) to the **epitympanic foramen of the facial canal** (or **aperture of the facial canal**) and the **stylomastoid foramen**.

The facial sulcus is well developed on the **body of the periotic** medial to the ***fossa incudis*** and on the medial face of the posterior process in *Tursiops* and other Odontoceti (Fordyce, 1994:160).

See further discussion under **stylomastoid foramen**.

= *facies encephalica* (caudomedial part) (*facies posterior partis petrosae*) = medial surface of the petrosal

– *facies encephalica* (rostrodorsal part) (*facies rostralis partis petrosae*)

The *facies encephalica* (rostrodorsal part) is that part of the cranial surface of the mammalian **petrosal** that faces anterodorsally (Schaller, 1992:22.10). The rostrodorsal part lies on the anterior side of the *crista partis petrosae*. In humans it is known as the *facies anterior partis petrosae* (Feneis, 1994:14.1).

This part of the periotic is not distinct in *Tursiops*.

= Fallopian aqueduct (*aqueductus Fallopii*) = *aqueduct of Fallopius*
See **facial canal**.

= Fallopian foramen (Novacek, 1986:58)
See proximal opening of the **facial canal**.

= *fenestra cochleae* (Schulte, 1917:396; Whitmore, 1953:132)
See **cochlear window** and ***fenestra rotunda*** of "Periotic Bone."

* ***fenestra ovalis*** (Figure 25m,v–x)

The mammalian **vestibular window, vestibular fenestra,** or **oval window**, which is occluded by the **footplate of the stapes**, lies just anterior and slightly dorsolateral to the **cochlear window** (Evans and Christensen, 1979:132).

The *fenestra ovalis* in *Tursiops* and other delphinids opens lateral to the ***fenestra rotunda*** at the lateral edge of the ***pars cochlearis***, just medial to the epitympanic orifice (or **facial foramen**, ***foramen faciale***) for the facial nerve, and anterior to the fossa for the stapedial muscle.

The term "*fenestra ovalis*" has been used widely in cetacean osteological literature. Equally acceptable common synonyms include ***fenestra vestibuli***, oval window, and vestibular window.

* ***fenestra rotunda*** (Figure 25b,e,m,q,v–x)

The *fenestra rotunda* lies at the posterolateral end of the promontory of the mammalian **petrosal.** It is closed by the secondary **tympanic membrane** (Evans and Christensen, 1979:132). The **cochlear window** may lie within a **cochlear fossula** (MacPhee, 1981:51).

The *fenestra rotunda* in *Tursiops* lies at the posterior edge of the ***pars cochlearis*** in an indistinct cochlear fossula.

Some Odontoceti carry a fissure between the *fenestra rotunda* and the **aperture for the cochlear aqueduct** that may reflect a common embryological opening (Kellogg, 1923:53, fig. 2).

The term "*fenestra rotunda*" has been used widely in cetacean osteological literature by Kellogg (e.g., 1936:116) and others. Equally acceptable common synonyms include ***fenestra cochleae***, cochlear window, and **round window**.

Not to be confused with the *fenestra rotunda* of **tympanic bulla**, of Boenninghaus (1904: fig. G, item 19).

= ***fenestra vestibuli***

See **vestibular window**.

= ***fissura petrooccipitalis***

See ***fissura petrosoparoccipitalis***.

– ***fissura petrosoparoccipitalis*** = *fissura petrooccipitalis* (Kellogg, 1936:114)

The *fissura petrosoparoccipitalis* is the fissure between the archaeocete periotic and the **paroccipital process**, into which may extend part of the **posterior sinus** and/or the **peribullary sinus** (Pompeckj, 1922, as interpreted by Kellogg, 1936:114). We understand Kellogg to mean that the fissure developed posterior and dorsal to the periotic, in which case the structure possibly does not include a component of posterior sinus.

Luo and Gingerich (1999:20, tbl. 5, #34b) noted that the **petrosoparoccipital fissure** in Neoceti and some Archaeoceti comprises the enlarged **basicapsular fissure** plus **jugular foramen**. Enlargement was attributed to an expanded "medial **pterygoid sinus**" (sic). McPhee (1981), however, implied that the basicapsular fissure is medial, not posterior, to the **periotic bone** (**petrosal**), in which case the petroso-paroccipital fissure would not include the basicapsular fissure.

This region is so modified in adult *Tursiops* by the development of the cranial hiatus, and particularly by the large dorsally developed excavation in the anterior face of the paroccipital process, that the term is not easily applicable.

See also **petrobasilar canal** and **ventral petrosal sinus**.

= ***foramen faciale*** = epitympanic foramen

The *foramen faciale* of Denker was cited by van der Klaauw (1931:173) and identified by MacPhee (1981:55) as the *apertura tympanica canalis facialis*, or foramen through which the mammalian facial nerve enters the middle ear. **Epitympanic foramen of the facial canal** or **aperture of the facial canal** (q.v.) are preferred terms.

See also **facial canal** and **stylomastoid foramen**.

= **foramen for the facial nerve**

See **stylomastoid foramen**.

– **foramen for the greater superficial petrosal nerve** (*foramen n. petrosus major*)

In mammals, the foramen for the greater superficial petrosal nerve is the opening of the **petrosal canal** in the petrosquamous suture just lateral to the **canal for the trigeminal nerve**.

See **petrosal canal** for discussion of the situation in *Tursiops*.

– **foramen for the *ramus superior* of the stapedial artery**

Various placentals have a foramen for the *ramus superior* of the stapedial artery as an aperture in the roof of the middle ear, such as in the **tympanic process of the alisphenoid** next to the ***foramen ovale***, or between the **petrosal** and squamosal (Wible and Gaudin, 2004:153). Sometimes the feature may be an incisure rather than a foramen.

A foramen for the *ramus superior* of the stapedial artery has not been identified in *Tursiops*, and may not exist, given the likely vestigial nature of stapedial circulation.

See section on arterial circulation and basicranial foramina in "Multi-element Complexes."

* ***foramen singulare*** (singular foramen) (Figure 25a,u)

The *foramen singulare* is situated ventral to the transverse crest of the mammalian **internal acoustic meatus**. The vestibular nerve fibers from the **ventral vestibular area** (*sacculus*) pass through the *foramen singulare* (Evans and Christensen, 1979:132). Gray (1918:143) said that the *foramen singulare* is the opening for the nerve to the posterior semicircular duct.

The *foramen singulare* in delphinids is located in the internal acoustic meatus, lateral to the transverse crest. We use the latinized term in preference to the ambiguous "singular foramen."

= ***foramen stylomastoideum*** (stylomastoid foramen) = *foramen faciale* of Denker (cited by van der Klaauw, 1931:173)

See ***foramen stylomastoideum primitivum***, ***foramen stylomastoideum tertium***, and **stylomastoid foramen**.

– ***foramen stylomastoideum definitivum***

Novacek (1986:56; fig. 20) and MacPhee (1981:63) identified this as the definite bony aperture for the exit of the facial nerve from the mammalian middle ear.

Tursiops lacks a *foramen stylomastoideum definitivum*.

– ***foramen stylomastoideum primitivum***

In some archaic artiodactyls (Whitmore, 1953) and archaic insectivores (Novacek, 1986 fig. 20) the distal path of the facial nerve as it exits the middle ear cavity is enclosed in a **stylomastoid canal** (q.v.), which starts proximally (internally) at the *foramen stylomastoideum primitivum*, and opens laterally at the **stylomastoid foramen** (q.v.) or the ***foramen stylomastoideum definitivum*** (reviewed by Van der Klaauw, 1931:171). MacPhee (1981:63) stated that the *foramen stylomastoideum primitivum* is strictly not a foramen at all but is the place where the facial nerve penetrates fibrous tissue adjacent to the **tympanohyal** on the way to the neck.

Tursiops lacks a *foramen stylomastoideum primitivum*.

– ***foramen stylomastoideum tertium***

Wible and Gaudin (2004:154) reviewed the *foramen stylomastoideum tertium* of Patterson et al. (1989), noting that the latter proposed the term *foramen stylomastoideum tertium* for an aperture on the euphractine (armadillo) skull base, to distinguish it from the ***foramen stylomastoideum primitivum*** and the ***foramen stylomastoideum definitivum***. The *foramen stylomastoideum tertium* is the exit for the facial nerve, which leaves the **external acoustic meatus** at a sizeable gap between the ectotympanic and the **paroccipital process** of the **petrosal**.

Tursiops lacks a *foramen stylomastoideum tertium*.

= fossa at the aperture for the *ductus endolymphaticus* (Kellogg, 1936:116)
See **aperture for the vestibular aqueduct**.

= fossa for the head of the malleus (*fossa capitis mallei*)
See **mallear fossa**.

* **fossa for the stapedius muscle** (*fossa m. stapedius*) (Figure 25b,e,m,o–q,u–w)

In mammals, the fossa for the stapedius muscle is located on the dorsal aspect of the **facial canal** just proximal to the **stylomastoid foramen** (Evans and Christensen, 1979:133).

In *Tursiops* the fossa for the stapedius muscle is located immediately posterior to the **vestibular window** or **oval window** (***fenestra ovalis***), just dorsal to the **facial sulcus**, and between the ***pars cochlearis*** and the posterior process (Kasuya, 1973:2).

* **fossa for the tensor tympani muscle** (*fossa m. tensor tympani*) (Figure 25w)

The fossa for the mammalian tensor tympani muscle is a spherical depression that lies anterior to the **vestibular window** and medial to the **epitympanic recess** (Evans and Christensen, 1979:132; not in Schaller, 1992). In humans this feature is termed the **semicanal for the tensor tympani muscle** and includes part of the **musculotubal canal of the sphenoid bone** (Feneis, 1994:12.29).

The tensor tympani muscle is minute but present in Neoceti (Yamada, 1953; Purves, 1966), in contrast to the large tensor tympani in many other mammals. The identity of the fossa for the tensor tympani muscle (***fossa muscularis major*** of Reysenbach de Haan, 1957:42) has been confused. Schulte (1917:397) said that the region between the **accessory ossicle** (**uncinate process** [of the tympanic bulla] of Schulte) and ***pars cochlearis*** may correspond to the **groove for the tensor tympani muscle**. Kellogg (e.g., 1936) and later authors (e.g., Fordyce, 1994, Luo and Gingerich, 1999:45) also identified the fossa as formed by a groove (or, in Delphinidae, a narrow cleft) between the **mallear fossa** and *pars cochlearis*, or alternatively on the “tympanic side of the periotic” (Luo and Gingerich, 1999:45). Yamada (1953), however, identified the muscle origin as the “medial side of the **tubal tubercle**” [= accessory ossicle of the **tympanic bulla**]. Fraser and Purves (1960:118, and fig. 27) indicated a similar origin for *Globicephala*, stating: “the tensor tympani arises from the dorsal wall of the **tympanic cavity** near that part which transmits the **Eustachian tube**.”

Tursiops lacks a clearly defined fossa for the tensor tympani muscle on the medial face of the accessory ossicle, but the ossicle may carry fine striations consistent with the origin of muscle fibers directed toward the **muscular process of the malleus** (Figure 25w).

* ***fossa incudis*** (Figure 25m,v)

In mammals, such as armadillos (Wible and Gaudin, 2004:142), the ***crus breve*** of the incus is suspended from the skull by a ligament to a small pit-like *fossa incudis*, which is situated in the **petrosal** lateral to the ***crista parotica*** and the **facial sulcus** or **facial canal**.

In Cetacea, the *fossa incudis* lies posterolateral to the **epitympanic foramen of the facial canal** or **aperture of the facial canal** in Archaeoceti and many Neoceti. It receives the *processus breve* of the incus (Pompeckj 1922: pl. 1, fig. 1; Kellogg, 1936:25).

The *fossa incudis* is distinct in *Tursiops* and other delphinids.

= *fossa muscularis major* (Reysenbach de Haan, 1957:42)
See **fossa for the tensor tympani muscle**.

= *fossa muscularis minor* (Reysenbach de Haan, 1957:42; Novacek, 1986:56)
See **fossa for the stapedius muscle**.

* ***fovea epitubaria*** = *fossa epitubaria* (Kellogg, 1936:25, 27, fig. 5) (Figures 5, 25m,s,v)

The *fovea epitubaria* (e.g., Pompeckj, 1922: Archaeoceti) is a concave depression on the ventral surface of the **anterior process of the periotic bone**, just posterior or posteromedial to the **anterior bullar facet** of some Odontoceti (Fordyce, 1994:160) and immediately in front of the **mallear fossa**. It receives the **accessory ossicle** of the **tympanic bulla**, which in *Tursiops* fuses with the periotic immediately in front of the mallear fossa. The *fovea epitubaria* is distinct from the anterior bullar facet. Kellogg (1936:27, fig. 5) stated that the *fovea epitubaria* lodges the ***processus tubarius*** (sic; accessory ossicle), but the feature that he labeled as *fovea epitubaria* is lateral to the fovea and instead represents the ventral part of the **anteroexternal sulcus** of the **periotic bone**.

In *Tursiops* and other delphinids the *fovea epitubaria* is so large as to obliterate the anterior bullar facet and occupies the ventrointernal surface of the anterior process of the periotic bone. In Odontoceti other than delphinoids, the depressed outline of the *fovea epitubaria* is visible laterally, but in *Tursiops* and other delphinids the fovea is obscured by the enlarged **parabullary ridge**.

= fundus of the internal acoustic meatus
See **internal acoustic meatus**.

– genu of the facial canal (*geniculum canalis facialis*)

The genu (knee) of the mammalian **facial canal** is the sharp turn that the facial canal makes in the **petrosal** in its course from the **internal acoustic meatus** to the **stylomastoid foramen**. The canal is slightly enlarged at the genu to accommodate the geniculate ganglion of the facial nerve. The genu may be enlarged to form a **supracochlear cavity** (q.v.).

In some cetaceans, a distinct canal for the greater superficial petrosal nerve arises at the genu, which probably is also the source of the minor superficial petrosal nerve; the condition in *Tursiops* is uncertain.

There have been no reported deviations of the genu in delphinids from the situation seen in the dog.

– groove for caudal meningeal artery (*sulcus a. meningea caudalis*)

The groove for the mammalian caudal meningeal artery (posterior meningeal artery) occurs on the lateral surface of the **petrosal** in equids (Schaller, 1992:22.5; not in Feneis, 1994). This appears to be absent in humans (Gray, 1918:557) and the dog (Evans and Christensen, 1979:658).

There is no obvious groove for the caudal meningeal artery on the periotic in *Tursiops*, and a close relationship with the meninges is unlikely, given the separation of the ear from the brain. Vascular structure around the ear has yet to be determined by dissection.

– groove for dorsal petrosal sinus (*sulcus sinus petrosi dorsalis*)

The groove for the dorsal petrosal sinus (groove for the superior petrosal sinus) lies on the surface of the **petrosal crest** in some mammals (Schaller, 1992:22.17; Feneis, 1994:14.10).

The venous sinus system in the odontocete cranium is extremely complex. The dorsal petrosal sinus presumably exists (Boenninghaus, 1904: pl. 13, fig. 13, item 11; fig. 14, item 6) but does not leave a recognizable sulcus on the periotic in *Tursiops*. For Archaeoceti, Pompeckj (1922: figs. 3, 4, 6, 7) identified a groove for a *sulcus peripetrosus superior* on the wall of the squamosal immediately dorsal to the **superior process**, but the latter sulcus is not clearly for the dorsal (superior) petrosal sinus.

– groove for occipital artery (*sulcus a. occipitalis*)

The groove for the occipital artery in humans lies on the posteroventral external surface of the **petrosal**, medial to the mastoid process and **mastoid notch** of the temporal bone and lateral to the occipital margin (Feneis, 1994:12.20). This feature was not mentioned for equids, bovids, caprids, suids, and canids (Sisson and Grossman, 1953).

The groove for the occipital artery is not recognizable in *Tursiops*. Vascular structure around the ear has yet to be determined by dissection.

– groove for sigmoid sinus (*sulcus sinus sigmoidei*)

The groove for the sigmoid sinus in humans lies on the posterodorsal aspect of the cranial surface of the **petrosal** (Feneis, 1994:12.19; not in Schaller, 1992). The sigmoid sinus passes over the posterior end of the petrosal in canids but does not leave an impression on that bone.

The venous sinus system in the odontocete cranium is extremely complex. The sigmoid sinus presumably exists but does not leave a recognizable groove on the periotic.

= groove for stapedial artery

See **stapedial artery groove.**

= groove for tensor tympani muscle

See **fossa for the tensor tympani muscle.**

– groove on ventral surface of the *pars cochlearis*

Schulte (1917:397) commented that the ventral surface of the ***pars cochlearis*** in *Kogia* becomes distinctly grooved toward the margin, anterior to the ***fenestra ovalis***. Such a groove is readily apparent in the anterior view of the periotics of young *K. simus* (USNM 550472). Schulte related the groove to the structure of the ***osseous tuba***.

Tursiops periotics have an indistinct groove on the ventral surface of the *pars cochlearis*, but it is much less developed than in *Kogia*.

See **musculotubal canal of the tympanic bulla.**

= *hiatus epitympanicus*

See **epitympanic recess.**

= *hiatus Fallopii* = aperture for the major petrosal nerve

The *hiatus Fallopii* is the anterior opening of the **petrosal canal**, and is widely recognized among eutherians (e.g., Novacek, 1986:59; Luo and Gingerich, 1999:42; Ross and Covert, 2000:243; Wible and Gaudin, 2004:155). The foramen is the exit for the greater petrosal nerve (also known as the palatine ramus of the facial nerve, or superficial petrosal nerve of some authors; Sanchez-Villagra and Wible, 2002:35). The foramen has also been named the **anterior fissure of the facial foramen**, the **hiatus of the facial canal** (*hiatus canalis facialis*), the hiatus for the greater petrosal nerve, the **opening for the major petrosal nerve** (*hiatus canalis nervi petrosi majoris*), and *hiatus Falopii* (which is a misspelling by Schulte, 1917). According to Wible (2003:172), Marshall and de Muizon (1995) used the term “median **lacerate foramen**” for the foramen for the greater petrosal nerve. Wible and Gaudin (2004:175) included **Fallopian aqueduct** as a synonym of *hiatus Fallopii*, citing McDowell (1958), but the latter identified the Fallopian aqueduct (McDowell, 1958:124) correctly as the path of the facial nerve through the **petrosal**, or **facial canal** in our use.

For the situation in *Tursiops*, see discussion under **petrosal canal** and under **aperture for the major petrosal nerve** (the latter used here as an alternative to *hiatus Fallopii*).

= hiatus of the facial canal (*hiatus canalis facialis*) (Gray, 1918:142; Whitmore, 1953)

See **petrosal canal.**

*** internal acoustic meatus** (*meatus acusticus internus*) (Figures 25c,e,l,o,p,t, 28)

The mammalian internal acoustic meatus lies just ventral to the **cerebellar fossa** on the posteromedial surface of the **petrosal**. Its opening is the **internal acoustic pore**. The internal acoustic meatus contains the transverse crest, the canal for the vestibulocochlear nerve, and the **canal for the facial nerve** (Whitmore, 1953:131; Evans and Christensen, 1979:132). It is also known as acoustic foramen (Owen, 1866a:40). Vesalius (1543:52; Vesalius et al., 1998:131) referred to the internal and external acoustic meati as the *quinti nervorum cerebri paris meatus, auditorius ve porus*.

The internal acoustic meatus in delphinids is located near the middle of the dorsal surface of the ***pars cochlearis***, at the base of the **cochlea**. Its opening is the **acoustic pore**. It contains the transverse crest, the canal for the vestibulocochlear nerve, the **spiral cribriform tract** (***tractus spiralis foraminosus***), the ***foramen singulare***, and the **ventral foramen of the facial canal** (internal aperture for the **facial canal** (**Fallopian aqueduct**)) (e.g., Kellogg, 1928: fig. 23; Kasuya, 1973; Fordyce, 1994:160).

– internal acoustic pore (*porus acusticus internus*)

The lip of the opening of the mammalian **internal acoustic meatus** is the internal acoustic pore. It lies on the posteromedial surface of the **petrosal** (Evans and Christensen, 1979:132).

The internal acoustic pore in delphinids is located near the middle of the dorsal surface of the ***pars cochlearis***.

Yamagiwa et al. (1999:294) referred to the *porus acusticus internus* in *Grampus* in a different sense, as the "bony exit for the vestibulocochlear and facial nerves" formed by the basioccipital, parietal, and exoccipital.

Given the difficulty of differentiating between the internal acoustic meatus (canal) and the lip of the internal acoustic meatus (internal acoustic pore), plus the differing use of internal acoustic pore by Yamigawa et al., we do not recommend using it.

= internal auditory canal

See **internal acoustic meatus**.

= internal auditory meatus (*meatus auditorius internus*)

See **internal acoustic meatus**.

= internal auditory meatus (internal auditory foramen)

See **internal acoustic pore**.

– intrajugular process of the periotic bone (*processus intrajugularis*)

In mammals, the intrajugular process of the **periotic bone** divides the **jugular foramen** into a posterolateral portion for the jugular vein and an anteromedial portion for the glossopharyngeal nerve, vagus nerve, and accessory nerve (Feneis, 1994:14.20).

This is not to be confused with the **jugular process** of the occipital in the dog, which is a bony process projecting posteroventrally alongside the **occipital condyles** (Evans and Christensen, 1979:151–153). The jugular process is also called the paracondylar or **paroccipital process**.

There is some question about the intrajugular process of the periotic bone in domestic animals. Schaller (1992:16.21) illustrated it as a process on the **occipital bone** (basioccipital) that divides the jugular foramen.

Due to the modification in the ear region of Neoceti, an intrajugular process of the periotic bone can no longer be recognized.

= labyrinthine part (*pars labyrintha*) (Turner, 1913:20)

See ***pars labyrintha***.

– lateral groove

Fordyce (1994:160) labeled a **shallow lateral groove** located mid-length on the lateral surface of the periotic in archaic Odontoceti, between the **lateral tuberosity** and **dorsal tuberosity**.

The lateral groove is not present in *Tursiops*.

– lateral projection of the anterior process

Geisler and Luo (1996:1052) identified a lateral projection or ridge on the **anterior process of the periotic bone** in Mysticeti. The projection forms the ventral edge of the **squamosal fossa**. Geisler and Luo (1996:1054) stated that this process can become developed to resemble the **ventrolateral tuberosity** (= lateral tuberosity of Barnes, 1978), but that it is not homologous.

Tursiops lacks a lateral projection on the anterior process.

*** lateral tuberosity** (Figure 25n)

In many Odontoceti the lateral tuberosity (Barnes, 1978:5) of the periotic is located posterolaterally on the **anterior process of the periotic bone**, lateral to the **vestibular window**, and carries the **mallear fossa** medially.

In *Tursiops* and other delphinoids the lateral tuberosity is small, but in some other Odontoceti it is a well-formed subcircular to subquadrate to irregular projection. The lateral tuberosity is closely approached by the edge of the **sigmoid process** of the **bulla**.

Luo and Gingerich (1999:45, e.g., fig. 20) proposed the term "**ventrolateral tuberosity**" for this feature. They also identified the term "**ventral tuberosity**" as a synonym, ascribing it to Fordyce (1994:160) who, however, used lateral tuberosity in the sense of Barnes. De Muizon (1987) proposed the term "ventral tuberosity."

See also ***prominentia canalis lateralis*** and ridge or **lateral projection of the anterior process**.

*** mallear fossa** (Figure 25m,v,x)

In the dog the **head of the malleus** lies in the **epitympanic recess** (Evans and Christensen, 1979:132, 1066, 1068), which is also called the **fossa for the head of the malleus** (Evans and Christensen, 1979:1068).

The mallear fossa (sensu Fordyce, 1994:160), or *fossa* (or *fovea*) *capitis mallei* of some authors (e.g., Pompeckj, 1922; de Muizon, 1987), or **facet for the malleus** (*Kogia*; Schulte, 1917:397), is a hemispherical depression that receives the head of the malleus. The fossa lies on the ventral surface of the **anterior process of the periotic bone**, immediately behind the ***fovea epitubaria*** and just medial to the **lateral tuberosity**. It is part of the epitympanic recess (Fordyce, 1994:160). The mallear fossa receives the head of the malleus.

In *Tursiops* the mallear fossa is small but well developed.

– mastoid canaliculus (*canaliculus mastoideus*)

The mastoid canaliculus is a small canal transmitting the auricular branch of the vagus nerve into the substance of the periotic in some mammals (MacPhee, 1981:57; Schaller, 1992:22.30; Feneis, 1994:14.25). In humans the mastoid canaliculus originates in the jugular fossa (Gray, 1918:144, 181). In horses it lies on the caudomedial aspect of the exoccipital margin of the petrous part of the temporal bone (Schaller, 1992:22.30).

The mastoid canaliculus has not been reported in *Tursiops*.

– mastoid cells

The mastoid cells or air cells in humans are cavities that occupy the mastoid process of the temporal bone and that communicate with the **tympanic antrum** (Gray, 1918:142; van der Klaauw, 1931:81ff.). The tympanic antrum in turn opens forward into the **epitympanic recess**.

The posterior process in *Tursiops* lacks mastoid cells, and there is no tympanic antrum.

– mastoid foramen (*foramen mastoideum*)

The mastoid foramen in mammals lies at the juncture of the exoccipital, **supraoccipital**, and the **petrosal** bones (Evans and Christensen, 1979:123, 133, 155; Schaller, 1992:10.29). This foramen appears to be variable in occurrence. In humans the mastoid foramen transmits a vein to the **transverse sinus** and a branch of the occipital artery to the dura (Gray, 1918:141; Feneis, 1994:12.21). Vesalius (1543:53; Vesalius et al., 1998:131) referred to the mastoid foramen as the *foramen id ad posteriorem regionem processus mammillaris*.

In *Tursiops* a single foramen or several grooves may open immediately dorsal to the **posterior process of the tympanic bulla** and at the anterolateral corner of the exoccipital. Its development varies ontogenetically. Study of soft tissues is needed to identify this foramen properly. A large foramen, perhaps the mastoid foramen, may open dorsal to the posterior process of the **tympanic bulla** in *Kogia* spp.

– mastoid notch (*incisura mastoidea*)

The mastoid notch in humans is a notch between the mastoid process of the temporal bone and the posterior portion of the squamosal (Feneis, 1994:12.18; not in Schaller, 1992), near the origins of the digastric muscle and *longus capitis* muscle (Gray, 1918:179). Gray (1918:141) identified it as the origin for the digastric. The mastoid notch lies on the posteroventral aspect of the external surface of the temporal. Novacek (1986:56) named this the groove for the digastric muscle.

Due to the separation of the periotic from the skull in Odontoceti, the mastoid process no longer contacts the squamosal, and the mastoid notch is absent.

– mastoid process of the petrosal (*processus mastoideus*)

The mastoid process of the mammalian **petrosal** lies between the **mastoid foramen** in the exoccipital and the **stylomastoid foramen** in the petrosal. The mastoid process is at the posterolateral corner of the petrosal (Evans and Christensen, 1979:133; Schaller, 1992:22.4; Novacek, 1986:54; 1993:462; Feneis, 1994:12.17). Vesalius (1543:22,23) referred to the mastoid process as the *mammillaris processus*, while Eustachius and Lancisius (1714:104, 105, 109) referred to it as the *processus mastoideus* but later (1714:112) referred to it as the *apophysis mammilaris*. Wible and Gaudin (2004:138) elaborated on MacPhee's (1981:57) concern that "mastoid process" is used with such variation in mammalian osteology that it is best avoided.

Past authors have used the term "mastoid" on the cetacean skull for features of the periotic bone, **tympanic bulla**, and squamosal bone. Because of such confused use in Cetacea, we use the terms **posterior process of the periotic bone** (q.v.) and **posterior process of the tympanic bulla** (q.v.), and recommend that "mastoid" not be used.

For the homology and contact relationships of "mastoid" elements, and references to past use, see discussion under **posterior process of the periotic bone** and **posterior process of the tympanic bulla** in "Tympanic Bulla."

= mastoid region

See **posterior process of the periotic bone**.

– mastoid tubercle

The mastoid tubercle (Novacek, 1986:56, fig. 20) is that part of the **mastoid process of the petrosal** that contributes ventrally to the **stylomastoid canal** (q.v.) in mammals. Novacek speculated that the mastoid tubercle might be partly composed of the **tympanohyal** (q.v.). See also **posterior process of the periotic bone**.

The tympanohyal region of the posterior process of the periotic bone in *Tursiops* and other delphinids, ventral to the **facial sulcus** and the stapedial muscle fossa, may take the form of a minute tubercle.

– medial surface of the petrosal (*facies medialis partis petrosae*)

The medial surface of the **petrosal** bone is that part of the cranial surface that is located on the posteromedial side of the mammalian *crista partis petrosae*, including the area around the **internal acoustic meatus** (Schaller, 1992:22.18). In humans it is known as the *facies posterior partis petrosae* (posterior surface of the petrous temporal) (Feneis, 1994:14.11).

The periotic in *Tursiops* is modified significantly from the situation in other mammals, so that medial surface can be used only in a general sense.

= median petrosal crest (Novacek, 1986:42, fig. 15)

See **petrosal crest**.

*** median promontorial groove** (Figure 25u,w)

In some Mysticeti and Archaeoceti (Geisler and Luo, 1996:1054; Luo and Gingerich, 1999:30), a median promontorial groove arises near the ***fenestra rotunda*** and extends around the medial rim of the **internal acoustic meatus**.

A poorly developed groove is present on the medial face of the ***pars cochlearis*** in *Tursiops*, but we have not found reports of a promontorial artery in *Tursiops*, and the homology with median promontorial groove has yet to be confirmed by dissection. The groove seems equally likely to mark the dorsolateral limit of the soft tissues of the **peribullary sinus** on the surface of the periotic.

– *modiolus*

The *modiolus* is the cone-shaped bony core of the mammalian **cochlea** (Schaller, 1992:532.24; Feneis, 1994:342.22). It contains the ganglionic canal for the cochlear nerve and forms the medial wall of the **spiral canal**.

The *modiolus* in Odontoceti is larger than that of other mammals (e.g., Luo and Marsh, 1996).

– occipital surface (*facies occipitalis*)

The *facies occipitalis* is that portion of the mammalian **petrosal** facing the exoccipital (Schaller, 1992:22.3; not in Feneis, 1994). Schaller illustrated it in the horse where it appears to be equivalent to the occipital margin. It is not illustrated elsewhere.

In *Tursiops* the periotic does not contact the exoccipital.

– opening for the lesser petrosal nerve (*hiatus canalis nervi petrosi minoris*)

In humans the opening for the lesser (or minor, or smaller) petrosal nerve is located on the anterolateral aspect of the cranial surface of the **petrosal** bone, just lateral to the opening for the greater petrosal nerve (Feneis, 1994:14.5; not in Schaller, 1992) and lateral to the opening of the **facial canal** (Gray, 1918:1047).

The lesser petrosal nerve in humans arises from the tympanic plexus, where it communicates with the tympanic branch of the glossopharyngeal (Gray, 1918:1047). It passes dorsally around the tensor tympani muscle, then anteriorly on the dorsolateral aspect of the **auditory tube** to the otic ganglion (Evans and Christensen, 1979:926). The nerve passes through the anterior part of the periotic just posterior to the ***foramen ovale*** (Feneis, 1994:290.16) and exits the middle cranial fossa through the sphenopalatine fissure below the *foramen ovale* to join the otic ganglion (Schaller, 1992:472.2, 474.21; Feneis, 1994:290.16). The lesser petrosal nerve bears parasympathetic fibers from the tympanic plexus to the otic ganglion (Feneis, 1994:294.15).

The opening for the lesser petrosal nerve has not been identified in *Tursiops*. It may be associated with one of the **anterointernal sulci** that lie on the medial surface of the **anterior process of the periotic bone**.

– opening for the major petrosal nerve (*hiatus canalis nervi petrosi majoris*)

In mammals the opening for the major petrosal nerve lies in the petrosquamous suture just lateral to the **canal for the trigeminal nerve** (Evans and Christensen, 1979:133). In humans the opening for the major petrosal nerve is located on the anterolateral aspect of the cranial surface of the **petrosal** just medial and posterior to the **opening for the lesser petrosal nerve**, lateral to the **pyramid**, and anterior to the **arcuate eminence** (Feneis, 1994:14.4). The major petrosal nerve runs in the **petrosal canal**.

In some specimens of *Tursiops* the petrosal canal exits from the periotic in the groove (**anterior incisure**) between the ***pars cochlearis*** and **anterior process of the periotic bone** on the anterior aspect of the periotic. The opening for the major petrosal nerve is 2–3 mm ventral to the dorsal surface of the cochlear process. The proximal end of the petrosal canal is 1–2 mm within the **facial canal.** In other specimens of *Tursiops*, such as those that we have illustrated, the petrosal canal appears to be nonexistent, the major petrosal nerve branching off the facial nerve cranial to the facial canal.

See further comments under **petrosal canal**.

= opisthotic portion of the periotic

See **posterior process of the periotic bone**.

– osseous labyrinth (*labyrinthus osseus*)

The mammalian osseous labyrinth consists of the **cochlea, semicircular canals**, and the **vestibule** and is contained in the **petrosal** (Gray, 1918:1047; Schaller, 1992:532.1; Evans and Christensen, 1979:132; Feneis, 1994:374.20). Eustachius and Lancisius (1714:107) referred to the osseous labyrinth as the *labyrhinthi ductus*. Eustachius and Lancisius (1714:107) referred to a part of the osseous labyrinth when they mentioned the *spiralis labyrinthi ductus*.

The osseous labyrinth in delphinids consists of the same elements as in the dog.

See ***pars labyrintha***.

– otic capsule

The mammalian otic capsule consists of the cartilaginous structure that surrounds the inner ear in the embryo.

= otic portion

Fraser and Purves (1960:34) used the term "otic portion" apparently for the body of the periotic (q.v.) in *Balaenoptera*.

See **body of the periotic**.

= oval window

See ***fenestra vestibuli***.

* **parabullary ridge** (Figure 25n,t,v,y)

The parabullary ridge (Fordyce, 1994:161) is a ridge on the periotic immediately lateral to the **anterior bullar facet** in some fossil Odontoceti. It may be equivalent to the "distinct ventral rim" or "ventral swelling" of de Muizon (1987:7).

Tursiops has a well-developed parabullary ridge, which is prominent especially on the lateral surface of the **anterior process of the periotic bone** about 5 mm dorsal and slightly lateral to the contact with the **accessory ossicle** of the **tympanic bulla.**

– *pars canalicularis* (canalicular part) = tympanic process (Wible et al., 2004:75)

MacPhee (1981:58) followed de Beer (1937) in recognizing the canalicular part as the posterodorsal portion of the mammalian **otic capsule** (of the periotic) that houses the **utricle** and **semicircular canals**. See also **body of the periotic, *pars cochlearis***, and ***pars labyrintha***.

The *pars canalicularis* is present but not distinct on the exterior of the periotic in *Tursiops*.

Luo and Gingerich (1999:45) observed that the *pars canalicularis* forms part of the cranial face of the periotic of Archaeoceti.

* ***pars cochlearis*** = cochlear part or cochlear portion (Figure 25b,d,l,o–q,w)

The *pars cochlearis* or **cochlear portion** is a rounded medial eminence on the mammalian periotic that contains the **cochlea.**

The *pars cochlearis* in *Tursiops* is a rounded medial eminence on the periotic that contains the cochlea and, dorsally, the **internal acoustic meatus** and associated structures within the **meatus**, and the apertures for the **cochlear aqueducts** and **vestibular aqueducts**. The anterior limit is at the **anterior incisure**; medially and posteriorly, the *pars cochlearis* passes into the **body of the periotic**, the ***pars canalicularis* / *pars labyrintha***, and the posterior process without obvious boundaries.

The term "cochlear portion" is an appropriate alternative.

– *pars labyrintha* (labyrinthine part)

The **labyrinthine part** of the mammalian periotic contains the **cochlea, vestibule**, and **semicircular canals** (Turner, 1913:20). This is in part synonymous with the ***pars canalicularis*** and with the ***pars vestibularis***.

In adult *Tursiops* the *pars labyrintha* is present but not distinct from other parts of the periotic.

= *pars mastoidea* (Anderson, 1879:502) = mastoid process

In this sense, applied to the odontocete *Platanista*, the *pars mastoidea* is not to be confused with that ventral part of *m. cleidocephalicus* that attaches to the mastoid process (Schaller, 1992:104.12).

See **posterior process of the periotic bone, posterior process of the tympanic bulla.**

= *pars vestibularis* (vestibular part or vestibular portion)

See **vestibular part, body of the periotic.**

= perilymphatic foramen (Luo and Gingerich, 1999: fig. 19)

See **cochlear aqueduct.**

* **periotic bone** (Figures 25a–e,l–q,t–x, 28)

The periotic bone (Mivart, 1892:69) in Cetacea is the equivalent of the petrous and mastoid parts of the temporal bone in other mammals. The **petrosal part of the temporal** bone is spatially separated from the squamous part in delphinids and other Cetacea.

We recommend the term "periotic bone" for *Tursiops* because of its long historical use for an element distinct from the temporal bone. The periotic contains the inner ear (**cochlea** and labyrinth), bounds the middle ear, serves as an origin for middle ear muscles, and transmits nerves and vessels.

The periotic bone also has been termed "cetotolite" (Owen, 1846:527) or "cetolith" (Yamada, 1953:18; Reysenbach de Haan, 1957). In other mammals, the petrosal part of the temporal bone has sometimes been loosely termed the "**pyramid**."

In *Tursiops* the periotic bone is sutured with the more ventrally placed **tympanic bulla**, but it has lost close sutural contact with the squamosal bone (squamous portion of the temporal of some other mammals). It lies on the ventral surface of the posterolateral margin of the skull, associated with but not contacting the **alisphenoid**, parietal, exoccipital, and basioccipital bones, and it lacks a mastoid exposure laterally on the skull wall.

Major parts of the periotic bone include the **anterior process**, the **body of the periotic** (including the ***pars vestibularis***), the **cochlear portion** or ***pars cochlearis***, and the posterior process (mastoid process of the periotic or ***pars mastoidea*** of past use).

See also **petrosal**.

– periotical processes

The periotical processes consist of both the anterior and posterior process of the cetacean periotic (Oelschläger, 1986a:353; not in Schaller, 1992; not in Feneis, 1994). We suggest that this term is of limited use.

– periotic canal (*canalis perioticus*) (McFarland et al., 1979:10) = internal acoustic meatus

The periotic canal is the passageway in the **petrosal** for the facial and auditory nerves and associated blood vessels (McFarland et al., 1979:10).

With the separation of the periotic from the tympanic portions of the temporal bone in Cetacea, the only place where the facial nerve and the auditory nerve run together through a bone is the **internal acoustic meatus**. The nerves do not run through a canal.

– periotic capsule

Not a postnatal term; not used by Schaller, 1992; or Feneis, 1994.

– petrobasilar canal = petrooccipital canal

In the dog the petrobasilar canal is bounded laterally by the **petrosal** and **tympanic bulla** and medially by the basioccipital bone. It parallels the **carotid canal of the sphenoid** and lies medial to it. The petrobasilar canal lies in the **petrooccipital fissure** and transmits the **ventral petrosal sinus** (Schaller, 1992:12.6; not in Feneis, 1994). It is also known as the petro-occipital canal (Evans and Christensen, 1979:134, 793).

The medial part of the petrobasilar canal in the mammalian basioccipital contains the ventral petrosal sinus (Evans and Christensen, 1979:134, 793) and has been termed the groove for the petrosal sinus, or *sulcus sinus petrosi ventralis* (Schaller, 1992:16.6).

The petrobasilar canal is not developed in *Tursiops* due to the separation of the **bulla** and periotic from the basioccipital. The ventral petrosal sinus probably occurs in *Tursiops* and is present in *Phocoena* (Boenninghaus, 1902; Fraser and Purves, 1960: fig. 2), but the anatomical situation with the ventral venous sinuses in delphinids is very complex and needs more descriptive work.

See also **ventral petrosal sinus**, **cranial hiatus**, and ***fissura petrosoparoccipitalis***.

– petrobasilar foramen

The petrobasilar foramen is the anterior opening of the mammalian **petrobasilar canal**. It lies just posteromedial to the **internal carotid foramen** (Evans and Christensen, 1979:156).

The petrobasilar canal does not exist in delphinids due to the separation of the **bulla** and periotic from adjacent parts of the braincase.

– petromastoid bridge

The petromastoid bridge is the bony contact between the *promontorium* dorsal to the **round window** (**cochlear window**) and the mastoid process in archaic mammals (Novacek, 1986:56).

The petromastoid bridge is not distinct in *Tursiops*, in delphinids, or in other Cetacea.

– petrooccipital canal (*canalis petrooccipitalis*)

See **petrobasilar canal**.

= petrooccipital fissure (*fissura petrooccipitalis*) = petrosoparoccipital fissure

See ***fissura petrosoparoccipitalis***, **petrobasilar canal**.

= petrosal (*pars petrosa*) = petrosal part of the temporal = periotic bone

The **petrosal part of the temporal** bone is located medially in the temporal complex and contains the inner ear. In some mammals it is slightly pyramidal in shape and is sometimes referred to as the **pyramid** (Evans and Christensen, 1979:129).

The petrosal part of the temporal bone is spatially separated from the squamous part in delphinids and other Cetacea and is widely known as the **periotic bone** (q.v.). This use, which we support for *Tursiops*, is historically widespread in cetacean literature.

*** petrosal canal** (*canalis petrosus*) (Figure 25a)

The petrosal canal or *hiatus canalis facialis* (Whitmore, 1953) is a small canal that runs anteriorly from the **genu of the facial canal** to exit in the petrosquamous suture, just lateral to the **canal for the trigeminal nerve** in the dog (Evans and Christensen, 1979:133), or on the anterior face of the periotic in artiodactyls. See also ***hiatus Fallopii***.

This appears to be the structure identified by Novacek (1986:59) for archaic mammals as the **facial canal within the *tegmen tympani***, for the intermedius branch of the facial nerve. Novacek identified this canal as opening at the *hiatus Fallopii*. For some Mysticeti, Geisler and Luo (1996: fig. 3) noted that the canal is in the form of a fissure that they termed the **anterior fissure of the facial foramen**.

The mammalian petrosal canal carries a branch of the facial nerve, the major petrosal nerve (*n. petrosus major*) (Evans and Christensen, 1979:922). The major petrosal nerve or greater petrosal nerve carries fibers that are destined for the pterygopalatine ganglion. The major petrosal nerve is also known as the greater superficial petrosal nerve in humans (Gray, 1918:892).

In some specimens of *Tursiops* the petrosal canal exits from the periotic in the **anterior incisure** or groove between the ***pars cochlearis*** and **anterior process** on the anterior aspect of the periotic. The aperture for the petrosal canal is 2–3 mm ventral to the dorsal surface of the cochlear process. The proximal end of the petrosal canal is 1–2 mm within the **facial canal**. In some specimens of *Tursiops* the petrosal canal cannot be identified as a discrete structure. In other Odontoceti, the petrosal canal may form as a reentrant in the anterior border of the internal aperture for the facial canal. These inferred relationships have yet to be established by dissection.

– petrosal crest

The petrosal crest in mammals is a sharp crest that lies on the medial surface of the petrous part of the temporal, just dorsal to the **internal acoustic meatus**, **cerebellar fossa**, and the **canal for the trigeminal nerve** (Evans and Christensen, 1979:130, 132; Schaller, 1992:22.16; not in Feneis, 1994). In the dog, the petrosal crest may be an anterior continuation of the *tentorium* cerebelli.

Whitmore termed this the "**dorsal crest** of the pars petrosa" in archaic artiodactyls: an elevated region that is posterior to and distinct from the **superior process** (Whitmore, 1953:131).

Novacek (1986:42, fig. 15) identified a **median petrosal crest** in the archaic insectivore *Leptictis*. This crest lies anterior to the internal acoustic meatus and medial to the **subarcuate fossa**.

The petrosal crest has not been reported for Cetacea; it is not homologous with the dorsal crest (q.v.).

– petrosal fossula (*fossula petrosa*)

The mammalian petrosal fossula is a small fossa that holds the distal ganglion of the glossopharyngeal nerve (Schaller, 1992:22.34). The petrosal fossula is located on the posteromedial aspect of the cranial surface of the **petrosal**, just dorsal to the **petrotympanic fissure** and **tympanomastoid fissure of the tympanic bulla**. In humans the petrosal fossula lies in the bony crest between the **carotid canal of the sphenoid** and the jugular fossa and houses the tympanic ganglion of the glossopharyngeal nerve (Feneis, 1994:14.29).

Tursiops appears to lack a petrosal fossula.

= petrosal part of the periotic

See **petrosal**.

= petrosal part of the temporal

See **petrosal**.

– petrosal ridge

The petrosal ridge is a feature on the *promontorium* of archaic mammals that marks the contact with the underlying **tympanic bulla** (Novacek, 1986:55).

Tursiops and other Neoceti lack a petrosal ridge.

= petrosoparoccipital fissure (Luo and Gingerich, 1999:20, tbl. 5, #34b)

See ***fissura petrosoparoccipitalis*** and **cranial hiatus**.

– petrosquamosal fissure (*fissura petrosquamosa*)

The petrosquamosal fissure lies on the dorsal surface of the **petrosal** and separates the latter from the squamosal in some mammals (goat, sheep, pig, horse; Schaller, 1992:22.37). In other species the petrosal and the squamosal are not separated by a fissure.

The contact between the periotic and squamosal has been greatly reduced in *Tursiops* and many other Odontoceti, so that the periotic is partly roofed dorsally by the squamosal and is loose in the macerated skull. The petrosquamosal fissure in the normal mammalian sense thus is absent.

– petrosquamosal suture

The petrosquamosal suture lies on the medial surface of the **squamous part of the temporal bone** and unites that with the **petrosal** (Gray, 1918:140:fig. 138, 142, 145). It is not given in Evan and Cristensen (1979:129–135), *Nomina Anatomica* (IANC, 1983), Schaller (1992:23E), or Feneis (1994:12D).

In odontocetes the sutural connections between the squamosal and the periotic have disappeared and the petrosquamosal suture does not occur.

= petrotympanic bone (Flower, 1885) = petro-tympanic bone

See **tympanoperiotic bone** of "Tympanic Bulla."

= petrotympanic fissure

See **petrotympanic fissure** (*fissura petrotympanica*) of "Tympanic Bulla."

– piriform fenestra

According to MacPhee (1981:59), in fetal mammals and some adults, the piriform fenestra is the large gap between the auditory capsule and its dorsal outgrowths (such as the ***tegmen tympani*** and **epitympanic wing** of the **petrosal**) and the epitympanic wing of the squamosal and sphenoid. Wahlert (2000:8) reviewed previous uses of "piriform fenestra." Wible and Gaudin (2004:162) noted that the piriform fenestra may be developed between the auditory capsule, **basisphenoid**, **alisphenoid**, and squamosal, and that it may be continuous with the **carotid foramen of the sphenoid** (see also Geisler, 2001: app. 2, 3); it is absent in the dog. Asher et al. (2003) stated that the piriform fenestra is present when the petrosal, alisphenoid, squamosal, and/or ectotympanic fail to ossify anterior to the promontory in the tympanic in fully grown individuals. See **tympanic roof**.

The piriform fenestra is present in young and adult *Tursiops* and forms part of the cranial hiatus (q.v. for details).

* **posterior bullar facet** (Figure 25m–o,v)

The cetacean posterior bullar facet is the entire ventral surface of the **posterior process of the periotic bone**. It articulates with the **posterior process of the tympanic bulla** (Fordyce, 1994:160).

The posterior bullar facet is well developed in *Tursiops*.

= posterior cochlear crest (Fordyce, 2002)

See **caudal tympanic process**.

= posterior division of the periotic (Anderson, 1879:515) = posterior process

– posterior margin of the petrosal bone (*margo posterior partis petrosae*)

The posterior margin of the petrosal bone is that portion of the posterior surface of the mammalian periotic that borders the **occipital bone** (occipital margin) (Feneis, 1994:14.17).

Due to the change in relationship of the periotic to the surrounding bones in cetaceans, the posterior margin of the periotic is restricted to the **posterior process of the periotic bone** where it contacts the **tympanic bulla**.

* **posterior process of the periotic bone** (mastoid process, *processus mastoideus*) (Figure 25a,e,l,n,q,t,w,x)

In Neoceti and some Archaeoceti the posterior process of the **periotic bone** lies posterior to the ***pars cochlearis*** and mainly consists of the **posterior bullar facet**. The posterior process forms the lateral wall of the **facial sulcus**. In most Odontoceti, but generally not Delphinidae, the posterior process of the periotic bone articulates with (but is not fused with) the **posttympanic process** of the squamosal. There is a wide body of literature about the process, its homology, and its relationships.

The posterior process of the periotic bone has often been discussed in the context of the mastoid process of other mammals. In mammals, the mastoid process forms the posterolateral corner of the **petrosal** (periotic bone) (Flower, 1885:131; Evans and Christensen, 1979:133); the mastoid has been defined as that portion of periotic bone posterior to a line joining the **stylomastoid foramen** and the **posterior lacerate foramen** (McDowell, 1958; Novacek, 1986). In noncetacean mammals, the term "mastoid" is applied to the periotic only, and generally is not used for the **tympanic bulla**. Following Flower (1868), Boenninghaus (1904), Pompeckj (1922), and others, we homologize the mastoid process in the traditional mammalian sense with the posteroventral eminence or posterior process of the periotic bone in *Tursiops*. The name "posterior process of the periotic bone" is used here, because the term "mastoid" also has been used previously for components of the squamosal bone and tympanic **bulla** in Neoceti. MacPhee (1981:57) similarly cautioned on the use of "mastoid."

The posterior process of the periotic bone has also been termed "*processus tympanicus ossis petrosi*" (Denker, 1902:429; Reysenbach de Haan, 1957). Lillie (1910:777) used the term "**opisthotic portion of the periotic**" for the posterior process of the tympanoperiotic of *Balaenoptera musculus*, but this process in *B. musculus* and other Mysticeti is formed mainly of tympanic bulla. Fraser and Purves (1960:77–80; e.g., pl. 8) used the term "mastoid process" for the **posterior process of the tympanic bulla** in some Odontoceti. We cannot identify in *Tursiops* or other Odontoceti any mastoid component in the tympanic bulla, and recommend that the term "mastoid" not be used for components of the tympanic bulla. Fraser and Purves (1960:77–80; pl. 7) also used mastoid process for the fused posterior process of the tympanic bulla plus posterior process of the periotic bone, as seen in Mysticeti. We do not follow this use of mastoid. See **posterior process of the tympanic bulla** for discussion.

In *Tursiops* and all other Odontoceti, the posterior process of the periotic bone is tightly sutured to the posterior process of the tympanic bulla. The suture may be plane, serrate, or sometimes foliate (the latter giving an impression of fusion), but it is not known to fuse with the tympanic bulla. In contrast, the posterior process of the periotic bone and tympanic bulla do fuse in Mysticeti, which has led to the confused terminology reviewed under posterior process of the tympanic bulla.

Further, the posterior process of the periotic bone in *Tursiops* is not known to fuse with adjacent skull elements. Fusion between the posterior process and adjacent elements is not known for sure among other Odontoceti, except the fossil group Squalodontidae in which the posterior process of the periotic bone may fuse with the **posttympanic process** of the squamosal.

The mastoid process in many mammals contributes to the wall of the braincase between the **mastoid foramen** (at the junction of petrosal, exoccipital, and squamous temporal bones) and the **stylomastoid foramen** of the **petrosal** (Sisson and Grossman, 1953:37, 71:fig. 48, 158:fig. 161; Evans and Christensen, 1979:133; Oelschläger, 1986b:fig. 6a; Novacek, 1993:472, 474). Archaeoceti show the expected mammalian condition, in which the posterior process of the periotic bone is exposed laterally on the skull wall, wedged ventrally between squamosal and exoccipital (Pompeckj, 1922; Kellogg, 1936: fig. 5, fig. 28, pl. 15 fig. 1). In Archaeoceti, the posterior process of the tympanic bulla is visible here in lateral view of the skull wall, where it sutures with the squamosal at the postmeatal crest, but the tympanic bulla does not significantly fill in the space between the squamosal and exoccipital.

Sometimes in noncetacean mammals, the mastoid process may not be exposed laterally on the skull wall, producing an "amastoid" condition of the skull in, for example, some artiodactyls (Whitmore, 1953:135). We interpret *Tursiops*, all other Odontoceti, and all Mysticeti as amastoid, with the posterior process of the periotic bone not exposed laterally. The region between squamosal and exoccipital may be altered when the squamosal and exoccipital become sutured more ventrally, or it may be filled by an enlarged posterior process of the tympanic bulla in some Odontoceti (Ziphiidae, Physeteridae, Kogiidae), or by an enlarged posterior process of the tympanic bulla to which the periotic bone is fused dorsomedially in most Mysticeti. See **posterior process of the tympanic bulla.**

Fraser and Purves (1960:77) identified in *Caperea* a "portion of the squamosal immediately anterior to the ***pars mastoidea*** [of tympanoperiotic], of a rugose and laminated appearance," which they interpreted as "a mastoid element" fused to what we identify as post-tympanic portion of squamosal (q.v.). This interpretation of Fraser and Purves led others to accept that a mastoid component of periotic has lost its primitive connection with periotic, and has become fused to the tympanic bulla and/or to the squamosal (Purves, 1966:340; Oelschläger, 1986a,b). However, we find no evidence among living or fossil mammals that any component of periotic or tympanic bulla loses its original connection through fusion with the squamosal bone.

* **posteroexternal foramen** (Figure 25c,e)

The posteroexternal foramen (Fordyce, 1994:161, 160) is located on the lateral surface of the **posterior process of the periotic bone** in some Archaeoceti and Neoceti. It is of uncertain function.

In *Tursiops* this part of the periotic carries many tiny foramina. The posteroexternal foramen was distinct in two of five periotics from different individuals. It is too small to be probed.

– **postpromontorial tympanic recess** = postpromontorial tympanic sinus (Wible and Rougier, 2000:94)

– **postpromontorial tympanic sinus**

In armadillos (Wible and Gaudin, 2004: fig. 4) the postpromontorial tympanic sinus is a depression between the fossa for the stapedial muscle and the ***fenestra ovalis***, and lodges a *diverticulum* of the *cavum tympani* in life.

Tursiops lacks a postpromontorial tympanic sinus.

– posttemporal canal

The posttemporal canal is present in some mammals as a structure between the **petrosal** (**periotic bone**) and squamosal, associated with the stapedial artery. In some armadillos (Wible and Gaudin, 2004:163) it lies near the most dorsal part of the laterally exposed mastoid process. It occurs in the horse but not in artiodactyls or the dog (Geisler and Luo, 1998; Wible and Gaudin, 2004:163). Geisler and Luo (1998:187) stated that it is absent from Cetacea, except for possibly some basal archaeocetes.

Tursiops is not known to have a posttemporal canal.

= primary facial foramen = ventral foramen of the facial canal

Ross and Covert (2000:243) used primary **facial foramen** as follows: "The primary facial foramen carries the facial nerve from the **internal acoustic meatus** to the *cavum supracochleare*." This is equivalent to the proximal (or cerebral, or internal, or dorsal) opening of the **facial canal**. Wible and Rougier (2000:118) attributed "primary facial foramen" to Wible (1990).

See **facial canal**.

– *processus cochleariformis*

In humans (Gray, 1918:145) the *processus cochleariformis*, or *septum canalis musculotubarii*, is a thin plate of bone that separates two canals that lead into the **tympanic cavity**, namely the canal for the tensor tympani (*semicanalis m. tensoris tympani*) and the canal for the bony part of the **auditory tube** (*semicanalis tubae auditivae*).

In *Kogia* Schulte (1917:397) identified the *processus cochleariformis* as a thin ledge that lies medial to the **accessory ossicle** (**uncinate process** [of the **tympanic bulla**] of Schulte) and projects medially and ventrally. The only structure apparent here in *Kogia* is the dorsomedial extremity of the **anterior process of the periotic bone**, which in turn is probably homologous with the **anterodorsal angle** (q.v.), which in *Kogia* is rotated medially and ventrally relative to the position in *Tursiops*. Dissection is needed to establish if a *processus cochlearis* is present.

– *processus cristae facialis*

Wible and Gaudin (2004:135), who attributed this term to Patterson et al. (1989), identified the *processus cristae facialis* as possibly the shelf that is continuous posteriorly with the *crista facialis* (here, **facial crest of the periotic**) or ***crista parotica***.

There is no evidence that a *processus cristae facialis* is present in *Tursiops*.

= *processus tubarius*

See **accessory ossicle** and ***processus tubarius* of the bulla** in "Tympanic Bulla."

– *prominentia canalis lateralis*

The *prominentia canalis lateralis* is an eminence that is closely applied to the squamosal in archaic artiodactyls (Whitmore, 1953:132). Its lower edge forms the ***tegmen tympani***.

The *prominentia canalis lateralis* is not a discrete structure in *Tursiops*. Whether the *prominentia canalis lateralis* is homologous with the lateral tuberosity is uncertain.

See **lateral tuberosity**.

= promontorial groove, median

See **median promontorial groove**.

– promontory of the *pars cochlearis* (*promontorium*)

See **cochlear portion** (***pars cochlearis***) in part.

The promontory of the mammalian **petrosal** is the eminence that forms the ventromedial part of the petrosal. It is directly medial to the fossa for the *m. tensor tympani* and the **facial canal** (Evans and Christensen, 1979:132). Whitmore (1953:132) and MacPhee (1981:61) stated that the *promontorium* is the bulge caused by the first turn of the **cochlea**. This structure is sometimes called the "promontory of the pyramid"; see **pyramid**.

For Archaeoceti, Luo and Gingerich (1999: fig. 19) identified the promontory as the ventromedial eminence of the ***pars cochlearis***.

In *Tursiops* the promontory of the periotic forms part of the eminence comprising the ventral part of the *pars cochlearis*. It is medial to the **vestibular window** (**oval window**) and has the **round window** in its posterior wall. Because the promontory is not distinct from other parts of the ear, it is not easily identifiable, so we recommend use of the term "*pars cochlearis*" (or **cochlear portion**).

= prootic portion of the periotic bone (Fraser and Purves, 1960:34)

See **anterior process of the periotic bone**.

= pyramid

In terrestrial mammals, the term "pyramid" has been used both for the **petrosal** (**periotic bone** (q.v.) of our use) and for the ***pars cochlearis*** (q.v.).

See **petrosal** (Evans and Christensen, 1979:129) and **periotic bone** entries above.

= pyramidal process of the periotic

Luo and Gingerich (1999: fig. 19) identified the pyramidal process of the periotic in Archaeoceti as the feature lateral to the **aperture for the vestibular aqueduct** and distinct from the **superior process**.

The indistinct **dorsal crest** of the **periotic bone** in *Tursiops* may carry an eminence just lateral to the aperture for the **vestibular aqueduct**, but it is not certain if this is homologous with the structure in Archaeoceti. See also **dorsal tuberosity**.

Similarly, it is not clear if a dorsal structure of the ***pars cochlearis*** in some Mysticeti (Geisler and Luo, 1996: fig. 3) is homologous.

= pyramidal prootic portion (Fraser and Purves, 1960:34)

See **anterior process of the periotic bone**.

= *recessus epitympanicus*

See **epitympanic recess**, **body of the periotic**, and ***tegmen tympani***.

= *regio mastoidea* = mastoid region

In *Kogia* Schulte (1917:396) described the "platelike *processus tympanicus* [of Denker] which Beauregard is no doubt right in interpreting as the *regio mastoidea*."

See **posterior process of the periotic bone**.

– rostral tympanic process

MacPhee (1981:63) identified the rostral **tympanic process** in mammals as arising from the ventral surface of the ***pars cochlearis*** in mammals.

Tursiops lacks a rostral tympanic process.

= round window (*fenestra rotunda*)

See **cochlear window** (= ***fenestra cochleae***).

– saccule (*sacculus*)

The saccule of the mammalian inner ear lies within the *recessus sphericus* or **ventral vestibular area** (q.v.). The saccule communicates with the cochlear duct, by way of the *canalis reuniens*, and the **endolymphatic duct** (Gray, 1918:1052).

Tursiops has a saccule.

= secondary facial foramen = stylomastoid foramen

Ross and Covert (2000:243) identified the secondary **facial foramen** as the epitympanic, ventral, **distal, or external opening of the facial canal** (**Fallopian aqueduct**). Sanchez-Villagra and Wible (2002:35) stated that almost all metatherians have a bony floor to the *cavum supracochleare*, and that the anterior and posterior edges of this floor have foramina that transmit the two major branches of the facial nerve. Sanchez-Villagra and Wible identified the anterior foramen as the ***hiatus Fallopii*** (for the palatine ramus or greater petrosal nerve), and the posterior foramen as the secondary facial foramen, which transmits the hyomandibular ramus.

= semicanal for the tensor tympani muscle (*semicanalis m. tensoris tympani*) = fossa for the tensor tympani muscle

See also ***processus cochleariformis*** and **musculotubal canal of the tympanic bulla**.

– semicircular canals

The mammalian semicircular canals are three in number and are designated the anterior canal, posterior canal, and lateral canal. The anterior semicircular canal is sometimes referred to as the superior semicircular canal. In the dog the semicircular canals lie in the **petrosal**, posterolateral and dorsal to the **cochlea** and **vestibule** (Evans and Christensen, 1979:1069, 1070).

In *Tursiops* and other Odontoceti the semicircular canals bear the same anatomical relationships as they do in the dog (Yamada and Yoshizaki, 1959; confirmed on USNM 241288, 241289).

– shallow lateral groove

Fordyce (1994:160) labeled a shallow **lateral groove** located midlength on the lateral surface of the periotic in archaic Odontoceti, between the **lateral tuberosity** and the **dorsal tuberosity**.

The shallow lateral groove is not present in *Tursiops*.

= singular foramen

See ***foramen singulare***.

= spherical recess (Evans and Christensen, 1979:1070)

See **ventral vestibular area**.

– spiral canal

The spiral canal is a cavity within the mammalian **cochlea** that is divided by the **spiral lamina** (q.v.).

*** spiral cribriform tract** (*tractus spiralis foraminosus*) (Figure 25a,u)

In mammals the spiral cribriform tract lies in the **internal acoustic meatus**, ventral to the transverse crest. The spiral cribriform tract passes the cochlear nerve (Evans and Christensen, 1979:132).

The spiral cribriform tract in delphinids lies lateral to the transverse crest.

– spiral lamina (*lamina spiralis ossea*)

The spiral lamina is a shelf projecting from the ***modiolus*** into the **spiral canal** of the mammalian **cochlea** (Schaller, 1992:532.29; Feneis, 1994:344.1). A secondary spiral lamina (*lamina spiralis secundaria*) projects from the opposite wall of the spiral canal of the cochlea on its basal turn only.

Odontoceti have a normal mammalian spiral lamina.

– squamosal fossa

Some Mysticeti have a squamosal fossa, which is a prominent groove on the lateral face of the periotic between the **anterior process of the periotic bone** and the **body of the periotic** (Geisler and Luo, 1996:1052, fig. 3.6). The squamosal fossa may be homologous with the **anteroexternal sulcus** (q.v.). See Watson and Fordyce (1993) for comment.

Tursiops lacks a squamosal fossa.

– stapedial artery groove

In some mammals the stapedial artery runs in a groove on the *promontorium* of the **petrosal** (***pars cochlearis*** of the **periotic bone** in the terminology used here for *Tursiops*), forming a promontorial stapedial artery groove (e.g., Wible and Gaudin, 2004:165) or sulcus for the stapedial artery.

Tursiops lacks a stapedial artery groove, and lacks grooves that in other mammals (e.g., Novacek, 1986:55) are attributable to carotid circulation through the middle ear.

See also **sulcus for the internal carotid artery**.

– stylohyal fossa

Wible and Gaudin (2004:137) followed Patterson et al. (1989) in identifying, in the yellow armadillo, a shallow, round, depressed stylohyal fossa on the **petrosal**; they commented that the round structure within the fossa is the terminal end of the **tympanohyal**.

Tursiops sometimes has a tiny tympanohyal on the posteroventral side of the periotic at the posterior of the **facial crest**, which occasionally forms a projection in a larger fossa. We have noted a more-obvious circular stylohyal fossa in *Physeter* and *Eubalaena*.

= styloid process

See **tympanohyal**.

– stylomastoid canal

In some archaic artiodactyls (Whitmore, 1953) the distal path of the facial nerve as it exits the middle ear cavity is enclosed in a stylomastoid canal, which starts proximally (internally) at the ***foramen stylomastoideum primitivum*** and opens laterally at the **stylomastoid foramen** (q.v.), also known as the ***foramen stylomastoideum definitivum*** (Novacek, 1986: fig. 20).

The stylomastoid canal is absent in *Tursiops*.

– stylomastoid foramen (*foramen stylomastoideum*)

In many mammals the stylomastoid foramen lies on the posterolateral surface of the **petrosal** posterior to the **mastoid process of the petrosal**. It marks the point where the facial nerve and stylomastoid artery (if present) pass onto the lateral face of the skull. The ventral margin of the stylomastoid foramen may be formed by the **tympanic bulla** (Gray, 1918:144,181; Schaller, 1992:22.32; Feneis, 1994:14.27). Vesalius (1543:53; Vesalius et al., 1998:131) referred to the stylomastoid foramen as the *foramen ex auditus organum amplitudinis medio exortu, ac illinc in posteriora porrectum . . . Paeparatur autem ramulo nervi quinti paris*.

Evans and Christensen (1979:231, 133, 662) indicated that, in the dog, the stylomastoid foramen is the lateral opening of the **facial canal** (q.v.). Wible and Rougier (2000:119) interpreted Evans and Christensen's definition of stylomastoid foramen to mean "the opening between the **petrosal**, the osseous bulla, and the **tympanohyal** (**tympanohyoid**) cartilage by which the facial nerve (hyomandibular branch) leaves the middle ear and the stylomastoid artery off the posterior (caudal) auricular enters." Whitmore (1953) named the more-distal (more-lateral) **canal for the facial nerve** as the **stylomastoid canal** (q.v.).

The stylomastoid foramen is absent in *Tursiops* and generally in other Neoceti. The facial nerve passes onto the lateral wall of the skull via a shallow to indistinct **facial sulcus**. Occasionally in Neoceti the facial sulcus may end abruptly at a distinct **lateral notch** on the **posterior process of the tympanic bulla**, which we recognize as the **stylomastoid notch**, and which we regard as homologous with the stylomastoid foramen. In *Kogia breviceps* (USNM 571648) a stylomastoid foramen is formed at the suture between the exoccipital and the posterior face of the posterior process of the tympanic bulla.

Van der Klaauw (1931:173) cited Hanke (1914:508) that the facial nerve in Odontoceti exits via the *fissura tympano-periotica*. The latter is not to be confused with the *fissura petro-tympanica* = **petrotympanic fissure** = ***fissura Glaseri***, which serves as the exit from the **bulla** for the *chorda tympani*. See ***fissura Glaseri***.

See also ***foramen stylomastoideum primitivum*** and ***foramen stylomastoideum definitivum***.

– stylomastoid fossa

The stylomastoid fossa is a square-shaped depression on the posterior face of the cetacean ***pars cochlearis*** dorsal to the fossa for the stapedial muscle (Geisler and Luo, 1996:1054). In some Cetacea the fossa may involve the base of the posterior process. Fraser and Purves (1960:39) apparently referred to this structure when they noted a "concavity on the postero-dorsal face of the '***pars mastoidea***' of the tympano-periotic." According to Fraser and Purves, the fossa is likely to accommodate a part of the **peribullary sinus** or the **posterior sinus**.

Tursiops lacks a stylomastoid fossa.

– stylomastoid notch

The stylomastoid notch is a semi-enclosed distal end of the **facial sulcus** on the lateral face of the skull, where the facial nerve exits the mammalian basicranium; it is regarded as homologous with the **stylomastoid foramen** (q.v.).

Geisler and Luo (1996:1054) and Luo and Gingerich (1999:45, and their fig. 2c) used stylomastoid notch for a feature on the periotic medial to the posterior process and between the posterior process and the ***pars cochlearis***.

The stylomastoid notch is present in *Tursiops*; the term "facial sulcus" seems more applicable, while "stylomastoid notch" is retained for the appropriate feature on the lateral face of the mammal skull.

See **facial sulcus**.

– subarcuate fossa (*fossa subarcuata*)

The subarcuate fossa is a deep depression posterior to the **internal acoustic meatus** in carnivores (Schaller, 1992:22.22) and other mammals (Novacek, 1986; Whitmore, 1953). In humans it lies in the same position relative to the internal acoustic meatus (Feneis, 1994:14.14). The subarcuate fossa lies in the hollow medial to the **petrosal crest** and posterior to the internal acoustic meatus. In infants the subarcuate fossa extends posteriorly as a blind tunnel under the anterior **semicircular canal** (Gray, 1918:143).

The subarcuate fossa has also been termed the "**cerebellar fossa**" (Evans and Christensen, 1979:130). The cerebellar fossa lies on the posteromedial surface of the **petrosal** and houses the paraflocculus of the cerebellum (Evans and Christensen, 1979:132).

The subarcuate fossa is not present in adult *Tursiops* or other Neoceti, but de Burlet (1913: figs. 10, 13) reported a subarcuate fossa in an embryo of *Phocoena phocoena*.

– sulcus for the internal carotid artery

In some mammals one or more sulci for the carotid artery may course across the *promontorium* (Novacek, 1986:55). The sulci may branch to produce sulci for the stapedial artery and the promontory artery.

Tursiops and other Neoceti lack sulci for the carotid artery.

– sulcus medialis

In some archaic mammals the *sulcus medialis* courses along the medial intracranial edge of the **petrosal;** it is probably for the ventral or inferior petrosal sinus (Novacek, 1986:59).

The *sulcus medialis* appears to be absent in *Tursiops* and other Neoceti. Dissection is needed to establish the path of the inferior or **ventral petrosal sinus** relative to the periotic and other bones.

See also **median promontorial groove**.

– superior margin of the petrosal (*margo superior partis petrosae*)

The superior margin of the mammalian **petrosal** bone is that portion of the dorsal cranial surface that borders the squamosal (Feneis, 1994:14.9).

Due to the change in the relationship of the periotic to the squamosal with the isolation of the ear apparatus from the rest of the skull in *Tursiops*, only the posteroventral corner of the periotic borders the squamosal. The superior margin has disappeared; its homologue includes the **dorsal crest** of the **periotic bone** (q.v.).

See also **superior process**.

– superior process = petrosal crest

The superior process is that dorsal part of the **periotic bone** (**petrosal**) that extends dorsolaterally on the cranial wall of the squamosal (Pompeckj, 1922; Whitmore, 1953) in mammals, including archaic artiodactyls, some Archaeoceti, and some Neoceti. The process may project laterally, rather than dorsally (Whitmore, 1953), to floor the temporal venous sinus. It is apparently distinct from the **petrosal crest**. The superior process is part of the ***tegmen tympani*** (Luo and Gingerich, 1999:41).

In *Tursiops* and other living Odontoceti the superior process is not distinct, having become obliterated through changes in contact relationships with the squamosal (Fordyce, 1994: fig. 9). The former position of the superior process is perhaps indicated by the **dorsal crest** of the periotic bone (q.v. Fordyce, 1994).

Previously, Kasuya (1973:2) identified the superior process of the periotic bone as the rounded dorsolateral eminence that lies between the **anterior process of the periotic bone** and **posterior process of the periotic bone**, lateral to the **cochlear portion**. De Muizon (1987:8) also seemed to apply the term in this way.

– supracochlear cavity

In some mammals a supracochlear cavity or *cavum supracochleare* is well developed as a space that houses the geniculate ganglion of the facial nerve (Wible and Gaudin, 2004:151). The cavity arises from the medial part of, or lies internal to, the **epitympanic recess** and penetrates the ***pars cochlearis*** dorsally (MacPhee, 1981:64; Ross and Covert, 2000).

Tursiops lacks a supracochlear cavity but, like many other mammals (Wible and Gaudin, 2004:151), is presumed to have a **genu of the facial canal**.

– suprameatal area = suprameatal fossa of the periotic

Bisconti (2005) mentioned, for an extinct right whale (Balaenidae), the suprameatal area of the **petrosal** (**periotic bone**), referring to the work of Luo and Gingerich (1999) who showed that in basilosaurids the suprameatal area of the periotic is high and flat to slightly concave. Bisconti's mention appears to refer to the **suprameatal fossa of the periotic** sensu Luo and Gingerich.

– suprameatal fossa of the periotic

Luo and Eastman (1995:436, fig. 1) proposed "suprameatal fossa" for the shallow depression between the **internal auditory meatus** and homologue of the **superior process** on the cranial face of the **periotic bone** in a squalodontoid odontocete. Previously, Fordyce (1994:161) referred to this feature through mention of the superior petrosal sinus or subarcuate (subfloccular) fossa, in turn influenced by Pompeckj (1922) and Kellogg (1936: figs. 5, 6). Kellogg (1936:117) did not name this area but identified it as the irregularly hollowed cerebral face of the periotic in the archaeocete *Zygorhiza kochii*. The suprameatal fossa of the periotic is well developed in Archaeoceti, forming much of the concave dorsal part of the periotic between the internal auditory meatus and the dorsal lip of the superior process (Luo and Gingerich, 1999:13, 26, 45, figs. 3, 19, item smf).

In *Tursiops* there is a variable and generally indistinct elongate depression lateral to the internal auditory meatus and medial to the vestigial **dorsal crest**; this might be the suprameatal fossa of the periotic.

The "suprameatal fossa of the cetacean periotic" should not be confused with the **suprameatal fossa** of some Carnivora, which is a depression immediately posterior to the bony **external auditory meatus** on the lateral wall of the skull (Wang et al., 2004, 2005; see also **suprameatal fossa** under "Squamosal Bone").

– *tegmen tympani*

The *tegmen tympani* in humans is a thin plate of bone (tegmen = roof) that separates the cranial cavity and **tympanic cavity**. It lies on the anterior surface of the **petrosal** close to its temporal margin. The tegmen is extended posteriorly to cover the **tympanic antrum** and anteriorly to cover the **fossa for the tensor tympani muscle**. It is limited laterally by the petrosquamous suture (Gray, 1918:1038). In the dog the *tegmen tympani* is a region of thin bone immediately dorsal to the **epitympanic hiatus** and the fossa for the tensor tympani muscle. Whitmore (1953:132) identified the *tegmen tympani* as lying lateral to the fossa for the tensor tympani muscle.

The *tegmen tympani* is identifiable in embryonic Cetacea (Ridewood, 1922) and occurs in adults, albeit as a structure that is greatly thickened dorsoventrally in many Archaeoceti (e.g., Luo and Gingerich, 1999: fig. 2) and Neoceti. The *tegmen tympani*, in the sense of a thin roof to the middle ear, is not readily applicable in adult *Tursiops*.

For cetaceans Kellogg used "***recessus epitympanicus***" (e.g., 1936:27) to refer to structures immediately ventral to the *tegmen tympani* of other authors, and (e.g., 1931) used "**body of the periotic**" to refer to that part of the **periotic bone** other than the **anterior process of the periotic bone**, ***pars cochlearis***, and **posterior process of the periotic bone**.

Tuberosity of the *tegmen tympani*, as used by Schulte (1917:397, 398), referred to the anterior process of the periotic bone.

= tegmental process (Yamada, 1953:20)

See **anterior process of the periotic bone**.

= *tractus spiralis foraminosus* = spiral cribriform tract

*** transverse crest of the internal acoustic meatus** (*crista transversa*) (Figure 25t,u)

The transverse crest of the **internal acoustic meatus** separates the opening of the **facial canal** from the ***tractus spiralis foraminosus*** in the dog (Evans and Christensen, 1979:132). This is the ***crista falciformis*** of humans (Gray, 1918:143).

In *Tursiops* the transverse crest of the internal acoustic meatus separates the internal aperture for the **facial canal** (**Fallopian aqueduct**) from the ***foramen singulare*** and the **spiral cribriform tract** (*tractus spiralis foraminosus*) (Kellogg, 1928: fig. 23; Kasuya, 1973:2). The crest is directed anteroposteriorly, rather than transversely, across the **meatus**.

= transverse septum (Luo and Gingerich, 1999:45)

See **transverse crest of the internal acoustic meatus**.

= transverse vascular channel (Luo and Gingerich, 1999:45, figs. 1, 14, item vf)

See **anteroexternal sulcus**. Note that further work is needed to determine whether the latter is homologous with the transverse (or dorsoventral) vascular channel or the vascular groove of Luo and Gingerich (1999:45).

– trigeminal impression (*impressio n. trigemini*)

The trigeminal impression is situated on the anterolateral portion of the cranial surface of the mammalian periotic, just posterior to the ***foramen ovale*** (Schaller, 1992:22.14; Feneis, 1994:14.8). It may also develop on the contiguous portion of **alisphenoid** (MacPhee, 1981:64). The trigeminal impression contains the posterior part of the semilunar ganglion of the trigeminal nerve.

In *Tursiops* and other Odontoceti the contact with the trigeminal nerve is lost and the trigeminal impression is absent due to the separation of the periotic from the skull.

= tuberosity of the *tegmen tympani* = anterior process of the periotic bone (Schulte, 1917:397)

– tympanic antrum

The tympanic antrum in humans is a large irregular cavity that develops toward the mastoid process, is roofed by the ***tegmen tympani***, and is continuous with the **tympanic cavity** (Gray, 1918:142).

Tursiops lacks a tympanic antrum.

= tympanic aperture of the facial canal (Reysenbach de Haan, 1957)

See **facial canal**.

– tympanic canaliculus (*canaliculus tympanicus*)

The mammalian tympanic canaliculus is a small canal for the tympanic branch of the glossopharyngeal nerve and inferior tympanic branch of the ascending pharyngeal branch of the **external carotid artery** (Schaller, 1992:22.33; Feneis, 1994:14.28). In humans the tympanic canaliculus lies between the **jugular foramen** and the **carotid canal of the sphenoid**. The tympanic branch of the glossopharyngeal nerve contributes to the tympanic plexus.

Presumably *Tursiops* has a tympanic nerve and tympanic plexus, but details have yet to be determined by dissection.

See also **opening for the lesser petrosal nerve**.

= tympanic process = caudal tympanic process (Wible et al., 2004:75)

– tympanic roof

"Tympanic roof" appears to be a general term for the roof of the middle ear, normally represented by the **petrosal** (**periotic bone**). See, for example, Wible and Rougier (2000:40), Asher et al. (2003), and Wible and Gaudin (2004).

Tursiops is inferred to have a tympanic roof, which, however, does not develop fully (see **piriform fenestra**). The term does not seem useful in describing adult specimens.

– tympanic surface of the periotic (*facies tympanica*) = tympanic surface of the petrosal

The tympanic surface of the **petrosal** bone in the dog is the ventrolateral surface that borders on the tympanic bone (Evans and Christensen, 1979:132).

In *Tursiops* the tympanic surface of the **periotic bone** is the ventral surface that faces the **tympanic bulla**. It bears the **anterior bullar facet** and **posterior bullar facet** and the **oval window**.

*** tympanohyal** (Figure 25k,m,o,t)

The tympanohyal cartilage is the most proximal of the hyoid elements. It runs between the **stylohyoid** and the **petrosal** (Evans and Christensen, 1979:148; Schaller, 1992:38.46; Sisson, 1910:64, figs. 27, 33). The tympanohyal is poorly developed in the dog. In humans the stylohyal fuses with the tympanohyal to form the **styloid process** or *processus styloideus* (Gray, 1918:145). Van der Klaauw (1931:239) and Sisson and Grossman (1953:71) used the term "hyoid process" (*processus hyoideus*) for the tympanohyal as fused to the **facial crest of the periotic** (q.v.). Eustachius and Lancisius (1714:98, 104, 109, 115) referred to the styloid process as the "***processus styliformis***" or "*styloides processus*."

Van der Klaauw (1931:239) suggested that the styloid process as formed by co-ossified tympanohyal and stylohyal be termed "*processus styliformis*," but this would introduce unnecessary confusion with the muscular process (**styliform process**) of the tympanic bone in some mammals.

In delphinids the base of the **tympanohyoid** is fused to the posteroventral side of the periotic (see Figure 25k,m,o,t,u). A vestigial tympanohyal is developed variably in *Tursiops*. Commonly, the tympanohyal in *Tursiops* and other Neoceti is marked by a small pit on the medial edge of the **posterior bullar facet**, immediately ventral to the **facial sulcus**. Van der Klaauw (1931:239) identified the point of fusion as the *crista facialis petrosi* or facial crest of the periotic. Occasionally the tympanohyal may be quite prominent (Owen, 1846:526, in *Physeter*; Oelschläger, 1986b; and our observations of Neoceti in the collections of the USNM).

The stylohyal has not been reported to fuse with the tympanohyal in *Tursiops*. Rather, in Odontoceti, the bony element usually identified as stylohyal articulates with the **paroccipital process** of the exoccipital. Dissection of *Tursiops* is needed to establish relationships between tympanohyal, paroccipital process, and stylohyal.

See also **tympanohyoid** under "Hyoid Apparatus."

– tympanomastoid fissure of the petrosal

Van der Klaauw (1931:174) stated that, in mammals, the common aperture for the facial nerve and the hyoid is termed the tympanomastoid fissure.

It seems unnecessary to apply this name to *Tursiops*.

= tympanoperiotic fissure (*fissura tympano-periotica*)

See **petrotympanic fissure** of "Tympanic Bulla" and **stylomastoid foramen**.

= upper tympanic aperture (Kasuya, 1973: fig. 1)

See **epitympanic hiatus**.

– utricle

The utricle is the cavity forming part of the labyrinth into which the **semicircular canals** communicate in humans (Gray, 1918:1051, 1052).

See ***pars canalicularis***.

– vascular foramen (associated with the periotic)

Luo and Gingerich (1999: fig. 18) showed a vascular foramen between the periotic and squamosal in Archaeoceti that is similar in position to that identified by Fordyce (1994) as perhaps for the middle meningeal artery.

See ***foramen spinosum***.

– ventral border of the petrosal bone (*margo ventralis partis petrosae*)

The ventral border of the mammalian **petrosal** bone is the cranial margin of the petrosal that borders the tympanic bone (Schaller, 1992:22.25).

In delphinids the ventral border of the periotic is limited to the articular surface of the **posterior process** and the portion of the **anterior process of the periotic bone** on which the **accessory ossicle** lies. See also **tympanic surface of the periotic**.

– ventral foramen of the facial canal

The ventral foramen of the cetacean **facial canal** lies on the **ventral surface of the petrosal**, just lateral to the **vestibular window** (e.g., Fordyce, 1994:160). The ventral foramen is the epitympanic, **distal, or external opening of the facial canal**.

See **facial canal** for further discussion.

– ventral petrosal sinus

The ventral petrosal sinus lies in the **petrobasilar canal** and connects the cavernous sinus with the sigmoid sinus in the dog (Evans and Christensen, 1979:793, 794). The feature is also termed the inferior petrosal sinus (e.g., MacPhee, 1981:56). It may be exposed ventrally in species in which the **basicapsular fissure** persists in adults.

The ventral petrosal sinus may exist in *Tursiops*, but the anatomical situation with the ventral venous sinuses in delphinids is very complex and needs adequate descriptive work. The petrobasilar canal is absent in *Tursiops*.

– ventral surface of the petrosal (*facies ventralis partis petrosae*)

The **ventral surface** of the mammalian **petrosal** is that portion of the external surface of the petrosal that is exposed ventrally (i.e., is not covered by the **tympanic bulla**) (Schaller, 1992:22.29; not in Feneis, 1994).

None of the ventral surface is external in *Tursiops*, so that in this sense the ventral surface does not exist. The ventral aspect of the periotic is partly equivalent to the **ventral border of the petrosal bone** and to the **tympanic surface of the periotic**.

= ventral tuberosity

Luo and Gingerich (1999:45) ascribed the term "ventral tuberosity" to Fordyce (1994), but it was used by de Muizon (1987:5).

See **lateral tuberosity**.

* **ventral vestibular area** (*area vestibularis saccularis* or *foramen acusticum inferius*) (Figure 25t)

The ventral **vestibular area** in mammals is located ventral (anteroventral) to the **transverse crest of the internal acoustic meatus** and contains the *sacculus*. Nerve fibers that come from the *sacculus* pass through the ***foramen singulare*** (Evans and Christensen, 1979:132). The structure has also been called the **spherical recess** for the **saccule** (Evans and Christensen, 1979:1070). It is separated from the **elliptical recess for the utricle** by the vestibular crus. The term "ventral vestibular area" seems clearer than "spherical recess."

Wible et al. (2001:8) used a broader definition for the extinct mammal *Prokennalestes*: the ventral vestibular area [foramen acusticum inferius of their use] is that part of the **internal acoustic meatus** that lies medial to the transverse crest, including the **spiral cribriform tract** and, although they did not mention it, the *foramen singulare*.

In *Tursiops* the ventral vestibular area in the sense of Wible et al. (2001:8) includes the spiral cribriform tract and the singular foramen or *foramen singulare*.

– ventrolateral ridge of the anterior process

Some Mysticeti have a lateral projection on the **anterior process of the periotic bone** that forms part of the border of the **squamosal fossa** between the anterior process and the **body of the periotic** (Geisler and Luo, 1996:1052, fig. 3.6).

Tursiops lacks a ventrolateral ridge on the anterior process.

= ventrolateral tuberosity (Luo and Gingerich, 1999:45)

See **lateral tuberosity**.

– vertical canal

The vertical canal in archaic Odontoceti opens dorsally into one of the **anterointernal sulci** (Fordyce, 1994:160). Its function is uncertain.

The vertical canal is not developed in *Tursiops*.

– vestibular aqueduct (*aqueductus* [*aquae-*] *vestibuli*)

The vestibular aqueduct in mammals runs from posteromedial side of the **vestibule** (Whitmore, 1953) posteroventrally to the posterior part of the of the cerebral surface of the **petrosal**. The vestibular aqueduct carries the **endolymphatic duct** (Evans and Christensen, 1979:133). It opens onto the surface of the petrosal in the **aperture for the vestibular aqueduct**.

The vestibular aqueduct in *Tursiops* bears the same anatomical relationships as in the dog. See **aperture for the vestibular aqueduct**.

= vestibular area

See **dorsal vestibular area** and **ventral vestibular area**.

= vestibular fenestra (*fenestra vestibuli*)

See ***fenestra ovalis***.

– vestibular fossa

The region adjacent to the mammalian vestibular region is sometimes termed the vestibular fossa (MacPhee, 1981:47).

– vestibular fossula

The mammalian **vestibular fenestra**, or ***fenestra ovalis*** for the **footplate of the stapes**, is situated in a shallow pit that is sometimes known as the vestibular fossula (MacPhee, 1981:47; Wible and Gaudin, 2004:134). There is an indistinct vestibular fossula in *Tursiops*.

– vestibular part (*pars vestibularis*)

The vestibular part is the dorsolateral part of the mammalian periotic that contains the **semicircular canals** (Whitmore, 1953:131).

Schulte (1917:396) used the term "***pars vestibularis***" broadly, for that part of the periotic in *Kogia* other than the ***pars cochlearis***.

In *Tursiops* and other Cetacea the vestibular part is continuous with other parts of the periotic, and is not recognized as a distinct structure.

See also **body of the periotic**.

= vestibular window = *fenestra ovalis*

Vestibular window is a common and equally acceptable synonym for ***fenestra ovalis*** (q.v.).

– vestibule (*vestibulum*)

The vestibule of the **petrosal** is the chamber where the three **semicircular canals** and **cochlea** join. The vestibule is located between the basal turn of the cochlea and the semicircular canals in the central portion of the petrosal in the dog (Evans and Christensen, 1979:133, 1069).

The vestibule in Odontoceti bears the same anatomical relationships as it does in the dog (Yamada and Yoshizaki, 1959; confirmed on USNM 241288, 241289.

TYMPANIC BULLA

Os Temporale / Pars Tympanica / Bulla Tympanica

FIGURES 3, 4, 6F, 25A–E, **25F–K**, 25R,S,W,X,Y, 29

The tympanic bulla (*bulla tympanica*) is an inflated bone that lies directly ventral to the mastoid process. It is formed of the tympanic part of the temporal and contains the fundus of the tympanic cavity (Evans and Christensen, 1979:129, 133, 134). The bulla was also referred to as the *processus petrosus ossis tympani* (sic) (Denker, 1902) or the tympanomastoid (Yamada, 1953:19; McFarland et al., 1979:7). Vesalius (1543:23) referred to the tympanic part of the temporal as merely the *os*.

The tympanic bulla in delphinids is a completely separate ossification consisting of the tympanic part of the temporal. It lies posterolaterally on the ventral surface of the skull, ventral to the periotic and ventromedial to the squamosal. It articulates with the periotic anteriorly and posteriorly.

*** accessory ossicle** (Figure 25a,d,f,g,I,j,r,w)

The term "accessory ossicle" as used in *Tursiops* follows Ridewood (1922:242), who cited van Kampen (1904:343, fig. 4), and many later cetologists. In Odontoceti the accessory ossicle is an elongate nodule with rounded edges that is fused to the dorsal part of the **outer lip** of the **bulla**, anterior to the **sigmoid process** and **petrotympanic fissure** (***fissura Glaseri***). Its dorsal surface carries a gently undulating facet that makes a plane suture with the ***fovea epitubaria*** of the periotic. Ventrally, the rounded medial edge of the accessory ossicle descends into the **tympanic cavity**.

In *Tursiops* the posterior quarter of the dorsal surface of the accessory ossicle is generally broken where the accessory ossicle fuses with the periotic just anterior to the **mallear fossa**; every specimen examined by microscope has shown fusion.

Luo (1998:276, 288) suggested that the accessory ossicle may be an evolutionary novelty for Odontoceti. All Odontoceti have an accessory ossicle, and the anterior of the periotic either lies close to the bulla or contacts the **periotic facet** of the bulla. Extant Mysticeti lack an accessory ossicle, and the periotic and bulla are separated widely but fused at a prominent **anterior pedicle**. We regard the accessory ossicle of *Tursiops* as partly homologous with the dorsal part of the anterior pedicle of Mysticeti, and note that a distinct accessory ossicle appears to be present in some extinct (stem-group) Mysticeti, in which it is extensively applied to the **anterior bullar facet**.

"Accessory ossicle" is preferred as a less ambiguous term than **tubal tubercle** (Yamada, 1953:20), **uncinate process, unciform process** (de Muizon, 1987, 1991), or ***processus tubarius* of the bulla**. Boenninghaus' (1904: fig. 10, item 3) label of the *processus tubarius bullae* shows that this term applies clearly to the accessory ossicle, but later use confused the nomenclature.

The accessory ossicle may be homologous with the wide massive portion of the anterolateral lip of the bulla (dorsal to the *fissura Glaseri*) in *Odocoileus virginianus* and *Ovis aries*.

= annulus (Fraser and Purves, 1960:65, 113)

See **tympanic ring**.

= ***anulus tendineus***

See **tympanic sulcus**.

= ***anulus tympanicus***

See **tympanic ring**.

– anterior angle

The anterior angle is a projection from the dorsal part of the **outer lip** anterior to the **accessory ossicle** in some Archaeoceti (Luo, 1998: figs. 5, 6). It is not clearly the same as the structure that de Muizon (1987) termed the "**anterolateral convexity**" (q.v.).

The **tympanic bulla** in *Tursiops* lacks an anterior angle.

= anterior aperture (Fraser and Purves, 1960:65, 70)

See **musculotubal canal of the tympanic bulla**.

= anterior apophysis (de Muizon, 1988)

See **muscular process of the tympanic bulla**.

= anterior bullar lip (Luo, 1998:288)

See **musculotubal canal of the tympanic bulla**.

= anterior bullar process (Luo and Gingerich, 1999:36, tbl. 4(16a))

See **anterior process of the tympanic bulla**.

– anterior conical process (*processus conicus anterior*)

Denker (1902:428, pl. 14, fig. 2, "p.c.a.") identified the *processus conicus anterior* in Odontoceti as the prominence at the distal (or anterolateral) end of the **mallear process**, adjacent to the **lateral groove**. (Beauregard, 1894:380, 381, fig. 2d, proposed the term as "*apophyse conique anterieure*.") It is part of the **anterior process of the tympanic bulla** in the sense of Boenninghaus (1904), but should not be confused with the (posterior) **conical process**, which is a modified part of the **tympanic ring** that lies posterior to the **sigmoid process**. We recommend using the term "anterior conical process." The anterior conical process is present but indistinct in *Tursiops*.

Ridewood (1922:241, fig. 10) incorrectly used the term "anterior conical process" for the sigmoid process, while van der Klaauw (1931:262) equated the ***processus tubarius* of the bulla** ("**accessory ossicle**" of our use) with the *processus conicus anterior* ("anterior conical process" of our use).

– anterior crus of the ectotympanic ring

The anterior crus is part of the primitive simple ring-shaped or horseshoe-shaped ectotympanic of eutherian mammals. (See, e.g., Ridewood, 1922:240; MacPhee, 1981; Novacek, 1986:51, 52; Luo and Gingerich, 1999.)

The ectotympanic is highly modified in *Tursiops* and other Cetacea to form the **tympanic bulla**. The anterior crus is the embryonic precursor to the **sigmoid process** (Ridewood, 1922; Luo, 1998:271, 284) and more-anterior structures, but it is not distinct in adult *Tursiops*.

= anterior entrance of the tympanic cavity (Fraser and Purves, 1960:15)
See **musculotubal canal of the tympanic bulla**.

= anterior opening of the tympanic cavity = anterior notch of the tympanic cleft, anterior notch for the Eustachian tube
See **tympanic cavity**.

= anterior orifice of the bulla (Fraser and Purves, 1960:74) = musculotubal canal of the tympanic bulla

*** anterior pedicle** (Figure 25f,m)

The anterior pedicle of Carte and Macalister (1868:253; anterior osseous pedicle, which they also termed "*processus anterior mallei*"), Lillie (1910:778), and others is that anterior part of the **tympanic bulla** in balaenopterids that fuses with the periotic just anterior to the **mallear fossa**. In Mysticeti the pedicle is narrow laterally but dorsoventrally prolonged; judging from the situation in some fossil stem-Mysticeti, it seems to be at least partly a modification of the **accessory ossicle**.

In *Tursiops* and other Odontoceti, the **bulla** and periotic are partly fused and partly sutured at the accessory ossicle, and there is no dorsoventrally prolonged anterior pedicle. Fraser and Purves mentioned the pedicles only in passing (1960:133) and referenced Kellogg (1938).

= anterior process (conical) of the tympanic bulla (*processus conicus anterior*)
See **anterior conical process**.

= anterior process of the external lip of the auditory bulla (Beauregard, 1894; Fraser and Purves, 1960:9) = anterodorsal crest of the tympanic bulla

– anterior process of the tympanic bulla

In reference to structures of the cetacean **bulla**, the term "anterior process" has had a history of ambiguous use. In noncetacean mammals, "anterior process" usually refers to structures associated with or arising from the **anterior crus of the ectotympanic ring** (q.v.). We recommend that the latter use be followed, noting that, if the components of the anterior crus are properly named in *Tursiops*, the term "anterior process" may be redundant.

In *Tursiops*, features of the more-dorsal part of the **outer lip**, from posterior to anterior, include the **sigmoid process, petrotympanic fissure, mallear ridge, sulcus for the *chorda tympani*, accessory ossicle**, and **anterodorsal crest of the tympanic bulla** (q.v.).

Several references illustrate the past state of nomenclature. Denker (1902) distinguished between the *processus conicus anterior*, the accessory ossicle, and the **anterior process**. Boenninghaus (1904: fig. 12) identified the anterior process of the bulla as including the sigmoid process and the ***processus tubarius* of the bulla** (or accessory ossicle).

Van der Klaauw (1931:262) stated that "the anterior process of the tympanic which is fused with the periotic is called the *processus tubarius* [or *processus conicus anterior*]. It forms, together with the *processus sigmoideus*, the *processus ossis anterior tympanici*." Van der Klaauw (1931:263) then indicated uncertainty about the identity of the *processus tubarius*, the **uncinate process** of Schulte, and the *processus conicus anterior*.

See **anterior pedicle, *processus tubarius* of the bulla,** and **accessory ossicle**.

Luo (1998:287) and Luo and Gingerich (1999:32; tbl. 4, #16a) equated the "anterior process" with the *processus tubarius*. They noted that in some Archaeoceti the anterior process (= *processus tubarius*) contacts the **squamosal bullar process**.

See **falciform process** of "Squamosal Bone."

– anterior spine

Kasuya (1973: fig.1) and de Muizon (1987:9, fig. 4) identified a prominent anterior spine of the **tympanic bulla** in fossil stem-Platanistidae and *Platanista*. The anterior spine is a prolonged muscular process. *Tursiops* lacks an anterior spine of the tympanic **bulla**.

Not to be confused with the **anterior tympanic spine**.

See **muscular process of the tympanic bulla**.

– anterior tympanic spine (*spina tympanica anterior*) = greater tympanic spine (*spina tympanica major*)

Van der Klaauw (1931:204) stated that, as a rule in mammals, the **tympanic crest** ends with **anterior** and **posterior tympanic spines** (*spina tympanica anterior* and *spina tympanica posterior*), which lie near the top of the **tympanic ring**. A line connecting the anterior and posterior tympanic spines marks the lower margin of the *membrana Shrapnelli* or *pars flaccida* (Bondy, 1907, cited by van der Klaauw, 1931). The development of anterior and posterior tympanic spines varies among mammalian species.

In humans the **greater tympanic spine** is located on the anterodorsal border of the tympanic ring (Feneis, 1994:16.6); it is bordered dorsally by the tympanic notch or **tympanic incisure** of the squamosal.

An anterior tympanic spine is not developed in *Tursiops*; it is probably represented by part of the **sigmoid process** of the **tympanic bulla**.

* **anterodorsal crest of the tympanic bulla [new term]** (Figure 25a,c,d,f,h,j,s)

The new term "anterodorsal crest of the tympanic bulla" is proposed here for the part of the **outer lip** of the cetacean **tympanic bulla** that lies anterior to the **accessory ossicle**.

In *Tursiops* and other delphinids the anterodorsal crest does not contact the periotic; it is thin-edged and descends toward the **musculotubal canal of the tympanic bulla.** In some other Odontoceti (e.g., *Physeter*, *Platanista*, many ziphiids), the anterodorsal crest is rounded transversely to form a **periotic facet** that is received by the **anterior bullar facet** of the **periotic bone.**

– anterolateral convexity

The anterolateral convexity is located on the anterolateral surface of the **tympanic bulla** in some species of Platanistoidea (de Muizon, 1987). It is most apparent in dorsal view. It is unlikely to be homologous with the similar structure that Luo (1998) termed the "**anterior angle**" (q.v.).

The anterolateral convexity does not occur in *Tursiops*.

= anteromedial angle of the involucrum (Luo and Gingerich, 1999: fig. 11)

See **anteromedial angle of the tympanic bulla**.

– anteromedial angle of the tympanic bulla

The anteromedial angle of the **tympanic bulla** of Luo and Gingerich (1999:31, also termed **anteromedial angle of the involucrum** of Luo and Gingerich, 1999: fig. 11) projects anteriorly or anteromedially from the anterior part of the **involucrum** in some Archaeoceti. This may be the same feature that Luo (1998:283) termed the medial angle of the involucrum. The homology is uncertain with the **anteromedial process of the tympanic bulla** of other mammals (See MacPhee, 1981:46).

The anteromedial angle of the tympanic **bulla** does not occur in *Tursiops*.

= anteromedial process of the tympanic bulla

This feature of some mammals (e.g., MacPhee, 1981:46) is probably the **anteromedial angle of the tympanic bulla**.

= antrum

MacPhee (1981:46, 57) equated the antrum of humans with the **mastoid cavity** of other mammals.

See ***diverticulum anterior***.

= aperture for the Eustachian tube

Kellogg (e.g., 1936:113) used this term for the musculotubal canal.

See **musculotubal canal of the tympanic bulla**.

= aperture for the paroccipital pneumatic sinus (*apertura posterior sinus pneumaticus paroccipitalis*) (van der Klaauw, 1931:263, who also termed it *apertura posterior*)

See **elliptical foramen**.

= ascial process (Ridewood, 1922: fig. 10C)

See **mallear process** and **mallear ridge**; see also **anterior process of the malleus** under "Malleus."

– auditory aperture (Clarke, 1948:980)

Clarke (1948:980) used auditory aperture as the term for the surface opening of the ear canal (**external auditory meatus**) in *Physeter* (Fraser and Purves, 1960:111). There appears to be no comparable term in human anatomy (Gray, 1918; Feneis, 1994) or the anatomy of domestic animals (Evans and Christensen, 1979; Schaller, 1992).

= basal pedicle

Kellogg (1936:114) mentioned the thin basal pedicle of the posterior process that originates just behind the **median process** (or **conical process**) on the **outer lip** of the **tympanic bulla** in Archaeoceti.

See **outer posterior pedicle**.

= bony tympanic tube (*ostium tympanicum tubae*) (Whitmore, 1953)

See **musculotubal canal of the tympanic bulla**.

= bulla

See **tympanic bulla**.

= bullar cavity

See **tympanic cavity**.

– bullar septum

One or more bullar septa may occur in mammals (van der Klaauw, 1931:209; MacPhee, 1981:63).

Tursiops has small anterior and posterior bullar septa associated with the **conical process**, **tympanic ring**, and **hypotympanic sinus**.

See ***diverticulum anterior*** and ***diverticulum posterior*** for details.

– carotid canal (*canalis caroticus*)

The carotid canal in the dog lies in the medial edge of the **bulla** (Evans and Christensen, 1979:134); it arises posteriorly at the **caudal carotid foramen** in the **tympano-occipital fissure**, and opens anteriorly at the rostral or cranial carotid foramen or ***foramen lacerum***. Flower (1885:141) termed this the internal carotid canal.

Several synonyms are applicable; the anterior opening of carotid canal is known as the caudal carotid foramen, the **rostral carotid foramen**, or the *foramen lacerum* (Evans and Christensen, 1979:134); while the posterior opening of the carotid canal is also known as the caudal carotid foramen (Evans and Christensen, 1979:134).

The carotid canal is not present in *Tursiops* or other Neoceti.

See also **carotid canal of the sphenoid** and **carotid foramen of the sphenoid** under "Sphenoid Bone."

= caudal carotid foramen

The caudal carotid foramen is the posterior opening of the **carotid canal** in the dog (Evans and Christensen, 1979:134)

The caudal carotid foramen is not present in Neoceti.

See **caudal carotid foramen of the sphenoid bone** and **carotid canal of the sphenoid** under "Sphenoid Bone."

= caudal lip of tympanic bulla (Schulte, 1917:396)

See **involucrum**.

– caudal ridge of sigmoid process

Schulte (1917:395) recognized two ridges arising from the apex of the **sigmoid process** in the **bulla** of *Kogia*. The caudal ridge, which becomes sharp toward the base of the sigmoid process, is homologous with the rounded external edge of the sigmoid process as seen in *Tursiops* and other odontocetes.

Schulte used the term "caudal" to indicate his perceived orientation of the feature on the tympanoperiotic in the *Kogia* skull; in life, the "caudal" ridge is actually ventral and slightly anterior (rostral), while the "rostral" ridge is dorsal and slightly posterior (caudal).

The external or lateral margin of the sigmoid process in *Tursiops* is rounded and not produced as a sharp ridge. For cetaceans in which a ridge might be present, the name external or lateral ridge of the sigmoid process seems better in light of the standardized directional terminology for the tympanoperiotic.

See **rostral ridge of sigmoid process**.

– caudal squamosal foot

The caudal squamosal foot is the anterior part of the **mallear plate** (q.v.) of the dorsal part of the ectotympanic in the archaic insectivore *Leptictis* (Novacek, 1986:51, fig. 19).

This structure cannot be homologized in *Tursiops*.

= *cavum epitympanicum* (Kellogg, 1936:113)

See **tympanic cavity**.

– *chordafortsatz*

Van der Klaauw (1931:208; see also MacPhee, 1981:50) cited Bondy (1907:326), originator of the term, that the mammalian *chordafortsatz* is a small bony or cartilaginous process that conducts the *chorda tympani* nerve toward the malleus.

The term refers to a "continuation process" for the *chorda tympani*.

The *chordafortsatz* is not clearly distinguishable in *Tursiops*, but see **sulcus for the *chorda tympani***.

– compound posterior process

In Mysticeti the **posterior process of the tympanic bulla** fuses with the **posterior process of the periotic bone** to form what Geisler and Luo (1996:1056) termed the compound posterior process.

Tursiops lacks a compound posterior process.

See **posterior process of the tympanic bulla**.

= concavity of the caudal lip of the bulla = concavity of the involucrum of the bulla (Schulte, 1917:397)

– concavity of the involucrum of the bulla

Schulte (1917:397) referred to the **concavity of the caudal lip of the bulla,** meaning a depression on the surface of the **involucrum** that is approached closely by the surface of the ***pars cochlearis*** of the periotic.

The ventral profile of the *pars cochlearis* of the periotic in *Tursiops* closely parallels the dorsal surface of the involucrum, resulting in a cavity or concavity similar to that of *Kogia*.

See also **medial petrotympanic fissure**.

= conical apophysis (Kellogg, 1969:26; Luo and Gingerich, 1999:36)

See **conical process**.

* **conical process** (*processus medius tympanici*) (Figures 25c,g,h, r,x,y, 29)

The conical process of the **tympanic bulla** is a small dorsal projection of the lateral wall of the cetacean **bulla** that lies between the **sigmoid process** and the posterior process (Kasuya, 1973:2). This structure is unique to Cetacea. The conical process, sigmoid process, and posterior process in part represent the highly modified **tympanic ring** of other mammals.

In *Tursiops* the conical process is excavated by the **hypotympanic sinus**, is associated with the anterior and posterior septa, and carries a ridge for the **tympanic membrane**.

According to Ridewood (1922:242), Beauregard (1894) proposed the term "*apophyse conique postérieure*." The conical process has also been termed the "*processus medius*" of Boenninghaus (1904:221), "***processus conicus posterior***" or "*processus medius bullae*" of van der Klaauw (1931:262), and "**median process**" or "**conical apophysis**" of Kellogg (1936:113). Luo and Gingerich (1999:36) termed it the **middle conical process**, or the **middle process**.

– *crista tympanica* of the meatus (meatal tube, inner)

In mammals the *crista tympanica* of the meatus, or **tympanic crest,** is formed where the ectotympanic wall of the **meatus** projects into the **tympanic cavity** (Whitmore, 1953:135). It is distinct from the **tympanic ring** (**tympanic annulus**). Luo (1998) termed this the "free inner end of the meatal tube."

Tursiops lacks a *crista tympanica* of the meatus, not to be confused with the tympanic crest in the sense of MacPhee (1981:51) and others.

See **tympanic crest**.

– distal plate of the posterior process of the tympanic bulla

Luo and Gingerich (1999: tbl. 3, #24) proposed the term "distal plate" for the cetacean homologue of the posterior wall of the **external auditory meatus**. For Odontoceti, Luo and Gingerich described it as the thick horizontal plate of the posterior process. The term is effectively synonymous with posterior process.

A distal plate is present in *Tursiops*.

* ***diverticulum anterior*** (Figure 25w)

The *diverticulum anterior* is also known as the **antrum** or anterior chamber of the **tympanic cavity** (Luo, 1998:280). MacPhee (1981:46, 57) equated the antrum of humans with the **mastoid cavity** of other mammals. In some Archaeoceti the *diverticulum anterior* is expanded dorsolaterally anterior to the **sigmoid process** and is separated from other parts of the tympanic cavity by one or more septa (*trabeculae*) that are present ventral to the sigmoid process.

In *Tursiops* a low anterior septum is identified provisionally on the medial face of the **outer lip**, extending anteroventrally from the base of the **conical process**; the *diverticulum anterior* is that part of the tympanic cavity anterior to the anterior septum.

See also ***diverticulum posterior***.

– *diverticulum posterior*

The *diverticulum posterior* is also known as the posterior chamber of the **tympanic cavity** (Luo, 1998:281). In some Archaeoceti the *diverticulum posterior* is expanded posterodorsally into the base of the posterior process, posterior to the posterior septum. In turn, the posterior septum arises from the posterior part of the **tympanic ring**.

In *Tursiops* the *diverticulum posterior* is that part of the tympanic cavity in the base of the posterior process or **posterior pedicle**; its anterior boundary is formed by a strong ridge that descends ventromedially from its origin on the posterior base of the **conical process**. The *diverticulum posterior* opens into the **elliptical foramen**.

See also ***diverticulum anterior***.

– ectotympanic part of the tympanic

The ectotympanic part of the tympanic bone represents the **tympanic ring** in many terrestrial mammals (Novacek, 1977). The element is incomplete dorsally at the tympanic notch or **tympanic incisure** (MacPhee, 1981:52). In Mysticeti (Ridewood, 1922:242; van der Klaauw, 1931:261; de Beer, 1937:341ff.) and all other Cetacea for which we can find accounts (e.g., Luo, 1998; Geisler, 2001; Geisler and Sanders, 2003; Uhen, 2004), the ectotympanic reportedly forms all of the **tympanic bulla**. Histological study of a range of living species would be helpful.

The auditory **bulla** of *Tursiops* is composed of the ectotympanic part of the tympanic bone.

* **elliptical foramen** (Figure 25e,k,w)

The elliptical foramen (**vertical cleft** or elongated aqueduct of Kellogg, 1936) is an opening in the wall of the cetacean **tympanic bulla** at its posterior end. It develops from the region of the ***diverticulum posterior***. The elliptical foramen is just ventral to the posterior process and just dorsal to the **outer posterior prominence** of the tympanic **bulla** (Kasuya, 1973) and, when present, it divides the base of the posterior process into the **inner** and **outer posterior pedicles**. The elliptical foramen transmits the **posterior sinus** (Fraser and Purves, 1960) to the apex of the **paroccipital process**. For the elliptical foramen, van der Klaauw (1931:263) used the term "*apertura posterior* for the *sinus pneumaticus paroccipitalis*," while Luo (1998:285) called it the "**pedicular foramen**," and Luo and Gingerich (1999: fig. 14) termed it the "**posterior cleft**." Fraser and Purves (1960: e.g., fig. 1) used the term "posterior aperture of the **tympanic cavity**."

The posterior sinus has also been termed the **paroccipital pneumatic sinus** (*sinus pneumaticus paroccipitalis* of van der Klaauw, 1931:37, 263), and the **posterior pterygoid sinus** (Luo, 1998:285).

– endotympanic part (*pars endotympanica*)

The endotympanic part or entotympanic **bulla** is the one or more skeletal or cartilage elements that form independently from other bullar elements (Novacek, 1977; MacPhee, 1981:52), including the ectotympanic part.

The cetacean tympanic bone lacks an endotympanic part (Ridewood, 1922:242; Novacek, 1977).

– epitympanic crest

The epitympanic crest (MacPhee, 1981:53) is a septum that borders the **epitympanic recess** and is associated with the stapedial artery in some primates.

The epitympanic crest is not identifiable in *Tursiops*.

– epitympanic recess

The epitympanic recess is bounded ventrally by structures of the **bulla** at the **tympanic incisure**. Details are discussed under "Periotic Bone."

= Eustachian cavity

See **tympanic cavity**.

= Eustachian end of the tympanic cleft (Turner, 1913:13)

See these features of the **tympanic bulla: musculotubal canal of the tympanic bulla, Eustachian notch**, and **Eustachian outlet**.

The term "Eustachian notch" should not be used for structures on the tympanic **bulla** because it also refers to a structure in the pterygoid.

See **Eustachian notch** under "Pterygoid Bone."

= Eustachian outlet (Kellogg, 1969:4)

Given that the term "**Eustachian notch**" is not appropriately applied to the cetacean **bulla**, the terms "Eustachian outlet" or "tympanic outlet" are appropriate alternative names for the **musculotubal canal of the tympanic bulla**. Kellogg (e.g., 1936:189, fig. 80) also used furrow or **aperture for the Eustachian tube**.

See **musculotubal canal of the tympanic bulla**.

= Eustachian tube (Luo, 1998; Luo and Gingerich, 1999:32)

See **musculotubal canal of the tympanic bulla** and **Eustachian outlet**.

The term "Eustachian tube" should be reserved for the soft tissue structure and not used for bony structures associated with the **tympanic bulla**.

= exoccipital contact (Luo and Gingerich, 1999)

See **exoccipital protuberance of the tympanic bulla**.

– exoccipital protuberance of the tympanic bulla

Luo and Gingerich (1999:31, and fig. 11) identified in Archaeoceti a feature termed the exoccipital protuberance that they also termed the **exoccipital contact** and **medial prominence**. (Medial prominence in this sense should not be confused with medial process or **conical process**.) The exoccipital protuberance lies on the **involucrum** of the **tympanic bulla**, internal to the **posterior pedicle**.

Tursiops lacks an exoccipital protuberance of the tympanic bulla.

– external acoustic meatus (*meatus acusticus externus*) = external auditory meatus

The external acoustic **meatus** in mammals is the canal from the external ear to the **tympanic membrane** (MacPhee, 1981:53). Vesalius (1543:23) referred to the external acoustic meatus as the *auditorii meatus* in a portion of his work, while in another (Vesalius, 1543:52; Vesalius et al., 1998:131) he referred to the external acoustic meatus (**auditory tube**) as the "*auditus organum petit, ac aer etiam in temporis ossis antrum auditus organo proprium, per id foramen sertur*." Eustachius and Lancisius (1714:105) referred to it as the "*auditorius [externus]* meatus *dissectus*." In the dog all but the dorsal part of the external acoustic meatus is formed by the tympanic part of the **bulla**. The dorsal part is formed by the **mastoid process of the petrosal** (Evans and

Christensen, 1979:134, 151). In the deer, *Odocoileus virginianus*, the dorsal part is formed by the squamosal (to the exclusion of **petrosal**), while the anterior, ventral, and posterior walls are formed by the **tympanic bulla**. In the sheep, *Ovis aries*, the external acoustic meatus is formed by a cylindrical tube of the bulla, with a small dorsal component of squamosal medially.

In some Archaeoceti the tympanic bulla forms a trough-like meatal tube that is part of the ventral wall of the proximal part of the **external auditory meatus** (Luo, 1998:278) and that may protrude internally into the **tympanic cavity**. In such whales the distal parts, and dorsal proximal parts, of the external acoustic meatus are formed by the squamosal.

The delphinid external acoustic meatus sensu stricto is mostly cartilaginous (e.g., Purves, 1966: fig. 4), with only a proximal bullar part formed by bone. It runs from near the dermis to the **lower tympanic aperture** of the bulla. In *Tursiops* the proximal bony bullar parts of the external acoustic meatus are the lateral part of the **sigmoid process**, **conical process**, and anterior face of posterior process.

For the external acoustic meatus, Luo and Gingerich (1999: fig. 21) used the name "**opening for the tympanic ligament**."

In *Tursiops* the squamosal carries a prominent ventral groove, the [bony] external acoustic meatus, sensu lato. The bony meatus originates laterally at the postglenoid or retroarticular notch, and terminates medially at the **spiny process**.

– external acoustic pore (*porus acusticus externus*)

The external acoustic pore in mammals is the external opening of the bony **external auditory meatus**. The external acoustic pore lies laterally on the posteroventral surface of the skull. The ventral part of this opening is composed of the **tympanic part of the temporal**, and the dorsal part is composed of the squamous part of the temporal (Evans and Christensen, 1979:150, 151).

Because the **external acoustic meatus** in delphinids is entirely cartilaginous, the external acoustic pore is not present.

= external auditory canal

See **external acoustic meatus**.

= external auditory meatus

See **external acoustic meatus**.

– external ridge

Luo and Gingerich (1999: tbl. 4, #15b) indicated that an external ridge is present on the anterior process of the ectotympanic of Archaeoceti and the extinct odontocete *Xenorophus*.

An external ridge cannot be identified in *Tursiops*.

= *fenestra rotunda* of the tympanic bulla

"***Fenestra rotunda***, of **tympanic bulla**" appears to be a mislabeling by Boenninghaus (1904: fig. G(19)).

See **musculotubal canal of the tympanic bulla**.

= *fissura Glaseri* (van der Klaauw, 1931; Kellogg, 1936; Whitmore, 1953; Novacek, 1986)

The names *fissura Glaseri* (or **Glaserian fissure**; Wible and Gaudin, 2004:155) and **petrotympanic fissure** (q.v.) both have wide use for mammals. However, MacPhee (1981:55) observed that the name "*fissura Glaseri*" is more appropriate than "petrotympanic fissure" because the latter name does not properly describe the feature in some mammals. Vesalius (1543:23) referred to the petrotympanic fissure as merely the linea (line). In the dog the *fissura Glaseri* lies at the anterolateral end of the **tympanic bulla**, just posterior to the **retroarticular process** (or **postglenoid process**) of the squamosal. In artiodactyls, the *fissura Glaseri* may be bounded by the *margo fissurae* of the squamosal (Whitmore, 1953). The *fissura Glaseri* serves as the exit from the **bulla** for the *chorda tympani* (Evans and Christensen, 1979:131, 133); in early ontogeny it serves as the exit for Meckel's cartilage (van der Klaauw, 1931:164).

The *fissura Glaseri* or petrotympanic fissure is present in *Tursiops* and other Neoceti at the point of fusion of the malleus to the bulla immediately anterior to the **sigmoid process**.

The synonym "petrotympanic fissure" should be avoided because of confusion with the **tympanoperiotic fissure**.

– folian process of the malleus (*processus folii* or *processus longus* of the malleus)

Van der Klaauw (1931:235) discussed the manner in which the folian process or anterior process (or *processus longus*) of the malleus may contribute to the mammalian **tympanic bulla**. The **anterior process of the malleus** lies in the ***sulcus malleolaris*** of the tympanic bulla, and often fuses with the **bulla**. Homologies are uncertain for the sometimes associated **accessory ossicle** of the malleus (*ossiculum accessorium malleoli*).

In *Tursiops* and other Neoceti the anterior process of the malleus is fused to the tympanic bulla.

See discussion under **mallear ridge** and **malleolar process**; see also "Malleus."

= *foramen lacerum*

Vesalius (1543:51; Vesalius et al., 1998:131) referred to the *foramen lacerum* as the *rimam hanc temporis ossi and occipitii communem*.

See **rostral carotid foramen, carotid canal of the sphenoid bone**, and ***foramen lacerum anterius***.

= *foramen lacerum anterius* (anterior lacerate foramen)

See **anterior lacerate foramen** under "Sphenoid Bone."

= Glaserian fissure (Luo, 1998)

See ***fissura Glaseri*** and **petrotympanic fissure**.

= greater tympanic spine

See **anterior tympanic spine**.

= groove for *anulus tendineus* (Kellogg, 1936)

See **tympanic sulcus**.

*** groove for facial nerve** (Figure 25f,i)

A groove for the facial nerve may be present on the **posterior process of the tympanic bulla** in Cetacea (van der Klaauw, 1931:263).

In *Tursiops* a groove is present variably on the posterior face of the posterior process of the **tympanic bulla**, just ventral to the suture with the **posterior process of the periotic bone**. Anteriorly, the groove passes into the **facial sulcus** of the periotic.

* **hypotympanic sinus** (Figure 25w)

Whitmore (1953:132) implied that this feature in archaic artiodactyls is broadly synonymous with the **tympanic cavity**. Earlier, van der Klaauw (1931:214) discriminated between the hypotympanic sinus and true tympanic cavity and indicated (1931:262) that the hypotympanic sinus is formed when the **external acoustic meatus** projects into the cavity of the **bulla**. It includes a lateral extension that excavates the **median process** or **conical process** (***processus conicus posterior*** or *processus medius bullae* of van der Klaauw).

In *Tursiops* and other delphinids the conical process is excavated ventrally by a cavity that is continuous with the tympanic cavity and that is presumed to be the hypotympanic sinus.

= **inner convexity** (Kellogg, 1936:115)

See **inner posterior prominence.**

= **inner pedicle**

See **inner posterior pedicle**.

* **inner posterior pedicle** (Figure 25f,k,s,x)

The **inner pedicle** of the cetacean **tympanic bulla** is the medial support between the **posterior process of the tympanic bulla** and the **inner posterior prominence** (Kasuya, 1973). It attaches to the **involucrum**. The inner **posterior pedicle** forms only when the base of the posterior process is split by the development of an **elliptical foramen** and **posterior sinus**. De Muizon (1987) termed this the "**medial pedicle.**"

The inner posterior pedicle is present in *Tursiops*.

* **inner posterior prominence** (Figures 25b,e,i,k,s, 29)

The inner posterior prominence (Kasuya, 1973) of the cetacean **tympanic bulla** is a ventral structure located on the medial side of the posterior surface of the tympanic **bulla.** In Odontoceti the feature is best seen in ventral view. Luo and Gingerich (1999:36, fig. 13) used the term "**medial posterior prominence**" for this feature.

In *Tursiops* the inner posterior prominence is the shorter of the two posterior prominences.

* **interprominential notch** (Figure 25e,k)

The interprominential notch (Kasuya, 1973) of the cetacean **tympanic bulla** lies on the posterior surface of the tympanic bulla between the **outer** and **inner posterior prominences.** It is continuous with the **median furrow** (Kasuya, 1973). For Archaeoceti Luo (1998:278, fig. 4) homologized the interprominential notch with the **tympanohyal sulcus**. Dissections of dolphins show that the path of hyoid elements is remote from this part of the **bulla**, so that we hesitate to accept this homology for *Tursiops*.

Tursiops has an interprominential notch, visible from the posterior or ventral surfaces.

See **sheath for the hyoid process.**

* **involucrum** (Figures 25b,d,f,j,s, 28)

The involucrum of the **tympanic bulla** is the rounded, dorsoventrally thickened, medial part of the tympanic **bulla**. The involucrum extends between the **inner pedicle** and the most anterior point of the medial wall (Kellogg, 1928; Yamada, 1953:19; Kasuya, 1973). Schulte (1917:396) used the term "caudal lip" for the involucrum in *Kogia*, with "caudal" referring to the relative position of the involucrum when the tympanoperiotic is articulated in the skull.

= **lacerate foramen** (*foramen lacerum*)

In the dog the lacerate foramen is located at the anterior margin of the **bulla**, lateral to the occipitosphenoid suture and medial to the **musculotubal canal of the tympanic bulla.** It has also been called the external carotid foramen (Evans and Christensen, 1979:134; McFarland et al., 1979:9). Davis (1964:52) identified the *foramen lacerum medium* (or *foramen lacerum anterius* of some authors) in carnivores as transmitting veins associated with pharyngeal circulation and the cavernous sinus and the internal carotid artery. In carnivores the lacerate foramen contains a loop of the internal carotid artery.

It has also been termed the median lacerate foramen in many mammals, although it seems that *foramen lacerum medium* sensu Flower (1885:123) strictly refers to the foramen that transmits the internal carotid artery to the braincase (McFarland et al., 1979:9). According to Wible (2003:172), Marshall and de Muizon (1995) used the term "median lacerate foramen" in another context, namely for the foramen for the greater petrosal nerve; see ***hiatus Fallopii*** of "Periotic Bone." See also comments under **carotid canal of the sphenoid** and **carotid foramen of the sphenoid**, under "Sphenoid Bone." The term "lacerate foramen" also has been used, as **posterior lacerate foramen**, for the **jugular foramen** in Odontoceti (see "Exoccipital Bone").

The lacerate foramen is not present in Neoceti.

* **lateral furrow** (Figure 25g,h,r)

The lateral furrow of the **tympanic bulla** in Odontoceti is a vertical feature located on the lateral surface of the **bulla** well anterior to the **sigmoid process** (Kasuya, 1973). It should not be confused with the groove that delimits the base of the sigmoid process. In some specimens the lateral furrow branches and becomes more complicated dorsally. Its function is not clear. The "lateral furrow" of Luo and Gingerich (1999:32) is a feature immediately anterior to the sigmoid process and may not be homologous with the lateral furrow in Odontoceti including *Tursiops*.

The lateral furrow is moderately developed in *Tursiops*, but more so in other nondelphinoid Odontoceti.

= **lateral posterior prominence** (Luo, 1998:34)

See **outer posterior prominence.**

= **lesser tympanic spine** (*spina tympanica minor*)

See **posterior tympanic spine.**

= **lip-like process** (Turner, 1913:16)

See **sigmoid process.**

= **longitudinal groove**

See **median furrow**.

* **lower tympanic aperture** (Figure 25h,s,w)

The lower tympanic aperture of the cetacean **tympanic bulla** is the opening on the posterolateral surface of the **bulla** that is bounded by the **sigmoid process**, the **conical process**, and the **outer posterior pedicle** of the tympanic bulla. The aperture opens dorsally at the **tympanic incisure**. This is the bony part of the **external acoustic meatus** and is the **tympanic aperture** (Yamada, 1953:20, Kasuya, 1973) or **tympanic annulus**.

Tursiops has a lower tympanic aperture.

See also **tympanic aperture, external acoustic meatus**.

– mallear plate

The dorsal part of the ectotympanic in the archaic insectivore *Leptictis* is flattened to form a mallear plate (Novacek, 1986:51, fig. 19). Anteriorly the mallear plate has a **rostral squamosal foot**; posteriorly it has a **caudal squamosal foot**. The rostral squamosal foot is probably homologous with the **anterior process** and anterior ossicle of the **tympanic bulla**, while the caudal squamosal foot is perhaps homologous with the posterior process of the **bulla**.

The term "mallear plate" is not applicable to *Tursiops*.

= mallear process (Turner, 1913:16)

The mallear process of the **tympanic bulla** in the sense of Luo (1998:275) referred to the structure in Cetacea that becomes fused to the **anterior process of the malleus**. That structure may be the **mallear ridge** (q.v.). For the anterior process of the malleus, Ridewood (1922: fig. 10C) named this the **ascial process**, and said that it is formed by the ***goniale***.

See **anterior process of the malleus; sigmoid process**.

*** mallear ridge** (Figure 25c,d,f,r,y)

The mallear ridge is located on the dorsolateral surface of the **tympanic bulla** immediately anterior to the **sigmoid process**, at least in Odontoceti (Fordyce, 1994:160). It descends obliquely laterally and ventrally from the medial part of the sigmoid process at the point of fusion of the malleus. Fordyce used the term for a surface feature without particular implications about embryonic origin; the feature is probably formed by the **anterior process of the malleus** (= **ascial process** of Ridewood, 1922:241). The **sulcus for the *chorda tympani*** lies medial and anterior to the ridge. The mallear ridge may be partly homologous with the **malleolar sulcus**. Luo and Gingerich (1999:18, tbl. 3, #20) referred to the mallear ridge as the **malleolar accessory ossicle**.

Tursiops has a well developed mallear ridge.

See **malleolar process** and **malleolar sulcus**.

= malleolar accessory ossicle

See **mallear ridge**.

– malleolar process = mallear ridge

Luo and Gingerich (1999:18, 46, tbl. 3, #20) used the term "malleolar process" or ridge for the site of attachment of the *processus gracilis* of the malleus in Archaeoceti. Their illustration (fig. 21) and text identify the malleolar process as the horizontal feature on the crest of the **outer lip** of the **tympanic bulla** medial to the groove or **sulcus for the *chorda tympani***.

In *Tursiops* and other Neoceti the **mallear ridge** lies posterior and lateral to the groove for the *chorda tympani*. The feature identified by Luo and Gingerich (1999: fig. 21) may be related to the **accessory ossicle** (= ***processus tubarius* of the bulla**).

– malleolar sulcus (*sulcus malleolaris*)

The malleolar sulcus of the **tympanic bulla** (van der Klaauw, 1931:235) carries the **anterior process of the malleus**, which in *Tursiops* and other Neoceti fuses with the **bulla**. The apparent region of fusion in Odontoceti is a ridge, rather than a sulcus, that Fordyce (1994) termed the "**mallear ridge**."

MacPhee (1981:57) identified the malleolar sulcus as a feature at the apex of the **anterior crus of the ectotympanic ring**, associated with the *chorda tympani*, ***goniale***, and Meckel's cartilage.

= mastoid cavity

Mastoid cavity in the sense of MacPhee (1981:46, 57) matches the **tympanic cavity** as used herein.

See **antrum, *diverticulum anterior***, and **tympanic cavity**.

= mastoid process of the tympanic bulla

See **posterior process of the periotic bone, posterior process of the tympanic bulla**.

– meatal tube, intrabullar part

In some Archaeoceti some of the **tympanic bulla** forms part of the ventral wall of the proximal part of the **external auditory meatus**. The resulting meatal tube is trough-shaped in dorsal view (Luo, 1998:278; Luo and Gingerich, 1999:32), and internally may protrude into the **tympanic cavity**. Other parts of the external auditory **meatus** are formed by the squamosal.

The projecting intrabullar part of the meatal tube may be supported by septa or *trabeculae*, and it carries the **tympanic ring** (***anulus tympanicus***).

There is no intrabullar part of the meatal tube in *Tursiops*. The septa (or *trabeculae*) are subtle structures identifiable adjacent to the **conical process** (e.g., Figure 25w).

= meatus

See **external acoustic meatus** of "Tympanic Bulla"; **spiny process** of "Squamosal Bone."

= medial angle of the tympanic bulla

See **anteromedial angle of the tympanic bulla**.

= medial conical process (Luo and Gingerich, 1999:18, tbl. 3, #20)

Also known as the **median process**.

Not to be confused with the **conical process**.

See **anteromedial angle of the tympanic bulla**.

– medial notch

In some Archaeoceti a medial notch is present on the medial and ventral surfaces of the **involucrum**, ventral to the **musculotubal canal of the tympanic bulla** (Luo and Gingerich, 1999:36, fig. 13).

The medial notch should not be confused with the **lateral groove**, nor the groove that delimits the base of the **sigmoid process**, nor the **median furrow**, all discussed elsewhere.

Tursiops lacks a medial notch.

= medial pedicle (de Muizon, 1987) = inner posterior pedicle

*** medial petrotympanic fissure** (Figure 25d,e)

Luo and Gingerich (1999: tbl. 4, #30) proposed the term "medial petrotympanic fissure" for the gap between the **involu-**

crum of the **tympanic bulla** and the *promontorium* (here, the ***pars cochlearis***) of the **petrosal** (**periotic bone**). The feature should not be confused with the **petrotympanic fissure** (or ***fissura Glaseri***).

Tursiops has a medial petrotympanic fissure.

= medial posterior prominence (Luo and Gingerich, 1999)

Luo and Gingerich (1999:36, fig. 13) used the term "medial posterior prominence" for what was earlier termed the **inner posterior prominence** (q.v.; Luo and Gingerich, 1999: fig. 10C, "mp"). They also termed it the **medial prominence**.

Luo and Gingerich (1999:29) discussed a tuberosity on the exoccipital that "serves to support the medial prominence of the bulla," implying that a dorsal feature on the **bulla** also has the appellation "medial." Elsewhere the dorsal feature of the bulla is termed **exoccipital contact** (their 'eoc', or **exoccipital protuberance**; Luo and Gingerich, 1999) on the dorsal side of the **involucrum**.

See **inner posterior prominence**.

= medial prominence

See **medial posterior prominence** and **inner posterior prominence**.

= medial prominence of the involucrum

In Archaeoceti (Luo and Gingerich, 1999:29) the **medial prominence** is dorsal to the posterior end of the **involucrum** and immediately internal to the posterior process. Luo and Gingerich also used the terms "**exoccipital protuberance of the tympanic bulla**" (Luo and Gingerich, 1999:31, fig. 11) and "**exoccipital contact**." The medial prominence contacts the adjacent **bullar process of the exoccipital bone** in some Archaeoceti and contacts the basioccipital of others (Luo, 1998:286).

The feature is not identifiable in *Tursiops*.

* **median furrow** (Figure 25b)

The median furrow of the cetacean **tympanic bulla** lies on the ventromedial surface of the tympanic **bulla** and extends from the **interprominential notch** anteriorly until it disappears (Kasuya, 1973). The appearance of the median furrow depends on the definition of the posterior prominences, since it lies between them. The feature should not be confused with the **medial notch** (q.v.) of Luo and Gingerich (1999). This has been also refered to as the **longitudinal groove**.

Tursiops has a well developed median furrow.

= median process (Kellogg, 1936) = conical process

= median ridge (Luo and Gingerich, 1999: tbl. 3, #29b)

See **ventral keel**.

= middle conical process (Luo and Gingerich, 1999:36)

Not to be confused with the **medial conical process**.

See **conical process**.

= middle process (Luo and Gingerich, 1999:36)

See **conical process**.

– muscular process of the tympanic bulla (*processus muscularis*)

The muscular process (**styliform process**, or ***processus styliformis*** of van der Klaauw, 1931) of the mammalian tympanic bone projects anteroventrally from the anterior border of the tympanic bone (Schaller, 1992:24.7). It is strongly developed in ungulates. Whitmore (1953) identified it as forming part of the **bony tympanic tube** (*ostium tympanicum tubae*) and part of the origin for the *m. levator veli palatini*. MacPhee (1981:61) identified it as for origins of the *m. tensor veli palatini* and *m. levator veli palatini*.

In Neoceti, the muscular process is an anterior projection of the **tympanic bulla** that lies ventral to the **auditory tube** (**Eustachian tube**). It is variable in *Tursiops* and other delphinids, appearing with age (Kasuya, 1973). Fraser and Purves (1960:19) mentioned that in *Delphinus delphis* the m. tensor palati is "associated with the styloid near its contact with the **bulla**." The latter use of styloid is not to be confused with the **styloid process** or *processus styloideus* as formed by the fused **tympanohyal** and stylohyal of other eutherians.

The muscular process of the tympanic bulla has also been termed the **anterior spine**, **anterior apophysis**, and **styloid apophysis** (Kasuya, 1973; de Muizon, 1987, 1988). Where the muscular process is present as a marked projection, as in *Platanista*, the term "anterior spine" would seem appropriate.

* **musculotubal canal of the tympanic bulla** (*canalis musculotubarius*) (Figure 25c,d,s,y)

In some mammals the musculotubal canal is a double or joint canal for the **auditory tube** (**Eustachian tube**) and the *m. tensor tympani* (Schaller, 1992:24.12; Feneis, 1994:12.28). The musculotubal canal lies in the anteromedial portion of the **tympanic bulla** and the caudal portion of the **temporal wing** of the sphenoid (Evans and Christensen, 1979:129). The musculotubal canal is just lateral to the ***foramen lacerum*** (external carotid foramen).

See Whitmore (1953) = **bony tympanic tube** (*ostium tympanicum tubae*) and Wible and Gaudin (2004:160).

The musculotubal canal in delphinids and other Cetacea has been modified by the separation of the osseous ear components, so that it is not a canal but is a U-shaped depression or semicanal at the apex of the tympanic **bulla**, lacking a dorsal bony roof. It is represented by the *semicanalis tubae auditivae* of the tympanic bulla and reportedly the *semicanalis musculus tensoris tympani* (Pilleri et al., 1987, pl. 16). However, the origin for the *m. tensor tympani* is on the **accessory ossicle** of the tympanic bulla, not on the thin **outer lip**. (See **fossa for the tensor tympani muscle** of "Periotic Bone.")

The musculotubal canal of the tympanic bulla has also been named the anterior notch of the **tympanic cleft** (Turner, 1913:19), the anterior notch for the **Eustachian tube** (Luo, 1998:283), the **Eustachian outlet**, the **Eustachian notch**, the **aperture for the Eustachian tube**, the groove on the outer lip border for the Eustachian canal, and the **anterior bullar lip**. Possibly, Schulte (1917:397) referred to the musculotubal canal when he mentioned the ***osseous tuba***. Boenninghaus (1904: fig. G) used the terms "***fenestra rotunda***" and "*tympanicum tubae Eustachii*."

"Eustachian notch" should not be used, since it applies to a structure on the pterygoid bone.

In *Tursiops* the terms musculotubal semicanal, Eustachian outlet, and tympanic outlet are appropriate for what is elsewhere termed the "musculotubal canal."

See also **musculotubal canal of the sphenoid bone**.

= opening for the tympanic ligament (Luo and Gingerich, 1999: fig. 21)

See **external acoustic meatus**.

= opisthotic portion of the periotic (Lillie, 1910:777)

See **posterior process of the tympanic bulla**.

= ***osseous tuba***

Schulte (1917:397) identified the *osseous tuba* as formed by the articulated **tympanic bulla** and periotic, and probably therefore meant the **musculotubal canal of the tympanic bulla**.

See also **groove on ventral surface of the** ***pars cochlearis***.

= outer convexity (Kellogg, 1936:115)

See **outer posterior prominence**.

* **outer lip** (Figure 25b,g,j,r,x)

Outer lip is a general term for the thin-walled part of the cetacean **bulla** that forms the lateral (outer, external) wall to the bullar portion of the **tympanic cavity**. The outer lip in Odontoceti includes the **anterodorsal crest of the tympanic bulla**, **anterolateral convexity**, **accessory ossicle**, **lateral furrow**, **sulcus for the** ***chorda tympani*** nerve, **mallear ridge**, **sigmoid process**, and the **conical process** and associated sinuses and septa; the outer lip often passes imperceptibly into the **outer posterior pedicle**.

The bulla in *Tursiops* has an outer lip.

* **outer posterior pedicle** (Figure 25k)

The outer **posterior pedicle** of the posterior process of the cetacean **tympanic bulla** is situated at the posterolateral surface of the **bulla**, lying between the posterior prominence, the **elliptical foramen**, and the **lower tympanic aperture**. It has been called outer pedicle (Kasuya, 1973:2). It arises from the **outer lip** posterior to the **conical process**.

The outer posterior pedicle is present in *Tursiops*.

* **outer posterior prominence** (Figures 6f, 25b,e,g,i,k,y, 29)

The outer posterior prominence of the cetacean **tympanic bulla** is a rounded eminence that lies on the posteroventral surface of the **bulla**, and supports the posterior process. It is separated by the **interprominential notch**, when the latter is developed, from the **inner posterior prominence** (Kasuya, 1973). The outer posterior prominence is usually the highest and most striking of the topographic features of the bulla.

Tursiops has a well-developed outer posterior prominence.

– pedicle foramen

The pedicle foramen of Luo and Gingerich (1999: fig. 21d) was illustrated as a small opening between the **inner** and **outer posterior pedicles** of the archaeocete whale *Saghacetus osiris* that is shown as separate from a more-ventral **elliptical foramen**. On accompanying figures, however (Luo and Gingerich, 1999: figs. 21c,e), the pedicle foramen is identified as the more-dorsal part of the elliptical foramen.

In *Tursiops* the elliptical foramen is the only major feature to pierce the **posterior pedicles**.

= pedicular foramen (Luo, 1998:285)

See **pedicle foramen**, **elliptical foramen**.

– periotic facet [new term]

In many nondelphinoid Odontoceti (e.g., *Physeter*, *Platanista*, many ziphiids), the thin **anterodorsal crest of the tympanic bulla** is rounded transversely to form a periotic facet (new term) that is received by the **anterior bullar facet** of the **periotic bone**. Previously, Fordyce (1994:158,160) used the name ***processus tubarius*** for this part of the anterodorsal crest, but the *processus tubarius* or **accessory ossicle** is a more-posterior structure.

Tursiops lacks a periotic facet on the anterodorsal crest of the **tympanic bulla**.

= petro-tympanic bone (Flower, 1885) = petrotympanic bone

See **tympanoperiotic bone**.

= petrotympanic fissure (*fissura petrotympanica*)

Van der Klaauw (1931:160) cited Hanke (1914:507) as reporting that the *fissura petrotympanica* is broad, but this use of the term apparently refers to some other structure.

The petrotympanic fissure should not be confused with the **medial petrotympanic fissure**.

See ***fissura Glaseri***.

= petrotympanic fissure, medial (Luo and Gingerich, 1999: tbl. 4, #30)

See **medial petrotympanic fissure**.

= petro-tympanic orifice (Fraser and Purves, 1960:9)

See **tympanic aperture** (Flower, 1885).

= posterior aperture (Fraser and Purves, 1960: e.g., fig. 1)

See **elliptical foramen**.

= posterior cleft (Luo and Gingerich, 1999: fig. 14)

See **elliptical foramen**.

= posterior conical apophysis

See **conical process**.

– posterior crus of ectotympanic ring

The posterior crus is part of the primitive, simple, ring-shaped or horseshoe-shaped ectotympanic of therian mammals; it articulates with the squamosal (see e.g., Ridewood, 1922:240 ff.; Novacek, 1986:51–52; Luo and Gingerich, 1999).

The ectotympanic is highly modified in *Tursiops* and other Neoceti to form the **tympanic bulla**. The anterior crus forms the **sigmoid process** and more-anterior features, while the posterior crus forms the **posterior process of the tympanic bulla**.

The posterior crus is not identifiable in adult *Tursiops*.

= posterior pedicle

See **inner posterior pedicle**, **outer posterior pedicle**.

* **posterior process of the tympanic bulla** (Figures 6f, 25b,c,e–g,r,x,y)

We are not aware of an elongate posterior process of the **tympanic bulla** in noncetacean mammals, but bullar features homologous with those of cetaceans can be identified. For clarity, we detail *Tursiops* first, then other mammals.

In *Tursiops* the posterior process of the tympanic **bulla** lies at the extreme posterodorsal end of the bulla and articulates with the periotic by a facet for the **posterior process of the periotic bone** that sutures with the **posterior bullar facet** of the periotic. In *Tursiops* the posterior process of the tympanic bulla carries regions that can be homologized with the facet for the **posterior meatal crest** (q.v.) and the facet for the **posttympanic process** (q.v.) (sensu Fordyce, 1994: fig. 11) of archaic Odontoceti. In young *Tursiops* the facet for the posterior meatal crest on the bulla is loosely sutured with the posterior meatal crest of the squamosal (q.v.), while the facet for the posttympanic process is loosely sutured with the small posttympanic process of the squamosal (q.v.). These features are usually obscure in adult *Tursiops*.

The posterior process of the tympanic bulla is connected to the remainder of the bulla by the **posterior pedicle**. If an **elliptical foramen** is present, the posterior pedicle is divided into an **inner pedicle** (q.v.; **inner posterior pedicle**) that attaches to the **involucrum**, and an outer pedicle (q.v.; **outer posterior pedicle**) that attaches to the **outer lip** posterior to the **conical process** (Kasuya, 1973). Yamada (1953) referred to the posterior process of the tympanic bulla as the mastoid process, but the bulla in *Tursiops* and other Odontoceti apparently lacks any component of the mastoid process of noncetacean mammals. See discussion under **mastoid process of the petrosal** in "Periotic Bone."

See also **distal plate of the posterior process of the tympanic bulla.**

Homologous features are seen in other mammals. In white-tailed deer (*Odocoileus virginianus*) and sheep (*Ovis aries*), such features occur in the posterior part of the tubular **external auditory meatus**, which is formed by the ectotympanic. In the deer (lateral view), the thin posterodorsal edge of the **external acoustic meatus** sutures with a thin plate of the **retrotympanic process** of the squamosal, immediately anterior to the mastoid process. Here, the posterodorsal edge of the external acoustic **meatus** probably represents the facet for the posterior meatal crest (q.v.) of the cetacean tympanic bulla, and perhaps also the facet for the posttympanic process. On the deer squamosal, the retrotympanic process is probably equivalent to the posterior meatal crest of the cetacean squamosal. Farther posteriorly, in deer, the bulla articulates narrowly with the **mastoid process of the petrosal** just lateral to the **tympanohyal**. In *Tursiops* this articulation is represented by contact of the posterior process of the tympanic bulla with the **posterior bullar facet** of the periotic.

The term "posterior process of the tympanic bulla" has had a confused history of use because of uncertain homology with the mastoid process or **posterior process of the periotic bone**. Flower (1872:218, 219, 234, pl. 29, caption) identified the large wedge-shaped posterior process of the tympanic bulla in Ziphiidae as comparable in position to the mastoid process of other mammals: "it differs from the ordinary mastoid in being united to the tympanic instead of the periotic." Later, Flower (1885:216) clearly differentiated the mastoid process of the periotic from the enlarged posterior process of the tympanic bulla, which merely "resembles in its relations the mastoid of ordinary mammals. . . ."

Schulte referred to the posterior process of the **tympanic bulla** in *Kogia* as the "'mastoid' process of the tympanic." (1917:392) or as the "tympano-mastoid" (1917:394). See also comment by Pompeckj (1922:63).

Van der Klaauw (1931:37) referred to the posterior process of the tympanic **bulla** as the *processus petrosus* [or *processus posterior*] of the tympanic.

Lillie (1910:777; see also Turner, 1913:14) used the term "**opisthotic portion of the periotic**" for the fused posterior process of the tympanic bulla plus periotic in *Balaenoptera musculus*.

Yamada (1953:19, fig. 17) and Fraser and Purves (1960: *Caperea*: pls. 5, 6; *Balaenoptera*: pl. 7; Ziphiidae: pls. 8–11) used the name "mastoid process" for the fused posterior process of tympanic bulla and periotic in Mysticeti. For Odontoceti Fraser and Purves (1960:77–80; e.g., pl. 8) also used "mastoid process" for the posterior process of the tympanic bulla and for the **posterior process of the periotic bone**.

We cannot identify in *Tursiops* or other Odontoceti any mastoid component in the tympanic bulla, and recommend that the term "mastoid" not be used for components of the tympanic bulla or, because of the above confusion, for components of periotic or squamosal.

Kellogg (e.g., 1928, 1931) identified the fused posterior process of tympanic bulla and periotic in Mysticeti merely as the "posterior process," without indicating a component of periotic.

The structure in young animals helps resolve the homology of the posterior process of the tympanic bulla, particularly in Mysticeti. In fetal or neonate *Tursiops* and many other Odontoceti and some archaic Mysticeti, the posterior process of the periotic bone and the posterior process of the tympanic bulla are short and subequal in size, are relatively smooth rather than rugose, lie within a somewhat open region between squamosal and exoccipital, and are not exposed prominently on the skull wall. Both processes are similarly short in Archaeoceti, which differ, however, in having the posterior process of the periotic bone exposed laterally on the skull wall (see discussion under Periotic). In fetal and/or neonate modern specimens, the posterior suture between the tympanic bulla and periotic is clearly visible, and is not fused.

The situation in neonate *Tursiops* is shown in Figure 25a–e. For Mysticeti, Kasuya (1973: pl. 1, fig. 9) illustrated fetal *Balaenoptera borealis*. Lillie (1915: pl. III, fig. 1) illustrated the tympanoperiotic of *Megaptera novaeangliae* in which the suture is visible between the posterior process of the tympanic bulla and the periotic. Van Beneden and Gervais (1869–1879) provided lateral and medial views of tympanoperiotics of fetal and juvenile *Balaena australis* (pl. I, II, fig. 10) in which there is a distinct suture between the posterior process of the tympanic bulla and the periotic. Van Beneden and Gervais also showed older specimens of *Balaena "antipodarum"* (pl. II, fig. 12), *Balaena mysticetus* (pl. VI, fig. 5), and *Megaptera "longimana"* (pls. X, XI, fig. 7) in which the suture between the posterior process of the tympanic bulla and the periotic are fused anteriorly but are still open posteriorly (distally). In adult Mysticeti, periotic and tympanic bulla are fully fused posteriorly to form the structure that is usually termed the posterior process of the tympanic bulla despite the contribution from the periotic. Table 8 is a summary of homologies of some bullar and associated structures in *Tursiops* and *Odocoileus*.

* **posterior tympanic spine** (*spina tympanica posterior*) = lesser tympanic spine (*spina tympanica minor*) (Figure 25s)

TABLE 8. A summary of homologies of some bullar and associated structures in *Tursiops* and *Odocoileus*.

Tursiops		*Odocoileus*
Sigmoid process of the bulla	=	Anterodorsal part of ectotympanic in external acoustic meatus
Conical process of the bulla	=	Floor of ectotympanic in external acoustic meatus
Posterior process of the bulla	=	Posterodorsal part of ectotympanic in external acoustic meatus
Facet (on the posterior process of the tympanic bulla) for the posterior meatal crest	=	Suture, in part, on posterodorsal part of ectotympanic at external acoustic meatus, for contact with squamosal
Facet (on the posterior process of the tympanic bulla) for the post-tympanic process	=	Suture, in part, on posterodorsal part of ectotympanic at external acoustic meatus, for contact with squamosal
Posterior meatal crest of the squamosal	=	Retrotympanic process in part, possibly the more medial portion
Post-tympanic process of the squamosal	=	Retrotympanic process in part, possibly the most lateral portion

The posterior tympanic spine is located on the posterodorsal border of the **tympanic ring** in mammals (Feneis, 1994:16.7; not in Schaller, 1992). The posterior tympanic spine, together with the **anterior tympanic spine**, marks the lower margin of the *membrana Shrapnelli* or *pars flaccida* (Bondy, 1907, cited by van der Klaauw, 1931). The development of anterior and posterior tympanic spines varies among mammalian species.

The tympanic ring or **tympanic annulus** is modified in cetaceans because of the development of the **sigmoid process** and **conical process**. A ridge that marks part of the tympanic ring was illustrated for *Phocoena phocoena* by Boenninghaus (1904: pl. 13, fig. 12A), and comparable structures exist in *Tursiops* (Figure 25w). A subhorizontal ridge extends posteriorly from the conical process and rises some way up the face of the outer pedicle of the posterior process. A projecting flange, originating from the outer pedicle of the posterior process, overhangs the ridge. The flange is probably homologous with the posterior tympanic spine.

Dissection is needed to identify the posterior boundary between the **tympanic membrane** and the *membrana Shrapnelli* (*pars flaccida*).

= **posteroexternal angle** (Kellogg, 1936)
See **outer posterior prominence**.

= **posterointernal angle** (Kellogg, 1936)
See **inner posterior prominence**.

= ***processus conicus posterior***
See **conical process** or **median process**.

= ***processus conicus posterior sive lateralis*** (Schulte, 1917:395)
See **conical process** or **median process**.

– ***processus perioticus***

"*Processus perioticus*" was used by Schulte (1917:396) without clear definition. It appears to refer to that portion of the posterior process of the **bulla** in *Kogia* that carries the facet for the **posterior process of the periotic bone**. Because the original definition is not clear, we recommend the term "*processus perioticus*" not be used. Schulte (1917:394) apparently also equated the *processus perioticus* with the ***processus petrosus ossis tympanici*** (= *processus conicus anterior* of Denker, 1902:428; pl. 14, fig. 2, "p.c.a.").

See **anterior conical process**.

– ***processus petrosus* of the tympanic**

Schulte (1917:396) identified the *processus petrosus* of the tympanic as that part of the **bulla** contacted posteriorly by the periotic, but did not define the "*processus petrosus*." He stated that "the *processus petrosus* [is reduced] to a plate of but moderate thickness," implying that the *processus petrosus* is distinct from his "tympano-mastoid." Because the original definition is not clear, we recommend the term "*processus petrosus* of the tympanic" not be used.

= ***processus petrosus ossis tympanici***
See **posterior process of the tympanic bulla** (Denker, 1902: pl. 14; Schulte, 1917:394).

= ***processus styliformis*** (van der Klaauw, 1931)
See **muscular process of the tympanic bulla**.

= ***processus tubarius* of the bulla** = accessory ossicle

Boenninghaus (1904: fig. G(6)) clearly identified the ***processus tubarius*** as the nodular structure on the dorsal part of the **outer lip**, also known as the **accessory ossicle** or **tubal tubercle**. Subsequently, the term "*processus tubarius*" has had a confused use.

Van der Klaauw (1931:132) identified the *processus tubarius* for mammals generally as the attachment for the cartilaginous **Eustachian tube** and the *m. tensor veli palatini*, sometimes forming an inward-pointing hook. Van der Klaauw (1931) also equated the *processus tubarius* with the *processus conicus anterior* (q.v.), but Denker (1902) indicated that the latter is a separate structure.

Fordyce (1994:158, 160) used *processus tubarius* for the enrolled or subcylindrical part of the **anterodorsal crest of the tympanic bulla** that sutures with the periotic in the fossil dolphin *Waipatia*; here, we use the term "**periotic facet**" for the suture on the anterodorsal part of the outer lip on various Neoceti and Archaeoceti. In *Tursiops* there is no periotic facet on the enrolled or subcylindrical anterodorsal thin outer edge of the **bulla** because this feature has been obliterated by an enlarged **accessory ossicle**.

Luo (1998:287) and Luo and Gingerich (1999:32, tbl. 4, #15, #16a) equated the *processus tubarius* with the whole of the **anterior process of the tympanic bulla**.

Van der Klaauw (1931:132) noted that Hanke (1914:508, 509) reported the *processus tubarius* as absent in Mysticeti. The process is, however, present but altered to form the narrow elongate **anterior pedicle** of the **tympanic bulla**.

See **accessory ossicle** for discussion.

* ***recessus meatus*** (Figure 25w)

The *recessus meatus* in mammals is that part of the **tympanic cavity** that extends laterally beyond the ***crista tympanica* of the meatus** (q.v.) (Whitmore, 1953:135).

Alternatively, van der Klaauw (1931:200) stated that the *recessus meatus* is the groove that sometimes occurs within the **meatus** lateral to the insertion of the **tympanic membrane**. MacPhee (1981:62) followed this definition; McDowell (1958:128) recognized the *recessus meatus* as the most proximal part of the bony **external auditory meatus**, set off from the meatus proper by its broader diameter In *Tursiops* a *recessus meatus* sensu Whitmore develops dorsolaterally via an excavation into the **conical process**. This recess is continuous with the tympanic cavity. In *Tursiops* the *recessus meatus* may be delimited by a **bullar septum**.

See **hypotympanic sinus**.

= rostral carotid foramen

The rostral carotid foramen or ***foramen lacerum*** is the anterior opening of the **carotid canal** in the dog (Evans and Christensen, 1979).

The rostral carotid foramen is not present in Neoceti.

See also **carotid canal**.

= rostral lip

Schulte (1917:395; cited by van der Klaauw, 1931:29) appeared to use the term "caudal lip" for the **involucrum** in *Kogia*, and "rostral lip" for the opposite structure, which therefore could include the whole of the **outer lip** of the **tympanic bulla**.

See **outer lip**.

– rostral ridge of sigmoid process

Schulte (1917:395) recognized two ridges, caudal and rostral, arising from the apex of the **sigmoid process** in the **bulla** of *Kogia*. Of these, the rostral ridge "continues into the free margin of the bulla losing its identity at the point where the malleus is anchylosed." The rostral ridge is thus homologous with the internal edge of the sigmoid process as seen in *Tursiops* and other odontocetes.

– rostral squamosal foot

The rostral squamosal foot is the anterior part of the **mallear plate** (q.v.) of the dorsal part of the ectotympanic in the archaic insectivore *Leptictis* (Novacek, 1986:51, fig. 19).

This structure cannot be homologized in *Tursiops*.

* **semicanal for the auditory tube** (*semicanalis tubae auditivae*) (Figure 25a)

The semicanal for the **auditory tube** lies at the anteromedial end of the **tympanic bulla** (Evans and Christensen, 1979:152, 153; Schaller, 1992:24.14). The semicanal for the auditory tube accounts for part of the **musculotubal canal of the tympanic bulla**. In humans the semicanal for the auditory tube accounts for the ventral part of the musculotubal canal (Feneis, 1994:12.30).

In *Tursiops* and other Odontoceti the semicanal for the auditory tube (= musculotubal semicanal, **Eustachian outlet**, and tympanic outlet) has been relatively enlarged and occupies most of the lumen of the tympanic **bulla**.

– semicanal for the *tensor veli palatini* muscle (*semicanalis m. tensoris veli palatini*)

The semicanal for the *tensor veli palatini* muscle lies anterolateral to the **semicanal for the auditory tube** in the anteroventral portion of the *pars tympanica* (Schaller, 1992:24.13).

According to Fraser and Purves (1960:11, 19) the Odontoceti *Phocoena phocoena* and *Delphinus delphis* have an *m. tensor veli palatini*. We could not find published details of its origin at the **tympanic bulla**.

* ***septum bullae*** (Figure 25w)

The *septum bullae* in canids is a shallow **transverse septum** in the ventral wall of the auditory cavity that divides the **tympanic bulla** (Schaller, 1992:24.9). It is also known as the septum of the meatal tube, and intrabullar part.

In some Archaeoceti the meatal tube protrudes into the **tympanic cavity** and is supported by septa or *trabeculae* (Luo, 1998:278). *Tursiops* appears to have two indistinct bullar septa, associated with the **conical process**. An anterior septum descends obliquely forward ventral to the **sigmoid process**, while the more robust and lower posterior septum descends gently posteriorly, toward the **inner posterior pedicle**.

See ***diverticulum anterior*** and ***diverticulum posterior*** for discussion.

– septum of the musculotubal canal (*septum canalis musculotubarii*)

The septum of the musculotubal canal divides the lateral **semicanal for the *tensor veli palatini* muscle** from the medial **semicanal for the auditory tube** (Schaller, 1992:24.15; Feneis, 1994:12.31).

It is not known if *Tursiops* has an *m. tensor veli palatini* that originates in the wall of the **auditory tube**. There is no bony septum of the musculotubal canal.

See **semicanal for the *tensor veli palatini* muscle**.

– sheath for the hyoid process (*vagina processus hyoidei*)

Schaller (1992:24.6) termed the sheath for the hyoid process the "*vagina processus styloidei*." Van der Klaauw (1931) used the same term for the canal that encloses the "top of the stylohyal and the tympanostyloid cartilage."

Schaller's term seems inappropriate, given the homology of the hyoid components; see "Hyoid Apparatus."

For archaic artiodactyls Whitmore (1953:134) identified the ***vagina processus hyoidei*** as the pit for the cranial end of the **tympanohyal**.

A small subcircular roughened surface is variably present in *Tursiops*; this is probably the *vagina processus hyoidei*.

– sheath for the styloid process (*vagina processus styloidei*)

Whitmore (1953) stated that, in archaic artiodactyls, the **sheath for the hyoid process** is the pit on the **tympanic bulla** that surrounds the cranial end of the **tympanohyal** bone. (The latter is in part the **styloid process**.) This structure is present in ruminants and the horse (Schaller, 1992:24.6), where it is termed the "sheath for the styloid process" (*vagina processus styloidei*). The sheath for the styloid process is formed by a sheet of the tympanic bone reflected around the base of the styloid process (Schaller, 1992:24.6; Feneis, 1994:16.10).

Luo (1998:278, and fig. 4) identified this feature in Archaeoceti as the **tympanohyal sulcus**, and homologized it with the **interprominential notch** of the tympanic **bulla**.

In *Tursiops* the tympanohyal, which in other mammals articulates with the stylohyal, is greatly reduced. Dissections have not shown that hyoid elements affect the surface topography of the tympanic bulla, and we hesitate to homologize the interprominential notch with the tympanohyal sulcus. However, the groove associated with the putative tympanohyal is reasonably homologized with the sheath for the hyoid process, for which "tympanohyal sulcus" is an appropriate alternative name. We cannot judge if the interprominential notch in *Tursiops* is functionally related to the sheath for the hyoid process.

*** sigmoid process** (Figures 25c–h,j,r,s,v–x,y, 29)

The sigmoid process of the **tympanic bulla** (Beauregard, 1894:380, 381, fig. 2s) lies on the dorsal margin of the **outer lip** of the **bulla**, anterior to the **conical process** and posterior to the ***fissura Glaseri***. The sigmoid process extends dorsolaterally and is usually complexly concave on its posterior surface (Yamada, 1953:20; Kasuya, 1973).

The **tympanic membrane** appears to insert subvertically in the middle of the posterior face of the sigmoid process. The lateral portion of the posterior face of the sigmoid process thus forms part of the anterior wall of the **external acoustic meatus**.

In the periotic of *Delphinus delphis* that we dissected, the laterally produced groove on the posterior surface of the apex of the sigmoid process seems to carry the start of the **middle sinus**.

Despite the suggestion of Hanke (1914:506, cited by van der Klaauw, 1931:37, 159), we know of no cetacean where the sigmoid process fuses with the periotic. In *Tursiops* the medial part of the sigmoid process closely approximates the periotic, to the extent that a gap cannot be seen between the elements, and thus might be said to suture, but the elements are not fused.

Turner (1913:16) named this the "**mallear process**" or "**lip-like process**." Van der Klaauw's (1931:262) comment on Turner did not make it clear that sigmoid process and mallear process are the same structure.

The sigmoid process is homologous with part of **tympanic annulus** of other mammals (Doran, 1878; Ridewood, 1922). It represents the modified anterior wall of the external acoustic **meatus**, and Luo (1998:294) regarded it as arising from the embryonic anterior crus. Structures transitional between some land mammals and *Tursiops* are seen in some archaeocete whales (Luo, 1998).

See **rostral ridge of sigmoid process**.

= styliform process (van der Klaauw, 1931:133; Whitmore, 1953)

Van der Klaauw (1931:133) noted possible confusion between the term "***processus styliformis***" or "styloideus," used here for the **muscular process of the tympanic bulla**, and the term "**styloid process**" or "*processus styloideus*," used for the fused **tympanohyal** and stylohyal of other eutherians.

See **muscular process of the tympanic bulla**.

= styloid apophysis (de Muizon, 1988)

See **muscular process of the tympanic bulla**.

*** sulcus for the *chorda tympani*** (*sulcus pro chorda tympani*) (Figures 25c,d,h,j, 26a)

In *Tursiops* and other Neoceti the *chorda tympani* lies in a sulcus that arises posteriorly at the **petrotympanic fissure** (= ***fissura Glaseri***) and runs anteriorly along the dorsal edge of the **outer lip** of the **tympanic bulla** (Kellogg, 1936:114; Archaeoceti: Pompeckj, 1922: pl. 2, fig. 8). The posteromedial part of the groove may be equivalent to the ***chordafortsatz***. Relationships are not clear with the **malleolar sulcus** (in the sense of MacPhee, 1981:57). The groove is bounded laterally and posteriorly by the **mallear ridge** and medially by the **accessory ossicle**. This interpretation differs significantly from that of Luo and Gingerich (1999: fig. 21).

= sulcus for the tympanohyal

See **tympanohyal sulcus**, **sheath for the hyoid process**, and **interprominential notch**.

= *sulcus malleolaris* = malleolar sulcus

= *trabeculae*, of meatal tube, intrabullar part = septa of meatal tube, intrabullar part

– transverse ridges

Transverse ridges (Kellogg, 1969:25) sometimes occur on the dorsal surface of the **involucrum** in Neoceti.

They are indistinct in *Tursiops*.

*** triangular opening** (Figure 25y)

The triangular opening lies on the lateral surface of the articulated **tympanic bulla** and periotic between the **sigmoid process** of the tympanic bulla, the **anterior process of the periotic bone**, and the malleus (Kasuya, 1973: fig. 1).

The triangular opening in *Tursiops* is further subdivided into an anterior division and a posterior division by a transverse crest coming off the lateral surface of the **bulla**, anterior to the sigmoid process and posterior to the malleus. This crest articulates with the **lateral tuberosity** (Fordyce, 1994:160) of the periotic.

= tubal canal (tubal foramen, tubal groove) (MacPhee, 1981:64)

See **musculotubal canal of the tympanic bulla**.

= tubal tubercle (*processus tubarius*)

See **accessory ossicle**.

= tympanic annulus (*anulus tympanicus*)

See **tympanic ring**.

*** tympanic aperture** (*apertura tympanica*) (Figure 29)

The tympanic aperture in cetaceans (Denker, 1902) is bounded ventrally by the **sigmoid process**, **conical process**, and

posterior process of the tympanic bulla. It is divided into the lower and **upper tympanic apertures** (Yamada, 1953; Kasuya, 1973: fig. 1). We prefer to use "**epitympanic hiatus**" to refer to the structure that was known as the upper tympanic aperture. As it now stands, the tympanic aperture consists of the combined **lower tympanic aperture** and epitympanic hiatus (q.v.).

The tympanic aperture is present in *Tursiops*.

* **tympanic bulla** (*bulla tympanica*) (Figures 3, 4, 6f, 29)

The tympanic bulla, when present in mammals (van der Klaauw, 1931; Novacek, 1977), is an inflated bone that lies directly ventral to the **mastoid process of the petrosal** (**periotic bone**). It is formed of the **tympanic part of the temporal** and contains the fundus of the **tympanic cavity** (Evans and Christensen, 1979:129, 133, 134). The **bulla** was also referred to as the *processus petrosus ossis tympani* (Denker, 1902) or the **tympanomastoid** (Schulte, 1917; Yamada, 1953:19).

In *Tursiops* and other delphinids the tympanic bulla is a completely separate ossification formed by the embryonic ectotympanic (de Beer, 1937:341ff). It lies posterolaterally on the ventral surface of the skull, ventral to the periotic and ventromedial to the squamosal. It articulates with the periotic anteriorly at the **accessory ossicle** and posteriorly at the posterior process. Anteriorly, it is closely approached by the **falciform process** of the squamosal bone.

* **tympanic cavity** (*cavum tympani*) (Figure 25f,h,j,r)

The tympanic cavity contains the middle ear (Gray, 1918:1037; Evans and Christensen, 1979:132; Schaller, 1992:534.12; Feneis, 1994:378.16). Eustachius and Lancisius (1714:105) referred to the tympanic cavity as the *cavitas tympani* or the *tympani cavitas*.

The tympanic cavity in the dog is enclosed by the **tympanic bulla** and the periotic. It consists of three parts: the fundic part, which is the largest part and entirely contained within the tympanic **bulla**; the tympanic cavity proper, which is located dorsal to the fundic part and opposite the **tympanic membrane**; and the **epitympanic recess**, which is located dorsal to the tympanic cavity proper and contains the incus, part of the stapes, and the **head of the malleus**. In cetacean literature the fundic part has long been termed the "tympanic cavity," without other qualification.

Whitmore (1953:132) used the term "**hypotympanic sinus**" for the tympanic cavity sensu lato of archaic artiodactyls. Van der Klaauw (1931:214) discriminated between the hypotympanic cavity and true tympanic cavity, but on page 262 implied that the hypotympanic sinus is a separate section of the tympanic cavity.

The tympanic cavity in *Tursiops*, other delphinids, and Neoceti in general is enclosed by the tympanic bulla and periotic. It communicates with the nasopharynx by means of the **auditory tube** (**Eustachian tube**).

The tympanic cavity has been termed the **Eustachian cavity** (by various authors) and the **bullar cavity** (Luo, 1998:284). Luo and Gingerich (1999:41) used the term "tympanic cavity" (and also peribullar cavity) apparently to refer to the cranial hiatus.

= **tympanic cleft** (Turner, 1913:13)

See **tympanic cavity**.

– **tympanic crest** (*crista tympanica*, or *margo sulci tympanici*)

MacPhee (1981:51) followed Bondy (1907) in recognizing the tympanic crest of mammals as a low semicircular ridge representing the dorsal margin of the **tympanic sulcus**. Van der Klaauw (1931:200) stated that occasionally the **tympanic groove** or sulcus may be missing, in which case the **tympanic membrane** attaches to the tympanic crest (*crista tympanica*, or *margo sulci tympanici*). The tympanic crest thus may be the same as the **tympanic ring** (q.v.) (= **tympanic annulus**).

Tursiops may have an tympanic crest. See **tympanic sulcus**.

= **tympanic groove**

See **tympanic crest**.

= **tympanic incisure**

See **tympanic notch**.

– **tympanic membrane** (eardrum) (*membrana tympani*)

The mammalian tympanic membrane (tympanum, tympanium) is not an osteological feature but is a membranous diaphragm that is supported by the **tympanic ring** (Evans and Christensen, 1979:134). The tympanic membrane intercepts airborne sounds and transmits them to the ossicular chain.

The tympanic membrane has been modified from a flat membrane in terrestrial mammals. In Mysticeti it forms an oval cone with the apex directed externally. This arrangement of the tympanic membrane has been termed the "glove finger" (Beauregard, 1894; Lillie, 1910:776, pl. lxxiv, fig. f; Fraser and Purves, 1954, 1960:10; Purves, 1966:336). The situation in Odontoceti is less clear. For example, Fleischer (1975) stated that the tympanic membrane is absent in *Kogia*. Purves (1966:336) did not mention the shape of the membrane but said that its fibrous portion forms a broad flattened triangular [tympanic] ligament that inserts on the malleus. McCormick et al. (1970:1423) indicated that the tympanic membrane in *Tursiops* is a small planar feature. According to McCormick et al. (1970) the tympanic membrane is attached only to the **lower tympanic aperture** (in the **tympanic bulla**).

See also **tympanic ring**.

* **tympanic notch** (*incisura tympanica*) (Figure 25c,f,g,y)

MacPhee (1981:52) noted that the mammalian tympanic notch is the feature at the open dorsal part of the horseshoe-shaped ectotympanic.

In many mammals the tympanic notch is bridged by part of the squamous part of the temporal where the **zygomatic process of the squamosal** is continued posterior to the **mandibular fossa** (Schaller, 1992:24.32; Feneis, 1994:16.9; our observations on *Odocoileus*). Such uses indicate that the tympanic notch is the gap between parts of the **bulla**, and not a part of the periotic or squamosal. The tympanic notch lies on the ventral surface of the extension of the zygomatic process that forms the posterior limit of the **supramastoid crest**. In humans the tympanic notch and adjacent temporal form the dorsal surface of the **external auditory meatus**.

For Archaeoceti, Kellogg (1936:113) identified the tympanic notch, which he termed *incisura Rivini*, as the gap in dorsal edge of **outer lip** of the **tympanic bulla**, between the dorsal rim of the **sigmoid process** and the anterior edge of the outer pedicle of the posterior process. The *incisura Rivini* connects the **lower tympanic aperture** with the **epitympanic hiatus**. The tympanic notch in some Odontoceti other than delphinids is roofed by the **spiny process** of the squamosal bone, which occupies the *hiatus epitympanicus* of the periotic.

The tympanic notch is present in *Tursiops*.

See ***hiatus epitympanicus*** or **epitympanic hiatus**.

* **tympanic opening of the auditory tube** (*ostium tympanicum tubae auditivae*) (Figure 25a)

The tympanic opening of the **auditory tube** lies in the anteromedial aspect of the **tympanic bulla** (Schaller, 1992:538.20). The tympanic opening of the auditory tube is the opening for the **semicanal for the auditory tube**, which is part of the **musculotubal canal of the tympanic bulla** (Evans and Christensen, 1979:152, 153).

In delphinids the tympanic opening of the auditory tube lies at the anteromedial end of the tympanic **bulla**.

= **tympanic part of the temporal** (*pars tympanica*)

The tympanic part of the temporal bone in mammals is that ossification that forms the **tympanic bulla**. The tympanic **bulla** contains most of the **tympanic cavity** (Evans and Christensen, 1979:134).

The term "temporal" is not appropriate for *Tursiops* because the squamosal, tympanic bulla (=tympanic part of the temporal), and periotic are separate elements; they are discussed separately here.

– **tympanic plate of the bulla** (Fleischer, 1978) (Figure 25g)

Fleischer (1975, 1978) used the term "tympanic plate" to refer to the thin ventrolateral portion of the **tympanic bulla**. Nummela et al. (1999a:63; 1999b: fig. 1) expanded the area. This is not to be confused with the **tympanic plate of the basioccipital bone**.

– **tympanic ring** (*anulus tympanicus*) (Figure 25w,x)

The tympanic ring in the dog is an annular-shaped process of the **tympanic part of the temporal** to which the **tympanic membrane** (q.v.) is attached (Evans and Christensen, 1979:134). In humans the tympanic ring is incomplete dorsally at the tympanic notch (Gray, 1918:146); it is the only portion of the tympanic part of the temporal in humans.

Van der Klaauw (1931:201) discussed the homology of parts of the tympanic ring, cautioning that the *crista tympanica* is not the same as the tympanic ring.

The tympanic ring in Neoceti is open dorsally at the tympanic notch, but otherwise is highly modified and has lost its ring shape; the shape is probably related to the structure of the tympanic membrane (q.v.). Dissection of *Delphinus delphis*, and observation of the **bulla**, reveals that the tympanic membrane attaches to the middle of the posterior face of the **sigmoid process**, to the ventromedial edge of the **conical process**, and to the ridge that runs posterodorsally from the ventromedial edge of the conical process; these features are equivalent to the tympanic ring. A comparable structure may be expected in *Tursiops*.

– **tympanic sulcus** (*sulcus tympanicus*)

The tympanic sulcus in mammals is a groove in the **tympanic ring** for the attachment of the **tympanic membrane** (Schaller, 1992:24.3; Feneis, 1994:16.8; see **tympanic ring**). Schulte (1917:396) used the term "drum" for tympanic membrane in *Kogia*. Van der Klaauw (1931:200) stated that occasionally the **tympanic groove** or sulcus may be missing, in which case the tympanic membrane attaches to the **tympanic crest** (*crista tympanica*). He also discriminated between the tympanic sulcus and the groove that may lie lateral to the insertion of the tympanic membrane; this groove has sometimes been termed the "***recessus meatus***."

The tympanic sulcus is poorly known in Neoceti (van der Klaauw, 1931:204). Archaeoceti show a grooved or depressed sulcus on the **conical process**, and the gray whale has a grooved sulcus at the base of the **sigmoid process**. Kellogg (1936) identified in Archaeoceti and in *Monodon* a groove on the conical process of the **tympanic bulla** as representing part of the **groove for *anulus tendineus***, or tympanic sulcus. In *Tursiops* the position of attachment of the tympanic membrane is readily identifiable as a ridge in some individuals, but there is no obvious groove (tympanic sulcus).

= **tympanohyal sulcus**

"**Tympanohyal** sulcus" is an appropriate alternative name for the **sheath for the hyoid process**.

See **sheath for the hyoid process** and **interprominential notch**.

= **tympanomastoid** (bone)

See **tympanic bulla**.

– **tympanomastoid fissure of the tympanic bulla** (*fissura tympanomastoidea*)

The tympanomastoid fissure of the tympanic bulla is formed at the external contact of the tympanic part with the **mastoid process of the** mammalian **petrosal** (Schaller, 1992:22.38).

The tympanomastoid fissure is present in Odontoceti as the articular surface of the **posterior process of the tympanic bulla** and **posterior process of the periotic bone**.

– **tympano-mastoid process** or **tympanomastoid process**

The tympano-mastoid process described by Schulte (1917:393, 394, 396) in *Kogia* is the greatly inflated **posterior process of the tympanic bulla** that has come to articulate with the **paroccipital process** of the exoccipital and exoccipital process of the squamosal. This large process is likely to be mistaken for the mastoid process in humans but bears no relation to it. The tympano-mastoid process is also developed in *Physeter* (Flower, 1868:321) and in ziphiids (Flower, 1872:218, pl. 29; Kernan, 1918:358) but not in delphinids.

We cannot identify in *Tursiops* or other Odontoceti any mastoid component in the tympanic **bulla**, and recommend that the term "tympano-mastoid" not be used in this manner.

See **posterior process of the tympanic bulla**.

– **tympano-occipital fissure** (*fissura tympano-occipitalis*)

In the dog the tympano-occipital fissure is formed by contact of the **tympanic part of the temporal** bone with the basioccipital (Evans and Christensen, 1979:135).

In *Tursiops* or other Odontoceti the **tympanic bulla** does not contact the basioccipital.

* **tympanoperiotic bone**

The tympanic and periotic portions of the temporal as seen in other mammals have become increasingly isolated from the cranium in cetaceans, much more so in Odontoceti than in Mysticeti. In many Odontoceti the tympanic and **periotic bones** are attached to the skull by a thin lamina of bone but are attached to each other by the articulation of the **posterior bullar facet** of the periotic with the **posterior process of the tympanic bulla**. The tympanic and periotic form a functional unit that is referred to as the tympanoperiotic bone (Anderson, 1879:508; Flower, 1885; Fordyce, 1994). It has also been called the petro-tympanic or **petrotympanic bone** (Owen, 1866a:30, 40), or the **otocrane** (Owen, 1866a:26, 29, 30, 35).

– tympanosquamosal fissure (*fissura tympanosquamosa*)

The tympanosquamosal fissure is the fissure formed where the tympanic bone contacts the squamosal bone on its cranial surface (Schaller, 1992:22.39). The tympanosquamosal fissure is present in sheep, goats, and horses, but is absent in other domestic animals.

The contact between the periotic and squamosal has been greatly reduced in delphinids, phocoenids, and iniids, and the tympanosquamosal fissure is absent (Kasuya, 1973:50, fig. 73). In other Odontoceti (e.g., the Ziphiidae, Platanistidae, Physeteridae) the tympanosquamosal fissure is present. Monodontids are equivocal.

There is no well-developed tympanosquamosal fissure in *Tursiops*, but sutures with the squamosal may occur in juveniles, between the **anterodorsal crest of the tympanic bulla** and the apex of the **falciform process**, and between the **posterior process of the tympanic bulla** and the **posterior meatal crest**. See **tympanosquamosal suture**.

– tympanosquamosal suture

The **posterior process of the tympanic bulla** in delphinids may suture with the squamosal via thin laminae of bone. These thin laminae go from the anterolateral margin of the posterior process to the **posterior meatal crest** of the squamosal. Because the **posttympanic process** is lost in *Tursiops*, there is no suture of squamosal and **bulla** here, contrasting with the situation in some nondelphinoid Odontoceti, e.g., *Platanista*.

= unciform process (de Muizon, 1987, 1991)

This is presumably a lapsus calami for **uncinate process**.

See **accessory ossicle**.

= uncinate process

Schulte (1917 396; see also van der Klaauw, 1931) used "uncinate process" (i.e., hooked process) to refer to the **accessory ossicle** (q.v.) in *Kogia* and possibly also for the part of the **outer lip** of the **bulla** anterior to the accessory ossicle. For the latter we prefer the term "**anterodorsal crest of the tympanic bulla**" (q.v.). This feature of the **tympanic bulla** should not be confused with the **uncinate process** of the ethmoid bone (q.v.).

See **accessory ossicle**, **tubal tubercle**.

= ***vagina processus hyoidei***

See **sheath for the hyoid process**.

= ventral groove = median furrow (de Muizon, 1987; Fordyce, 1994:149)

* **ventral keel** (Figure 25b)

The ventral keel of the cetacean **tympanic bulla** lies on the ventromedial margin of the tympanic **bulla**. The ventral keel is an anterior continuation of the eminence of the **inner posterior prominence** (Kasuya, 1973). The ventral keel commonly has a very rugose surface, but it is sharply developed only in a few species of Odontoceti. The structure in *Tursiops* is rounded.

Luo (1998:290) suggested that the ventral keel is present only in Mysticeti. Oishi and Hasegawa (1995) discussed the structures in mysticetes.

Luo and Gingerich (1999: tbl. 3, #29b) used the term "**median ridge**," apparently for the ventral keel.

= vertical cleft (Kellogg, 1936: fig. 34)

See **elliptical foramen**.

AUDITORY OSSICLES

Ossicula Auditus

With the evolutionary transition from reptiles to mammals, one of the elements that changed was the composition of the lower jaw and structure of the ear. The reptilian articular bone of the lower jaw became the incus and the quadrate bone of the skull became the malleus. The three bones are present in all mammals (Gray, 1918:1044–1046; Evans and Christensen, 1979:1065–1067; Schaller, 1992:536; Feneis, 1994:382). Eustachius and Lancisius (1714:10, 19, 20, 97) referred to these bones as the *auditus ossicula*; the malleus as the *maleus os*, the incus as the *incudi os simile*, and the stapes as the *os stapedi simile* or the *stapedi os simile*.

The three auditory ossicles, malleus, incus, and stapes, are considered separately below.

MALLEUS

FIGURES 25R,S, 26A–F

* **anterior process of the malleus** (*processus gracilis*, *processus anterior*, *processus folianus*) (Figures 25f, 26a,b,d,e)

In humans (Gray, 1918:1044; Feneis, 1994:382.17) the **anterior process** is a small projection that arises below the neck and is connected to the **petrotympanic fissure** by ligamentous fibers. This process in the dog (Evans and Christensen, 1979:1066) is largely embedded in the **tympanic membrane**. The anterior process is also called the **rostral process** (Evans and Christensen, 1979:1066, fig. 19:6a) or **long process**; it is formed partly by an embryonic element, the ***goniale***. The process contacts or is fused with the **bulla** in various groups of mammals (e.g., Novacek, 1986:51, Luo and Gingerich, 1999: tbl. 3, #20, comment).

Van der Klaauw (1931:235) discussed the manner in which the anterior process (or *processus longus*) of the malleus may contribute to the **tympanic bulla**. The anterior process of the malleus lies in the ***sulcus malleolaris*** of the tympanic bulla and often fuses with the bulla. Homologies are uncertain for the sometimes-associated **malleolar accessory ossicle** (*ossiculum accessorium malleoli*).

In *Tursiops* and other Cetacea the anterior process (e.g., Kellogg, 1927) is an elongate robust projection that is fused with the **outer lip** of the tympanic bulla at the **mallear ridge**, where the medial part of the **sigmoid process** contacts the outer lip. The anterior process of the malleus carries a groove on its anterodorsal surface.

* **articular surfaces of the malleus** (Figure 26f)

The **facet for the incus** on the **head of the malleus** has two articular surfaces that contact the **body of the incus** at the incudomalleolar joint in the **epitympanic recess** (Gray, 1918:1044; Evans and Christensen, 1979:1066).

In *Tursiops* the articulation faces dorsomedially and posteriorly. As in other mammals, the upper facet is larger, the lower smaller.

* **facet for the incus** (Figure 26b)

The head of the malleus carries a facet for the incus. This facet faces dorsomedially and posteriorly and is divided into two articular surfaces.

* **foramen for the *chorda tympani*** (Figures 25r, 26a,b,e)

In the dog the nerve for the *chorda tympani* leaves the middle ear "under a fine bridge of bone of the **tympanic ring**" (Evans and Christensen, 1979:133), and continues through a canal in the lateral wall of the **bulla**.

In *Tursiops* and other Cetacea the nerve for the *chorda tympani* exits the middle ear via a small foramen for the *chorda tympani* in the malleus, just medial to the junction of the two articular surfaces of the **facet for the incus**.

= ***goniale***

See **anterior process of the malleus**.

* **groove on the malleus** (Figure 26f)

Delphinoids carry a prominent oblique groove that arises near the **facet for the incus** and traverses the dorsomedial face. Kellogg (1927:29) identified this groove as separating the **tubercule of the malleus** (with insertions for *m. tensor tympani* and the tympanic ligament) from the facet for the incus.

= **handle of the malleus** (Evans and Christensen, 1979:1066)

See **manubrium of the malleus**.

* **head of the malleus** (*caput mallei*, *capitulum mallei*) (Figure 26d)

In the dog (Evans and Christensen, 1979:1066), the head of the malleus (*capitulum mallei*) is one of three main parts of the malleus; it adjoins the neck. The head of the malleus carries the articular surfaces.

In *Tursiops* and other Delphinidae the dorsolaterally placed head of the malleus is subspherical and carries the **facet for the incus**. It articulates closely with the **mallear fossa** of the periotic. The head of the malleus merges indistinctly into the neck of the malleus.

* **insertion for the tendon of the *m. tensor tympani*** (Figure 26a,c)

The apex of the **tubercule of the malleus**, which in *Tursiops* is the most anterior part of the malleus, carries a small oval pit that is the insertion for the tendon of the *m. tensor tympani*. In other Cetacea this insertion may lie more dorsally.

– **lateral process** (*processus lateralis*)

In humans (Gray, 1918:1044) the lateral process arises from the **manubrium of the malleus**, is directed laterally, and is attached to the upper part of the **tympanic membrane** at the position of the tympanomalleolar folds that border the *pars flaccida* (*membrana Shrapnelli*). The lateral process in the dog (Evans and Christensen, 1979:1066) is the most dorsal attachment of the manubrium to the tympanic membrane. The lateral process is also known as the short process (*processus brevis*). The position of the lateral process in *Tursiops* is unknown.

= **long process** (Evans and Christensen, 1979:1066)

See **anterior process of the malleus**.

* **manubrium of the malleus** (*manubrium mallei*) (Figures 25x, 26b,c)

In humans (Gray, 1918:1044) and the dog (Evans and Christensen, 1979:1066) the manubrium of the malleus, or **handle of the malleus**, is an elongate process, the long lateral margin of which is connected with the **tympanic membrane**.

In *Tursiops* and other Delphinidae the manubrium of the malleus is an indistinct prominence marking the insertion of the tympanic ligament on the ventromedial border of the malleus. The position of the manubrium of the malleus is variable within the Odontoceti.

* **muscular process of the malleus** (*processus muscularis*) (Figure 26a,c)

The muscular process carries the insertion for the *m. tensor tympani* (q.v.). In the dog (Evans and Christensen, 1979:1066) the small muscular process projects medially and rostrally from the base of the **manubrium of the malleus**. A small hook on the apex of the muscular process of the malleus forms the insertion for the tendon of the *m. tensor tympani*. In humans, the muscular process is on the medial side near the upper end of the manubrium.

In *Tursiops* the muscular process is the most apical part of the prominent and anteriorly prolonged **tubercule of the malleus**. The process carries a small pit, the insertion for the tendon of the *m. tensor tympani*, on the apex. In other odontocetes (e.g., Platanistoidea; de Muizon, 1987) the muscular process of the malleus may lie away from the apex of the manubrium.

– **neck of the malleus** (*collum mallei*)

In the dog (Evans and Christensen, 1979:1066) the neck of the malleus is an elongate region that links the **head of the malleus** with the muscular and **lateral processes** and the **manubrium of the malleus**. In humans (Gray 1918:1044) this is a narrow restricted region below the head of the malleus.

The neck of the malleus is not distinct in *Tursiops* or other Delphinidae.

= **rostral process** (Evans and Christensen, 1979:1066)

See **anterior process of the malleus**.

* **tubercule of the malleus** (*tuberculum mallei*) (Figure 26a)

The tubercule of the malleus in *Tursiops* is the stout anterior end of the malleus that includes the **manubrium of the malleus** and the **muscular process of the malleus** (see also Kellogg, 1927: fig. 13). Published literature gives the impression that "muscular process" and "tubercule" are used interchangeably. Among different groups of odontocetes the positions of muscular process and manubrium vary (de Muizon, 1987, 1991; Kellogg, 1927; and of *Tursiops* in this work).

INCUS

FIGURES 25W,X, **26G–L**

* **articular surfaces of the incus** (Figure 26g,h,k)

Two articular surfaces on the **body of the incus** contact the malleus at the incudomalleolar joint in the **epitympanic recess** of the **petrosal** (Gray, 1918:1044; Evans and Christensen, 1979:1066).

In *Tursiops* the articular surfaces are oriented anteriorly and slightly dorsolaterally. The upper facet is larger, the lower smaller.

* **body of the incus** (*corpus incudis*) (Figure 26g–j)

In humans (Gray, 1918:1044) the body of the incus is the main part of the incus. It carries two distinct projections, the ***crus breve*** and the ***crus longum***, and has an articular surface that carries two facets for contact with the malleus.

In *Tursiops* the body of the incus is enlarged and merges with the indistinct *crus longum*.

* ***crus breve*** (*processus brevis* (Anderson, 1878:521)) (Figure 26g,h,k,l)

In the dog (Evans and Christensen, 1979:1066) the short crus, or *crus breve*, of the incus points caudally into the ***fossa incudis*** of the **petrosal**.

In *Tursiops* the *crus breve* of the incus is a delicate lateral projection from the **body of the incus**.

* ***crus longum*** (*processus longus* (Anderson, 1878:521)) (Figure 26i,j)

In humans (Gray, 1918:1044) the *crus longum* is a distinct projection from the **body of the incus**.

In *Tursiops* the *crus longum* is a short, robust posteromedial part that is not distinct from the body of the incus.

* **facet for the malleus** (Figure 26g,h,k)

In *Tursiops* the anterior part of the **body of the incus** carries a facet for the malleus. This facet faces anteriorly and slightly dorsolaterally and is divided into two articular surfaces.

* **lenticular process** (*processus lenticularis*, *os lenticulare*) (Figure 26g–j,l)

In humans (Gray, 1918:1044) the lenticular process is a rounded projection on the end of the ***crus longum***. The lenticular process articulates with the **articular facet** on the **head of the stapes.**

In *Tursiops* the lenticular process is a small dorsomedial projection on the posterior part of the **body of the incus**.

STAPES

FIGURES 25V,X, **26M–R**

* **anterior crus of the stapes** (*crus anterius*) (Figure 26o–q)

The anterior crus of the stapes, or rostral crus of the stapes, is the more anterior of the two stapedial crura.

* **articular facet** (Figure 26n)

The **head of the stapes** carries an articular facet for contact with the **lenticular process** or ***crus longum*** of the incus (Kellogg, 1927:29, 31).

* **base of the stapes** (*basis stapedis*) (Figure 26o,q,r)

The base of the stapes is the flattened oval plate of the stapes (Gray, 1918:1045) that articulates with the periotic at the *fenestra vestibularis* (***fenestra ovalis***, **oval window**). The base is also known as the "**footplate of the stapes**" (Kellogg, 1927:31).

= footplate of the stapes

See **base of the stapes.**

* **head of the stapes** (*caput stapedis*, *capitulum stapedius*) (Figure 26n,p,q)

The head of the stapes is at the opposite end to the **base of the stapes.** It carries the **articular facet** for contact with the **lenticular process** or ***crus longum*** of the incus (Gray, 1918:1045).

* **muscular process of the stapes** (Figure 26o,p,r)

In the dog (Evans and Christensen, 1979:1067) the muscular process on the posteromedial face of the **neck of the malleus** marks the attachment of the stapedial muscle.

A muscular process of the stapes is well developed in *Tursiops*.

– neck of the stapes

In humans (Gray, 1918:1045) the neck of the stapes is the constricted part of the stapes between the **head of the stapes** and the **stapedial foramen.** It carries the **muscular process of the stapes** (q.v.) on the posterointernal face.

There is no obvious neck of the stapes in *Tursiops*.

* **posterior crus of the stapes** (*crus posterius*) (Figure 26o,p,r)

The posterior or caudal crus of the stapes is the more posterior of the two stapedial crura.

* **stapedial foramen** (Figure 26o,p)

The stapedial foramen is the foramen that opens, in humans (Gray, 1918:1045), between the two stapedial crura. The stapedial foramen is also known as the intercrural aperture or intercrural foramen (Kellogg, 1927:31).

In *Tursiops* the anterior and posterior crura are close together, and the stapedial foramen is vestigial.

* **umbo** (Figure 26m)

The umbo is the concavity on the vestibular face of the **footplate of the stapes** (Kellogg, 1927:31).

The umbo is well developed in *Tursiops*.

VOMER

FIGURES 27, 29, **31A**

The vomer is the ventral midline portion of the rostrum and is the only unpaired bone in the rostrum. The vomer forms an important link between the facial bones of the rostrum and the mesethmoid of the cranium. The vomer also contributes to the ventral part of the nasal septum.

The vomer in cetaceans has taken over entirely the separation of the right and left nasal passages. The vomer forms the floor of the mesorostral canal, through which the mesorostral cartilage of the mesethmoid protrudes. In ziphiids, where the elements of the rostrum fuse, the vomer forms the mesorostral ossification (Schulte, 1917:374, 375, 378, 380, 381, 384–388, 400).

= **alar process of the vomer** (Anderson, 1879:511) = wings of the vomer

= **aliform process** (Owen, 1866b–1868(vol. 2):420) = alar process of the vomer

– **base of the vomer** (Evans and Christensen, 1979:146)

Evans and Christensen (1979:146) discussed the vomer as follows:

> The sagittal part is formed of two thin, bony leaves, *laminae laterales*, which unite ventrally to form a sulcus, *sulcus septi nasi*, which in turn receives the **cartilaginous nasal septum** rostrally and the **bony nasal septum**, or **perpendicular plate** of the ethmoid caudally. It articulates ventrally with the **palatine processes of the maxillae**, with the caudal parts of the palatine processes of the incisive bones, and with the rostral parts of the **horizontal portions of the palatine bones**. This caudal articulation is at the palatine suture and the ventrorostral half of the base of the vomer. The **sagittal part of the vomer** is sharply forked at each end. The rostral notch is the **incisive incisure** (*incisura incisiva*); the caudal is the **sphenoidal incisure** (*incisura sphenoidalis*).

Evans and Christensen did not identify the "base of the vomer" on any illustrations, although he labeled the articulation with the palatine on figure 4–34 (Evans and Christensen, 1979:146). This articulation is on the posterolateral aspect of the wings (horizontal part) and not the sagittal part. Due to this inconsistency, we have not chosen to use the base of the vomer in this work.

– **bony nasal septum** (*septum nasi osseum*)

The bony nasal septum consists of the **perpendicular plate** of the ethmoid bone (Gray, 1918:194; Evans and Christensen, 1979:135; Schaller, 1992:14.2; Feneis, 1994:32.2;) and the **sagittal part of the vomer**. In many mammals, including humans and dogs, the **cartilaginous nasal septum** attaches to the anteroventral part of the bony nasal septum.

In delphinids the **mesethmoid** (**perpendicular plate** of the ethmoid bone) has come to lie internal to the **nasal plate** of the vomer, and the latter bone makes up the nasal septum.

– **cartilaginous nasal septum** (*cartilago septi nasi*)

The cartilaginous nasal septum is attached to the anterior margin of the **perpendicular plate** of the ethmoid bone and **sagittal part of the vomer** (Gray, 1918:194, 992; Evans and Christensen, 1979:158; Schaller, 1992:176.6; Feneis, 1994:134.22). The cartilaginous nasal septum separates the anterior part of the nasal cavity.

The entire **nasal septum** in delphinids is formed by the vomer, without cartilaginous component. The homologue of the cartilaginous nasal septum is attached to the **mesethmoid** as the **mesorostral cartilage**.

= **choanal crest of the vomer** (*crista choanalis vomeris*) = vomerine crest (*crista vomeris*)

= **fusiform crest** (Kernan, 1918:352) = mesorostral ossification

= **groove for nasal septum** = median vomerine groove (*sulcus septi nasi* / *sulcus vomeris* / *sulcus septalis*) = mesorostral canal

* **horizontal part of the vomer** (Figure 27b–d)

The vomer consists of two parts, the horizontal part and the sagittal part. The horizontal part of the vomer consists of the wings (*ala vomeris*) (Schaller, 1992:30.11).

The **wings of the vomer** are well developed in delphinids.

* **incisive incisure** (*incisura incisiva*) (Figure 27a,c,d)

The incisive incisure is a notch in the midline at the anterior end of the **sagittal part of the vomer** (Evans and Christensen, 1979:146). This term is not in the *Nomina Anatomica Veterinaria* (Schaller, 1992:30.8).

The incisive incisure is present in some *Tursiops*.

* **lateral sheet** (*lamina laterale*) (Figure 27a,c)

The lateral sheets are composed of the **sagittal part of the vomer**. They unite ventrally to form the sulcus (**groove) for the nasal septum**. This sulcus receives the **cartilaginous nasal septum** anteriorly and the **mesethmoid** ossification posteriorly (Evans and Christensen, 1979:146). The vomer in humans and many other mammals is reduced and the lateral sheet is not differentiated (Schaller, 1992:30.8; Feneis, 1994:20.28). This term is not in the *Nomina Anatomica Veterinaria*.

In cetaceans the bulk of the vomer is composed of the lateral sheets.

= **median vomerine groove** = groove for nasal septum (*sulcus vomeris* / *sulcus septi nasi* / *sulcus septalis*) = mesorostral canal

= **mesorostral bone** = mesorostral ossification (Turner, 1872)

* **mesorostral canal** (Figures 1, 8a, 27a,d)

The mesorostral canal lies on the dorsal midline of the rostrum. It is bounded by the premaxillae laterally and by the vomer ventrally (Flower, 1878; Heyning, 1989a:5). The mesorostral canal is limited posteriorly by the **mesethmoid.** It has also been called the mesorostral furrow (Turner, 1880:5) or the vomerine gutter (Schulte, 1917:400).

The mesorostral canal is present in all cetaceans. It is homologous with the **groove for nasal septum** (*sulcus vomeris* [*sulcus septalis*]), which is formed by the ventral fusion of the lateral sheets of the vomer (Schaller, 1992:30.9). In terrestrial mammals it receives the **cartilaginous nasal septum** anteriorly and the mesethmoid ossification posteriorly (Evans and Christensen, 1979:146).

– mesorostral ossification

The mesorostral ossification occurs only in ziphiids and is a result of the dorsal expansion of the vomer (Fraser, 1942). It is usually found in adult males of the ziphiid genera, *Mesoplodon*, *Ziphius*, and *Berardius* (Heyning, 1984).

* **nasal plates** (Anderson, 1879:508, 521, 522) (Figure 27a–c)

Anderson described the vomer as follows:

> Vomer (pl. XL, fig. 1, vo). – This is directed downwards and forwards, but has a twist to the left side. It may be resolved, into three portions: 1st, the expanded. plates which invest the under surface of the orbito-sphenoid and a portion of the **basisphenoid**; 2nd, the thin nasal plate between them; 3rd, a division consisting of two wings, between which the **mesethmoid cartilage** (me) is received, the latter terminating below and anteriorly in a thin vertical plate wedged between the **vertical plates** of the maxillae, the posterior extremities of which are applied. to a lateral expansion on its posterior border. (Anderson, 1879: 521

Anderson's plate XL is a disarticulated near-term fetus. Figure 1 of that plate is an oblique posteroventral view. We have interpreted the "nasal plate" in his description to mean that part of the lateral lamina that is exposed in the nasal passage.

* **nasal septum** (*septum nasale*) (Figures 1, 2, 27a,b)

The nasal septum serves to divide the right and left nasal cavities (Gray, 1918:194; Evans and Christensen, 1979:158; Schaller, 1992:176.6; Feneis, 1994:136.4). It comprises of the **perpendicular plates** of the ethmoid bone and vomer and the **cartilaginous nasal septum**. Vesalius (1543:23) referred to the nasal septum as the *septum amplitudine narii*. Eustachius and Lancisius (1714:112) referred to the nasal septum as the *septo medio ipsius nasi*.

In delphinids the **mesethmoid** (perpendicular plate of the ethmoid bone) has come to lie internal to the **nasal plate** of the vomer and the latter bone makes up the nasal septum. Schulte (1917:372, 373, 378, 384) referred to it as the internarial septum or the narial septum (Schulte, 1917:385).

* **palatal part of the vomer** (Owen, 1866a:27) (Figure 2)

The vomer is not present on the palatal surface of the skull in terrestrial mammals (Evans and Christensen, 1979:145, 146; Schaller, 1992:30.8) nor in humans (Gray, 1918:170; Feneis, 1994:20.28, 25).

In cetaceans the rostrum has become extended anteriorly and the relationship of the bones has changed slightly. The vomer is exposed on the palatal surface of the skull and that portion of the bone is known as the palatal part of the vomer.

* **prenarial process of the vomer** (Schulte, 1917:385) (Figure 27a–c)

The prenarial process is a midlateral process that occurs on the vomer just anterior to the bony nares (Schulte, 1917:385). The prenarial process was described in *Kogia* where it is very marked on the left. Schulte (1917:378, 384) also referred to the prenarial process as the tuberosity of the vomer or the prenarial tubercle.

Tursiops has a well-developed prenarial process.

* **sagittal part of the vomer** (Figure 27a,c)

The sagittal part of the vomer is composed of two thin plates, the *lamina laterales*, which unite ventrally to form the *sulcus septi nasi*. This sulcus receives the **cartilaginous nasal septum** anteriorly and the **mesethmoid** ossification posteriorly (Evans and Christensen, 1979:146). This term is not in the *Nomina Anatomica Veterinaria*.

In Cetacea the bulk of the vomer is composed of the sagittal part.

* **sphenoidal incisure** (*incisura sphenoidalis*) (Figure 27a,b,e)

The sphenoidal incisure of the vomer is a fork on the posterior end of the **sagittal part of the vomer** (Evans and Christensen, 1979:146). This is contrary to the use of this term (*incisura sphenoidalis*) in the *Nomina Anatomica Veterinaria* (Schaller, 1992:28.17), where it referred to a notch in the anteroventral portion of the frontal that receives the wing of the ethmoid in ruminants and horses.

The sphenoidal incisure is prominent in young delphinids, tending to change into a shallow concavity in older specimens. The sphenoidal incisure is visible on the ventral aspect of the skull.

* **vomerine crest** (*crista vomeris*) (Figures 2, 27b,c)

The vomerine crest is the ventral crest on the caudal part of the vomer (Evans and Christensen, 1979:146; Schaller, 1992:30.10). It is homologous with the **choanal crest of the vomer** that separates the two nasal passages (**choanae**) in humans (Schaller, 1992:30.10; Feneis, 1994:20.30a).

The vomerine crest is readily seen on the ventral aspect of the skull of delphinids. The crest is better developed in adults.

– wedge-shaped part of the vomer (*pars cuneiformis vomeris*)

The wedge-shaped part of the vomer is the most anterior portion in humans that has a wedge-shaped form in lateral view (Feneis, 1994:20.30b). It forms the base of the **cartilaginous nasal septum** (Gray, 1918:194).

In odontocetes the vomer has changed its shape markedly, particularly with respect to the cartilaginous nasal septum. The part of the delphinid vomer that is homologous with the wedge-shaped part of vomer in humans is the entire dorsal aspect of the medial portion of the vomer that forms the floor of the **mesorostral canal**.

* **wings of the vomer** (*ala vomeris*) (Figure 27b–d)

The wings of the vomer, or *ala vomeris*, constitute the **horizontal part of the vomer** (Schulte, 1917:385, 392, 394; Evans and Christensen, 1979:146; Schaller, 1992:30.11). They lie at right angles to the sagittal part, flaring laterally and articulating with the sphenoid, ethmoid, and palatine bones. The wings of the vomer are also known as the **alar process of the vomer** or ala of the vomer (Schulte, 1917:374, 381, 385, 386, 393). Schulte (1917:394) referred to the wings of the vomer as the "*processus alaris*."

In delphinids the wings of the vomer are paired lateral structures, at the posterior end of the vomer. The anterior surface of the wings of the vomer forms part of the posterodorsal wall of the nasal passage. The wings lie against the elements of the ethmoid posteriorly.

MULTI-ELEMENT COMPLEXES: STRUCTURES SHARED BY ADJACENT BONES

TOPOGRAPHIC FEATURES

The Rostrum

The term "rostrum" is derived from the Latin word for beak. The cetacean rostrum is defined generally as that portion of the skull that is anterior to the cranium. In terrestrial mammals, like the dog, the rostrum is formed principally by the nose. In cetaceans, where the skull has been subjected to "telescoping" (q.v.), the nasal passages have come to lie against the cranium and form the posterior boundary of the rostrum.

The odontocete rostrum consists of the maxilla, premaxilla, and vomer (Flower 1885:213).

The nasal bone, which in terrestrial mammals forms an important part of the rostrum, in odontocetes has become part of the anterior wall of the cranium.

The rostrum forms the upper jaw and functions primarily in feeding. The posterior portions of the rostrum, which form part of the facial region, function in the generation and modification of acoustic signals.

Antorbital Region

In strict morphometric terms, the rostrum is limited posteriorly by a line drawn between the apices of the **antorbital notches** (see Appendix B). These notches contain the facial nerve where it emerges from the suborbital region and spreads out over the facial region of the skull.

The dorsal portion of the antorbital region blends into the facial region and consists of elements of the maxilla, premaxilla, frontal, and in some cases, the lacrimal. The dorsal portion bears a number of eminences, tubercles, crests, or ridges that have been given a variety of confusing names. We have grouped the names that pertain to the same structure in Diagram 2.

Facial Region

The face is defined in humans as the "front of the head from the top of the forehead to the bottom of the chin, and from ear to ear" (Webster's New World Dictionary, College Ed., 1960:519). In cetaceans we have attempted to use the equivalent area of the skull and defined the facial region as the area into which the maxilla and premaxilla expand during telescoping. This area includes the entire dorsal surface of the rostrum (maxilla and premaxilla), the **ascending process of the maxilla**, the **nasal process of the premaxilla**, the **external surface of the frontal**, and the nasal bones. The facial region is bounded posteriorly by the **nuchal crest** and laterally by the **orbitotemporal crest**. The facial region includes the external nares.

Hinton and Pycraft (1922:233), in their treatment of the anatomy of *Lipotes*, described "a pair of large floating bones placed on each side of the subcutaneous narial slit, and forming together its posterior lip." No further mention was made of these structures and the dissection material was ultimately lost. There seemed to be some doubt as to the nature of the "floating bones" because Hinton (1936:185) said, "The superficial valves are controlled by a pair of special 'bones,' which if not truly ossified are formed of very dense fibrous tissue." Zhou and Qian (1981:120, 126) also treated *Lipotes* and found that the "floating bones" were the tendon of insertion of the *m. maxillonasolabialis pars externa*. That muscle had hypertrophied into what Zhou and Qian termed the "maxillonasalis tendinous plate", and it was not bone.

The Palate and Pterygopalatine Fossa

The palatal area of the skull is expanded with the increase in relative size of the rostrum. The palate is primarily a surface feature that consists of the bones of the skull that form the mouth cavity. The palate ends at the posterior margin of the pterygoids where the pharynx begins. The palate consists of maxilla, premaxilla, vomer (in cases where the vomer has a palatal exposure), palatine, and pterygoid. The **soft palate** is the shelf of soft tissue that stretches between the pterygoid hamuli, in cases where the pterygoid hamuli are separated (e.g., the phocoenids). *Tursiops* does not have a soft palate.

The pterygopalatine fossa (supermaxillary fossae of Schulte, 1917:373; **infratemporal fossa** of Davis, 1964:48) is a complex issue in mammalian anatomy and is rendered more complex in odontocetes by the incursion of the anterior lobe of the **pterygoid sinus**.

The pterygopalatine fossa is bounded posteriorly by the **orbital part of the frontal**, from which it is separated by the **ventral orbital crest**. From the pterygopalatine fossa the **pterygopalatine canal** leads anteriorly via the pterygopalatine sulcus to the **greater palatine sulcus**.

The **palatine canal** in *Tursiops* lies along the palatomaxillary suture. It runs from the **sphenopalatine foramen** in the pterygopalatine fossa anteriorly to exit via the **major palatine foramen** and **minor palatine foramen**.

The sphenopalatine ganglion (pterygopalatine ganglion) in humans is the largest of the four parasympathetic ganglia associated with the cranial nerves (Dox et al., 1979:177). The sphenopalatine ganglion sends postganglionic parasympathetic fibers to the lacrimal glands, the nasal and oral cavities, and the upper part of the pharynx.

The sphenopalatine foramen lies just anterior to the middle of the **ethmoidal crest of the palatine** on the medial (vomerine) surface of the palatine bone.

The concept of the pterygopalatine fossa seems to be the space bounded by the **orbit**, the palatine, and the area posterior to the **ventral infraorbital foramen** of the maxilla, into which space open the sphenopalatine foramen, the ventral infraorbital foramen, and the **posterior palatine foramen**. In *Tursiops* the pterygopalatine fossa is bounded by the low rounded ventral orbital crest dorsolaterally, the **lateral lamina of the palatine** bone medially, and the ventral infraorbital foramen anteriorly.

The pterygopalatine fossa contains the pterygopalatine ganglion (sphenopalatine ganglion), maxillary nerve, infraorbital nerve, maxillary artery and maxillary vein, and the origins of the *m. pterygoideus*.

The Cranium

The cranium is defined as the bones forming the enclosure of the brain. Vesalius (1543:25) referred to the cranium as the *caput*. The cranium consists of the **occipital shield** (exoccipital, supraoccipital) posteriorly; the interparietal dorsally; the parietal and the squamosal laterally; the frontal and the ethmoid anteriorly; the basioccipital, tympanoperiotic, and sphenoid ventrally.

Internally the cranium consists of two major cavities or fossae, the **cerebral fossa**, which houses the cerebral hemispheres, and the **cerebellar fossa**, which lodges the cerebellum.

Vertex

The vertex has assumed a new role in the cetacean skull as a result of the posterior movement of the external nares. The vertex in terrestrial mammals was a craniometric point, defined as the most dorsal point on the skull, and did not have a definite function. In cetaceans, and particularly in some odontocetes such as the ziphiids, it serves as a nexus for many groups of muscles. The vertex serves as a foundation on which the muscles that control the movements of the nasal passage and associated diverticula rely.

The vertex is primarily centered on the nasal bones. In groups in which the vertex is more highly developed, such as the ziphiids, the vertex consists of the nasals and surrounding portions of the maxillae, premaxillae, and frontals. The vertex is surrounded by a dense matrix of connective tissue, so the bony elements are fused together and function as one.

Occipital Area

The occipital area has become more a part of the locomotor system of cetaceans and is the anterior insertion of the series of extremely well-developed epaxial muscles. The occipital area consists of the interparietal, supraoccipital, and exoccipital ossifications. The basioccipital forms part of the ventral surface of the skull and has not been considered part of the occipital area. The dorsal elements of the occipital area (interparietal, **supraoccipital**) have been termed the **occipital shield** or the **occiput**.

Zygomatic Arch and Temporal Fossa

The **temporal fossa** has been modified in its relationship to the zygomatic arch and the **orbit**. The primitive mammalian zygomatic arch consisted of the jugal (= malar, zygomatic), which spanned the ventral border of the temporal fossa. In the dog the zygomatic arch extends from the **zygomatic process of the squamosal** to the **zygomatic process of the frontal** bone and the maxilla. This bony bridge (the jugal) closes the temporal fossa ventrolaterally.

In the delphinids the ventrolateral border of the temporal fossa consists of the zygomatic process of the squamosal posteriorly and the **postorbital process of the frontal bone** anteriorly. The jugal has moved ventrally and runs from the zygomatic process of the squamosal to articulate with the lacrimal and the maxilla ventral to the **preorbital process of the frontal**. The jugal in odontocetes has been reduced to a slender rod that forms the ventral border of the orbit.

Orbit and Orbital Fissure

The **orbit** in generalized mammals is partially closed by the frontal, maxilla, and jugal. It is open posteriorly where it borders on the **temporal fossa**.

The orbit in cetaceans is open on the ventral portion. In delphinids the orbit is formed primarily by the frontal, with minor contributions by the jugal and lacrimal. The maxilla does not take part in formation of the orbit in odontocetes.

The **orbital fissure** in most mammals lies in the sphenoid in the sutures between the **orbitosphenoid** and the **alisphenoid**. The orbital fissure is located slightly posterolateral to the **optic canal** and transmits the ophthalmic nerve, oculomotor nerve, trochlear nerve, and anastomotic artery.

The term "orbital fissure" is applicable only in young delphinids. In adults the orbital fissure is divided into the **inferior orbital fissure**, which transmits the zygomatic nerve, infraorbital nerve, and infraorbital vessels, and the **superior orbital fissure**, which transmits the ophthalmic, oculomotor, trochlear, and abducens nerves, as well as the superior ophthalmic vein.

In mammals, including delphinids, the optic canal transmits only the optic nerve and opens laterally by the **optic foramen**.

Basicranium

The most striking modifications have occurred in the ventral portion of the cranial vault, known as the basicranium. Vesalius (1543:25) referred to the basicranium as the *calvariae basim*. The basicranium is an inordinately complex area in vertebrates in general, but is extremely so in cetaceans.

The concept of the mammalian temporal bone has become modified in Cetacea (see introductory discussion under "Periotic Bone," **mastoid process of the petrosal**, and introductory discussion under "Tympanic Bulla" in the preceding section of the Lexicon). This has resulted in our treating the temporal bone under "Tympanoperiotic Complex" (Periotic Bone and Tympanic Bulla) and "Squamosal Bone."

Tympanoperiotic

Cetaceans have modified that portion of the temporal bone that deals with the ear into a single element, the tympanoperiotic. The tympanoperiotic is further broken down into the middle ear, which contains the **tympanic cavity** and auditory ossicles and is known as the **tympanic bulla**, and the inner ear, which contains the **cochlea** and **semicircular canals** and is known as the **periotic bone**. The periotic is homologous with the petrous temporal or **petrosal** of other mammals.

The tympanic **bulla** and periotic bone are joined by a complex interdigitation of their posterior processes. In odontocetes this joint is never fused. The tympanic bulla and periotic are also joined variably by their **anterior processes**. This joint is highly variable and details of its confused terminology are discussed under anterior process of both tympanic bulla and periotic in the preceding section of the Lexicon.

The functional reasons for this separation no doubt involve the increasingly complex sense of hearing, a topic that is still under theoretical discussion. In delphinids the only attachment remaining between the tympanic bulla and periotic bone is the delicate bony process that bridges the gap between the posterior process and the **posttympanic process** of the squamosal.

Cranial Hiatus

Another result of modifications associated with hearing in cetaceans is the isolation of the tympanoperiotic from the other bones of the basicranium, resulting in an opening or cranial hiatus. The cranial hiatus is more complete in odontocetes than mysticetes and has resulted in skulls that frequently lose the tympanoperiotic elements on decomposition.

In delphinids the cranial hiatus is the confluence of the **posterior lacerate foramen** (**jugular foramen**) and the **internal acoustic meatus**.

Pterygoid Sinus Complex

One of the most striking modifications of the basicranium of cetaceans is the development of an anterior extension of the **Eustachian tube** (**auditory tube**). That extension has developed into a series of air sinuses known as the **pterygoid sinus** complex. In some delphinids the sinus system extends from the **pterygoid hamulus** (hamular lobe of pterygoid sinus), the posterior portion of the maxilla (anterior lobe of pterygoid sinus), through the orbital area (postorbital and preorbital lobes of pterygoid sinus), posterior to the nasal passage (**basisphenoidal sinus** in phocoenids), in the **tympanosquamosal recess** of the squamosal (**middle sinus**), around the tympanoperiotic (**peribullary sinus**), and into the **paroccipital process** (**posterior sinus**).

Venous Sinus System

Correlated with the development of the **pterygoid sinus** system is a complex system of venous sinuses. They have been described by Fraser and Purves (1960) as a system of fibro-venous plexuses associated with the entire air sinus system.

Mandible and Mandibular Foramen

The most striking change in the mandible is the development of a large **mandibular foramen** and **mandibular canal** in odontocetes. The lumen of this extends virtually the whole height of the mandible. The mandibular canal in mammals transmits the mandibular nerve and mandibular vessels, but in odontocetes the fatty material that is present in most foramina hypertrophies into the intra-mandibular fat body and occupies better than 95% of the lumen. The chemical composition of this fat body and the anatomical position have led researchers to hypothesize that it functions as a pathway for sound reception.

TRANSMISSION OF VESSELS, NERVES, AND PASSAGES

Infraorbital Complex

The nomenclature of the elements of the infraorbital complex have become extremely complicated, more as a function of historical lack of consensus than anything else (see earlier discussion under **infraorbital canal** of "Maxilla").

The infraorbital complex consists primarily of the infraorbital nerves and vessels that supply the rostrum and facial areas. The nerves are infraorbital branches from the maxillary nerve and the vessels are infraorbital branches of the maxillary artery and vein.

Nasal Passages

Nares

Nares (*naris*) is a term used historically for both soft tissues and bones. In Cetacea it has been used for the external opening of the respiratory apparatus (blowhole), for the distal or external or facial bony openings associated with the nasals and premaxillae, and (generally with a qualifier) for the proximal or internal bony opening or openings associated with the palatines, pterygoids, vomer, and **basisphenoid** at the nasopharynx.

Table 9 shows the variation in terminology for the narial openings used in publications on Cetacea and some other mammals.

For *Tursiops* we use "**external bony nares**" for the distal or external or facial bony openings associated with the nasals and premaxillae, and "internal bony nares" or "**choanae**" for the proximal or internal bony opening or openings associated with the palatines, pterygoids, vomer, and basisphenoid at the nasopharynx.

One of the most obvious modifications in the delphinids is the movement of the external bony nares dorsally and posteriorly. This occurred while the rostrum was growing in relative length, resulting in heads with the external bony nares opening on top.

The rostral elements (premaxilla, maxilla, vomer) still bear the same relative relationship to the nasal passage, even though the relationship has shifted from a lateral to a vertical one (see Figure 31a). The anterior narial wall is formed by the premaxillae, vomer, palatine, and pterygoid. The posterior palatal elements (palatine, pterygoid) still form the bulk of the lateral walls of the nasal passage. The medial narial wall is the **nasal septum**, the bony element of which is the vomer. The posterior narial wall is formed by the nasals, **mesethmoid**, and vomer.

The nasal septum is formed principally by the vomer instead of the ethmoid. The ethmoid (**mesethmoid**) forms the dorsal margin of the nasal septum in very young animals but as the animal ages the vomer displaces the mesethmoid. In adults the mesethmoid is restricted to the posterodorsal wall of the nasal passage lying between the vomer ventrally and the nasals dorsally.

The internal bony nares (choanae) are formed by the pterygoids anterolaterally and the vomer posteriorly. Fraser and Purves (1960:20) used the term "posterior narial aperture" in speaking of the internal bony nares. The pterygoids have expanded to displace the palatines in forming the anterior border of the internal nares. Most of this pterygoid hypertrophy can be correlated with the development of the **pterygoid sinuses**. Fraser and Purves (1960:12) used the term "**false choanae**" in a discussion of Boenninghaus' (1904) treatment of the naso-pharyngeal muscle mass that rises into the nose through the "false choanae," which appear to be the internal bony nares. Anderson (1879:451) referred to the internal bony nares as the "internal nasal aperture." Vesalius (1543:53; Vesalius et al., 1998:131) referred to the internal nares [posterior nares] as the "*ampla narium foramina septo quodam insigni x notato interstinct, and in fauciam amplitudinem e naribus tedentia*."

The terms "spiracle" and "spiracular" have had ambiguous use in cetacean anatomy. Spiracle is an uncommon but occasionally used term for the cetacean blowhole. The **spiracular plate** of the premaxilla (**premaxillary sac fossa** of our use) is a bony structure associated with the bony external nares, with the implication that nares equate to spiracles. The term "**spiracular surface of the vertex**" as used in ziphiids (Heyning, 1989a) refers to the **nasal process of the premaxilla** or the posterodorsal portion of the premaxilla near the vertex of the skull. Spiracle is also applied to the first gill opening in fish (Romer, 1962). Accord-

TABLE 9. Terminology for narial openings used by selected authors. Page numbers refer to the citation given in the first column; a dash (–) indicates opening not mentioned in the citation.

	Narial terminology		
Author, date	**External opening**	**Bony opening at premaxillae and nasals**	**Bony opening at palatines and pterygoids**
Bianucci, 2001	—	External nares	Internal nares
Evans and Christensen, 1979	Nostril or nares, p. 507	External nasal opening or piriform aperture, p. 150; bony nasal aperture, p. 508	*Choanae*, p. 514; succeeded posteriorly by basipharyngeal canal or choanal region, pp. 153–154
Flower, 1868, *Physeter*	—	Blowhole, p. 317	—
Flower, 1872	—	Superior narial aperture, p. 217	—
Flower, 1885	—	Anterior nares, p. 124	Posterior nares, p. 124
Fordyce, 1994	—	Bony nares	*Choanae* (posterior nares)
Fordyce, 2002	—	External nares	Internal nares (*choanae*)
Fraser and Purves, 1960	Blowhole	Nares, p. 107	Bony nares, pp. 11, 20; bony nasopharynx, p. 12; *choanae*, p. 37; posterior nares, p. 68
Geisler and Sanders, 2003	Blowhole	External bony nares, p. 36	Internal bony nares
Ichishima and Kimura, 2001	—	Bony nares	—
Lambert, 2005	Blowhole	Bony nares	*Choanae*
Luo et al., 2002	—	—	Internal choanae, char 241.
Morgane et al., 1980	Blowhole	Bony nares, p. 15	—
de Muizon and Domning, 2002	—	Bony nares	*Choanae*
Schulte, 1917	Blowhole	Nares, p. 371; nostril, p. 371ff.	—
True, 1910	—	Blowhole, p. 13; superior orifices of nares, p. 26; anterior nares, p. 50	—
Wible and Gaudin, 2004	—	External nasal aperture, p. 119	*Choanae* or internal nasal aperture

ingly, we consider the terms “spiracle” and “spiracular” to be too ambiguous to apply to *Tursiops*.

Nasal Cavity

The nasal cavity (*cavum nasi*) in mammals (Gray, 1918:994; Evan and Christensen, 1979:158; Schaller, 1992:14.1, 176.1; Feneis, 1994:32.1, 134.18) consists of the facial part of the respiratory tract. The nasal cavity is the space between the external nares and the **choanae** and is lined by the premaxillae, maxillae, frontals, nasals, vomer, ethmoid, palatine, and pterygoids. Vesalius (1543:25) referred to the nasal cavity as the *narium*.

The nasal cavity in odontocetes has moved posterodorsally in the skull in response to demands of an aquatic existence. In delphinids the **external bony nares** are formed of the premaxillae, maxillae, frontals, and nasals. The nasal passage is lined by the **mesethmoid**, palatines, vomer, and the pterygoids. The choanae consist of the posterior borders of the pterygoids and the vomer.

Basipharyngeal Canal

The basipharyngeal canal or choanal region in the dog (Evans and Christensen, 1979:153, 154) is the osseous part of the nasal pharynx that extends from the **choanae** to the caudal borders of the pterygoids, with contributions from pterygoid, palatine, vomer, **basisphenoid**, and **presphenoid**. Wible et al. (2005) stated that the basipharyngeal canal is the nasopharyngeal passage behind the choanae.

Tursiops has a basipharyngeal canal that is bounded dorsally and laterally by the pterygoids and vomer; the lateral borders of the basipharyngeal canal are the **pharyngeal crests** behind which lie the **basioccipital crests**. See also **entopterygoid crest**.

Paranasal Sinuses

Cetaceans have lost the paranasal sinus system (frontal, maxillary, and sphenoid sinuses). This may have been the result of the posterior movement of the nasal passages or the development of the **pterygoid sinus** system.

Arterial Circulation and Basicranial Foramina

In many mammals the internal carotid artery supplies the brain via the promontorial and stapedial arteries (McDowell, 1958:122; Novacek, 1986; Wesley-Hunt and Flynn, 2005). Both the latter arteries traverse the middle ear and may leave distinct sulci on the **periotic bone** (**petrosal**), the **tympanic bulla**, and nearby bones (McDowell, 1958; Novacek, 1986). In contrast to many eutherian mammals, the internal carotid circulation in Odontoceti and Mysticeti is greatly reduced (Boenninghaus, 1904; Walmsley, 1938:141), and the main supply to the brain is via spinal meningeal arteries (e.g., Viamonte et al., 1968:1233; Vogl and Fisher, 1981a). The internal carotid artery has been shown (Vogl and Fisher, 1981b) to be nonpatent in *Monodon*, while angiograms for *Tursiops* show that the internal carotid artery forms a truncated and atrophied system that extends to the base of the skull but does not supply the brain directly (Viamonte et al., 1968:1231). The internal carotid artery has not been shown, by corrosion casting or angiograms, to be patent in other living species. Nevertheless, the **carotid foramen of the sphenoid** is consistently patent in Neoceti, even in species (e.g., of *Kogia*) in which the skull base is modified to become extremely disparate from other eutherian mammals. Further, the internal carotid artery can sometimes be traced through the carotid foramen and into the braincase in Cetacea (J. G. Mead, pers. obs.), although it is not known if the internal carotid artery in such cases is patent.

Also of note, the **stapedial foramen** is reduced and often nonpatent in Odontoceti (Doran, 1878) and, in contrast to some other mammals (McDowell, 1958), is unlikely to transmit a stapedial artery. In Mysticeti the stapedial foramen is commonly patent but small (Doran, 1878). Stapedial circulation is relevant to endocranial supply, because, according to McDowell (1958:126), the mammalian stapedial artery may have a branch, the middle meningeal artery, that enters the braincase via the ***foramen spinosum***. If the middle meningeal artery is a branch of the stapedial artery, it seems, given a reduced or absent stapedial artery in Cetacea, that the so-called *foramen spinosum* may be misidentified. However, Fraser and Purves (1960:26) noted that "in terrestrial mammals the middle meningeal artery is a conspicuous branch of the first portion of the internal maxillary, and anastomoses with the internal carotid. In at least one of the injected specimens evidence of an intra-cranial blood supply from this source has been established; and it cannot be assumed that this artery has atrophied, notwithstanding the apparent atrophy of the internal carotid."

Figures

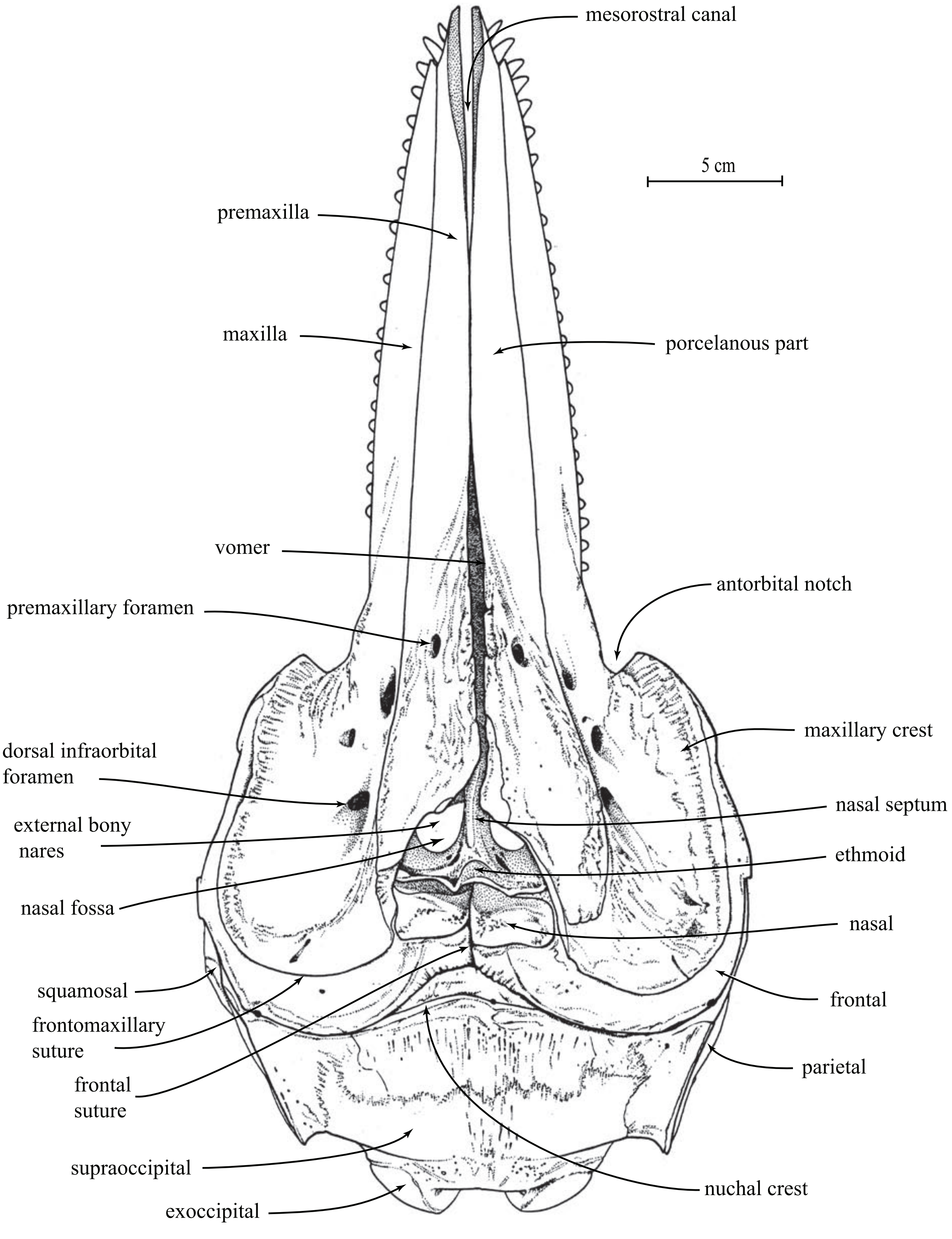


FIGURE 1. Intact skull of adult specimen, dorsal view (USNM 550403).

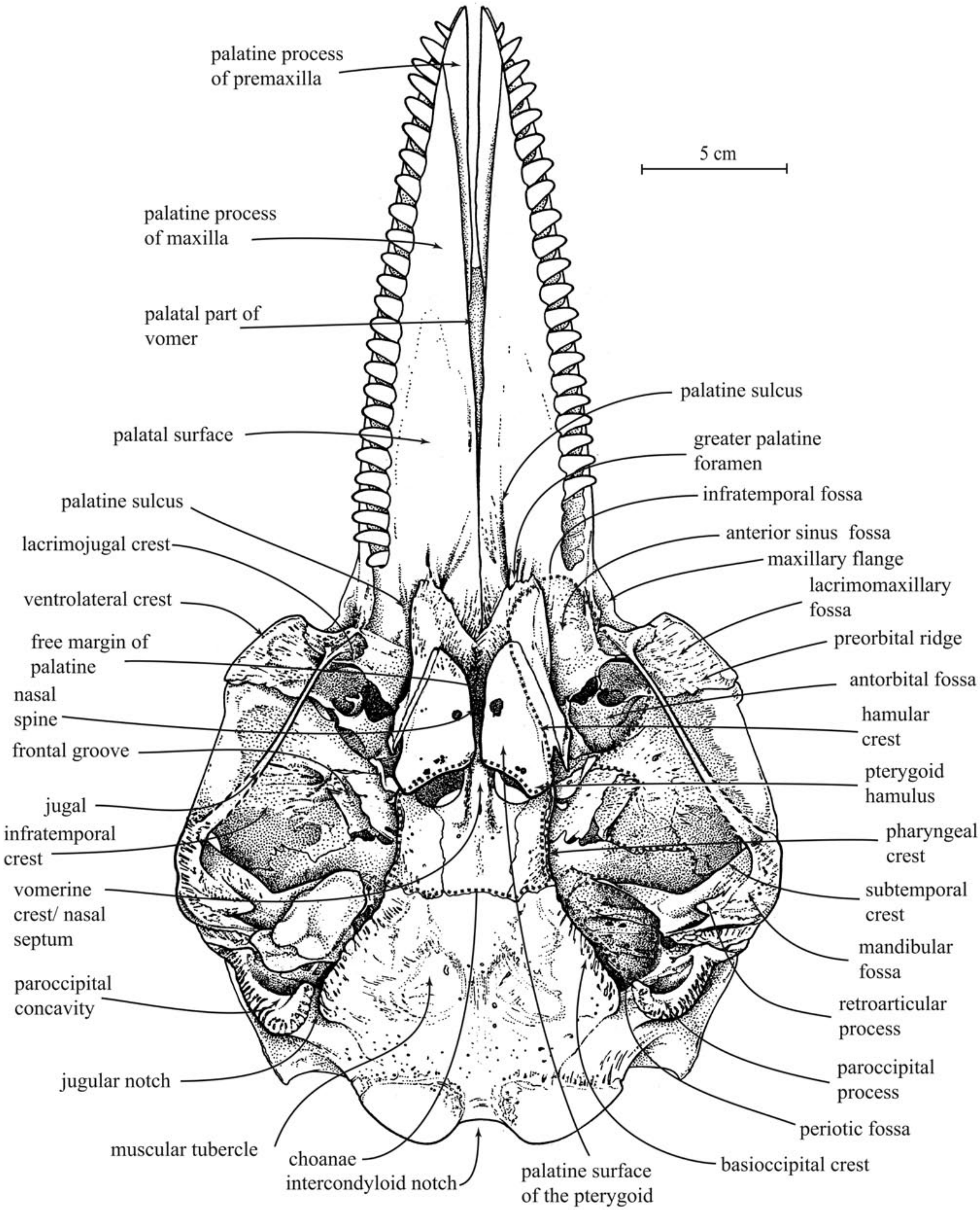


FIGURE 2. Intact skull of adult specimen, ventral view (USNM 550403).

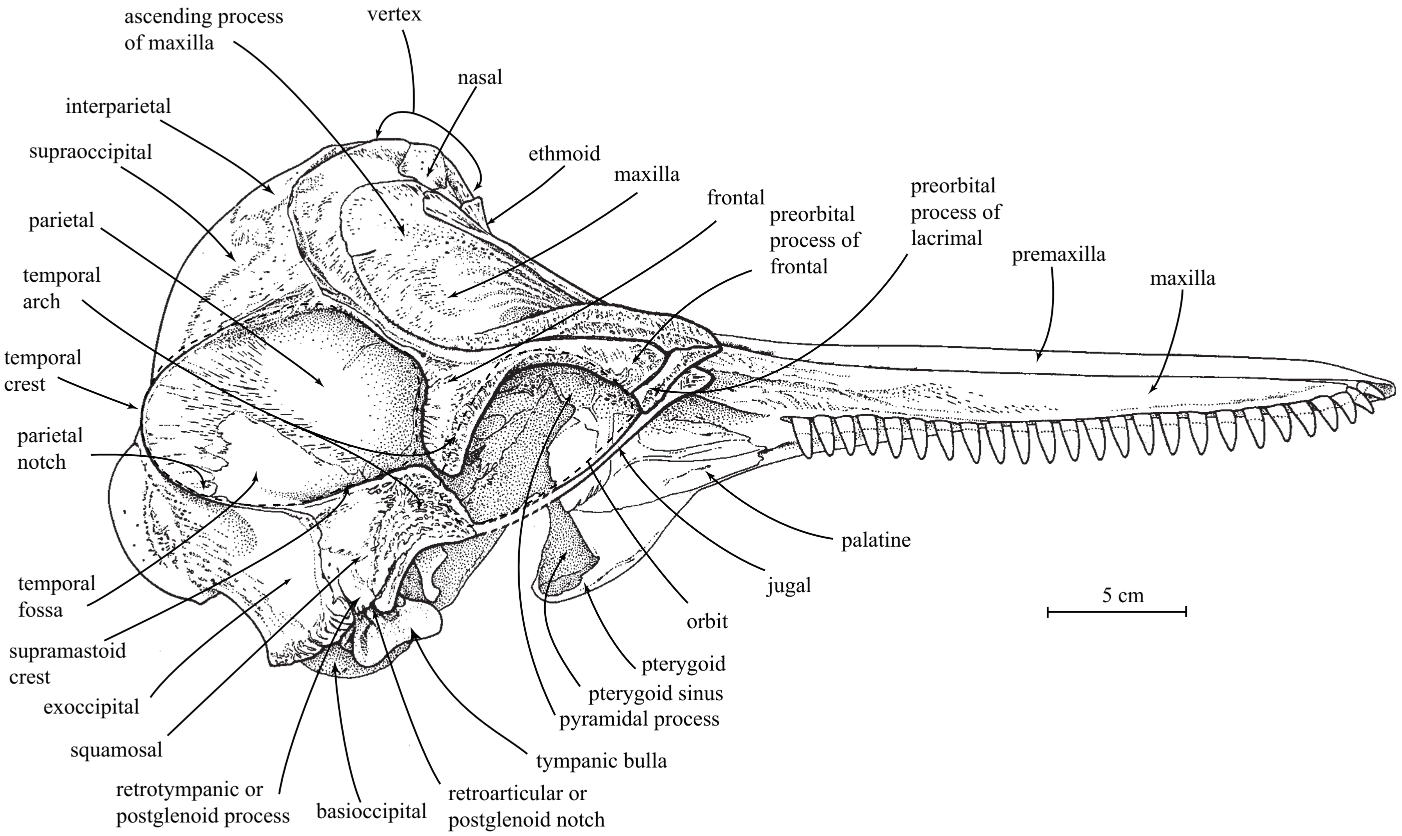


FIGURE 3. Intact skull of adult specimen, lateral view (USNM 550403).

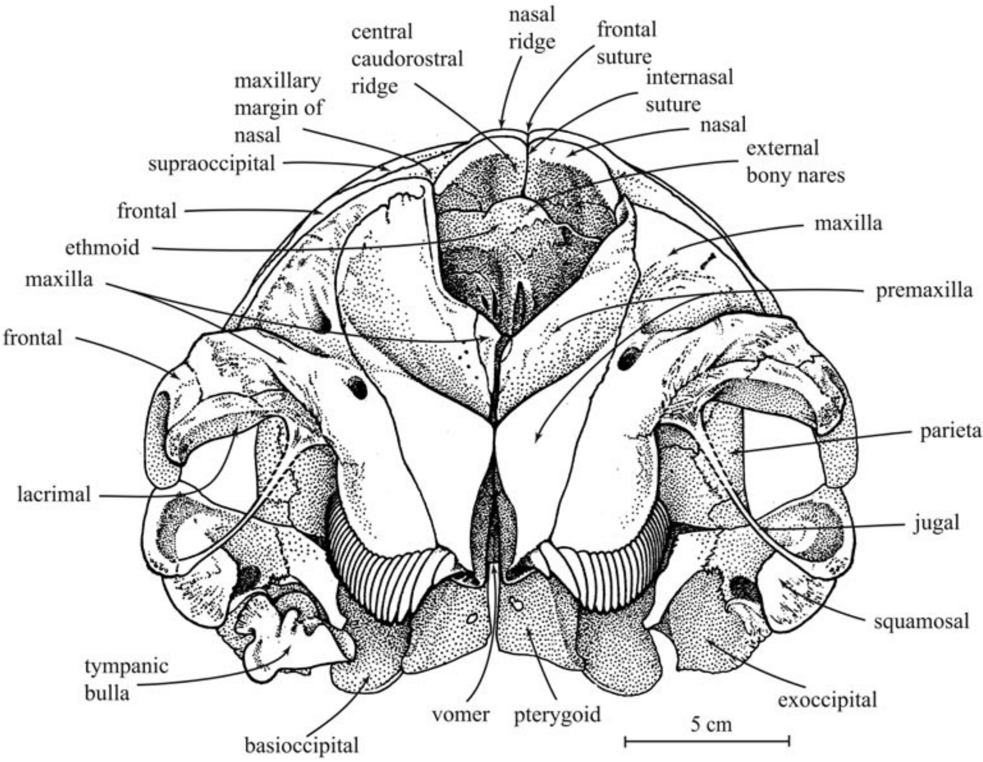


FIGURE 4. Intact skull of adult specimen, anterior view (USNM 550403).

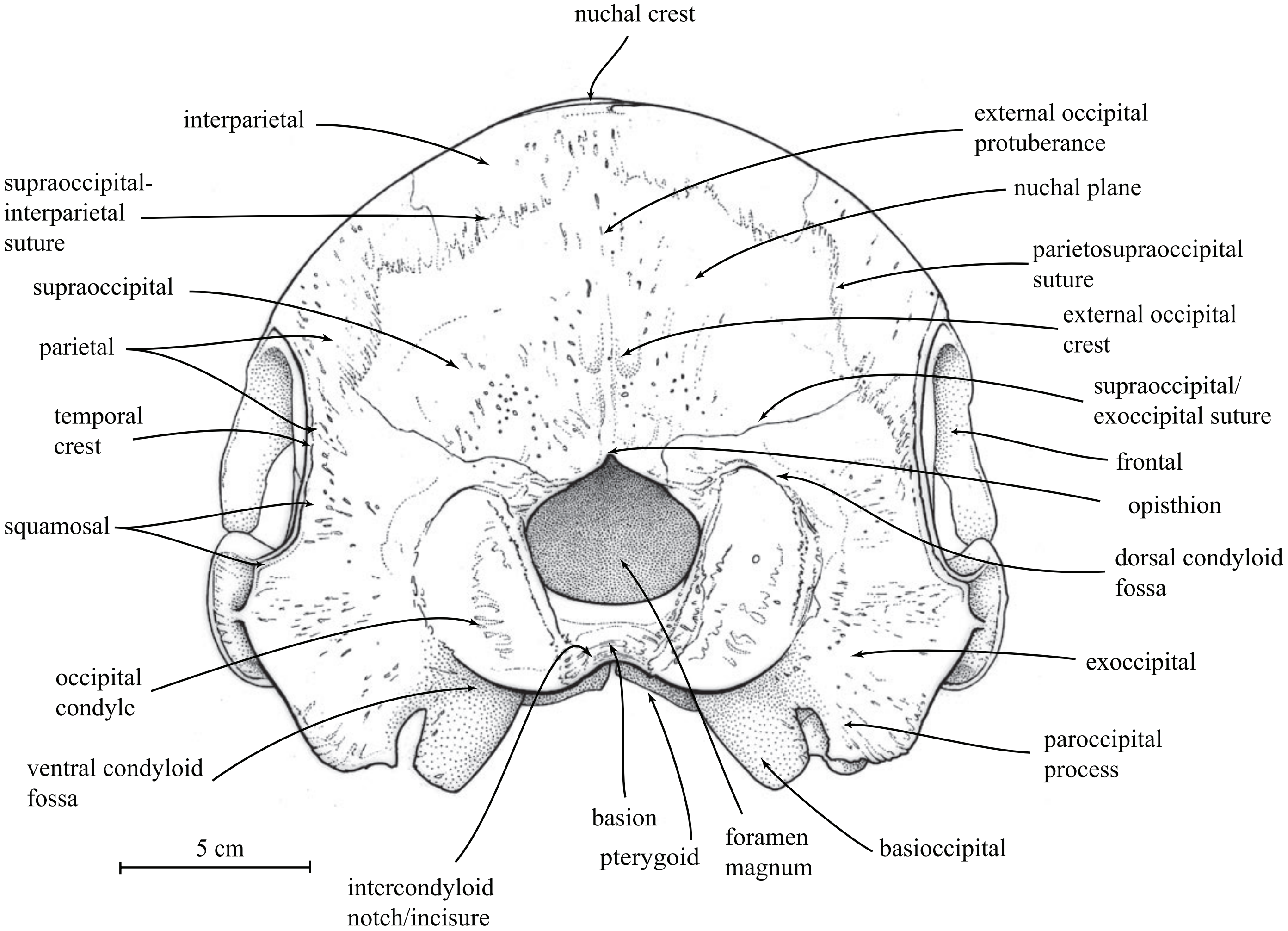


FIGURE 5. Intact skull of adult specimen, posterior view (USNM 550403).

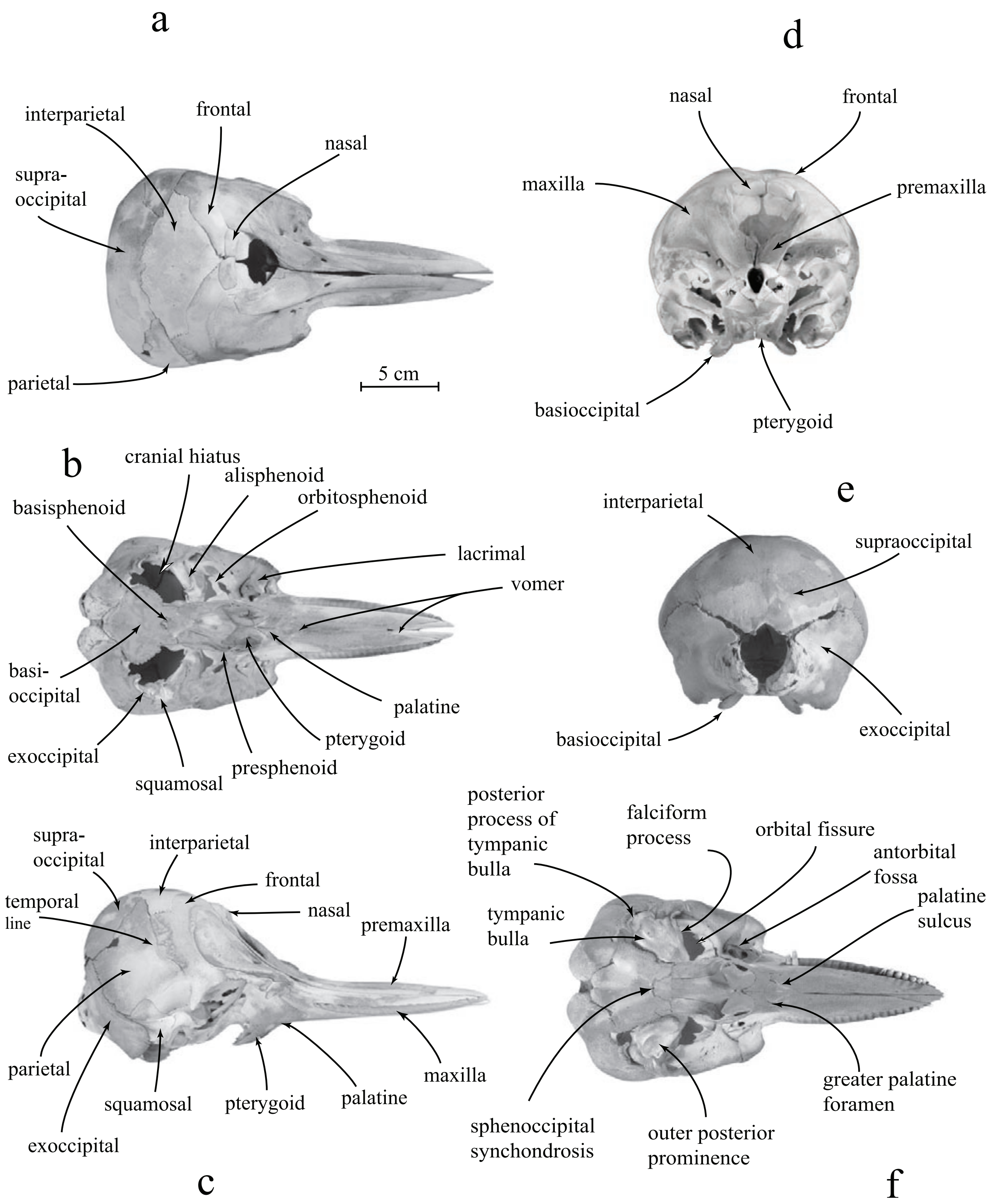


FIGURE 6a–f. Intact neonatal skull (USNM 550835). (a) dorsal view, (b) ventral view, (c) right lateral view, (d) anterior view, (e) posterior view, (f) ventral view with tympanoperiotics in place (USNM 500851).

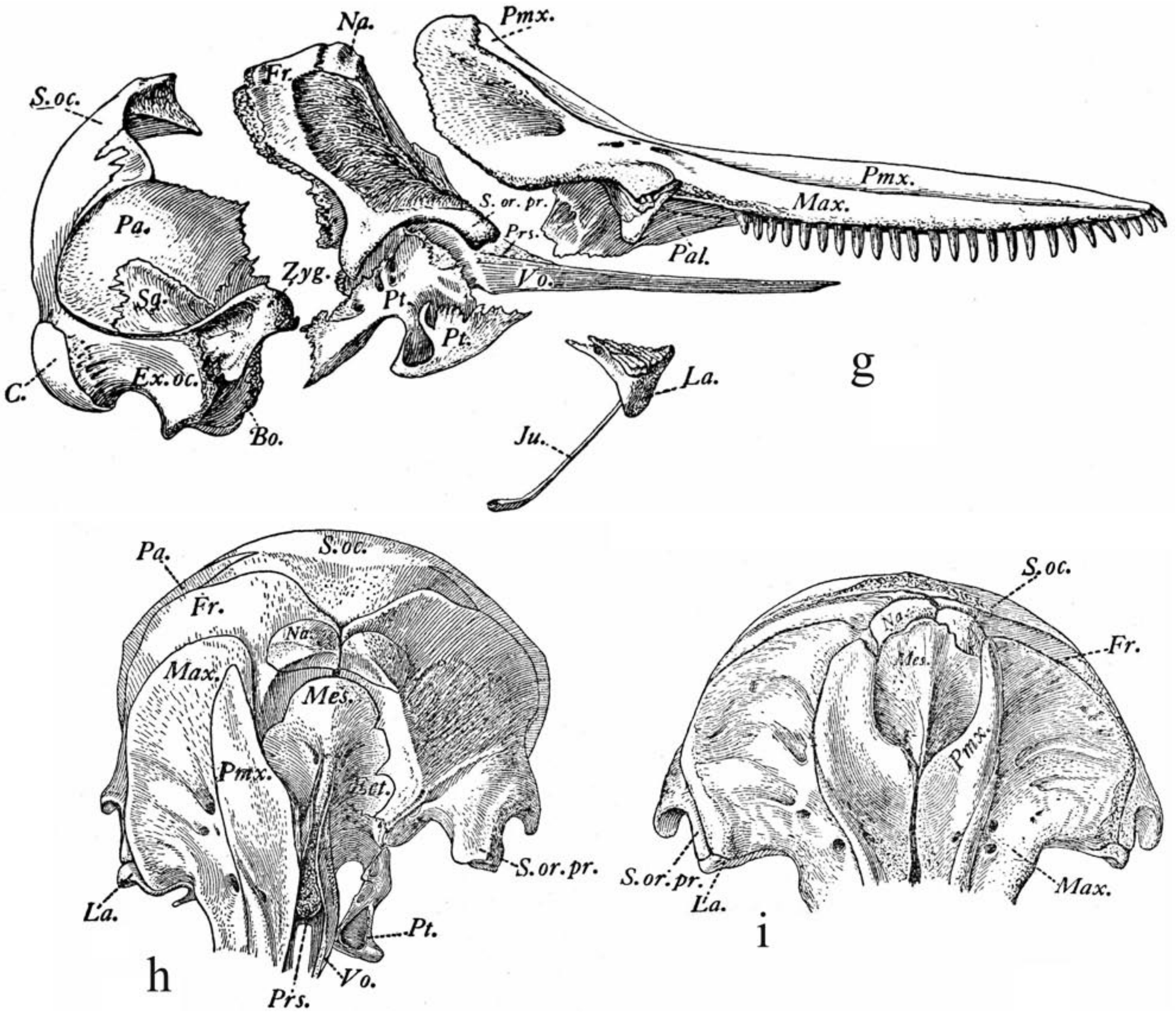


FIGURE 6g–i. Disarticulated neonatal skull (g), right lateral view; anterodorsal views showing some ontogenetic changes in (h) young and (i) adult skulls (from Kellogg, 1928, figs. 3, 22; specimen numbers not indicated).

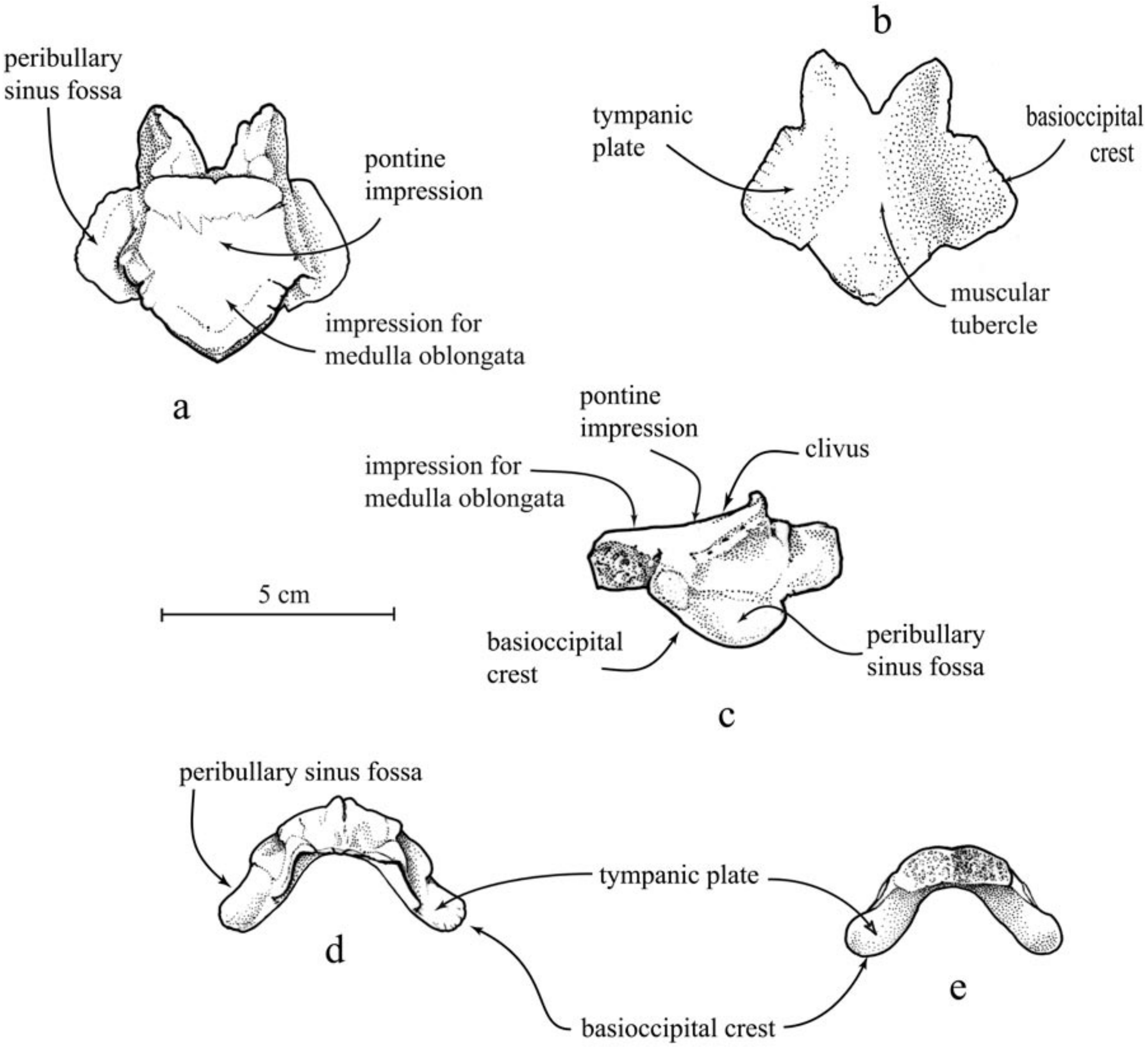


FIGURE 7. Disarticulated neonatal skull, basioccipital (USNM 504560).

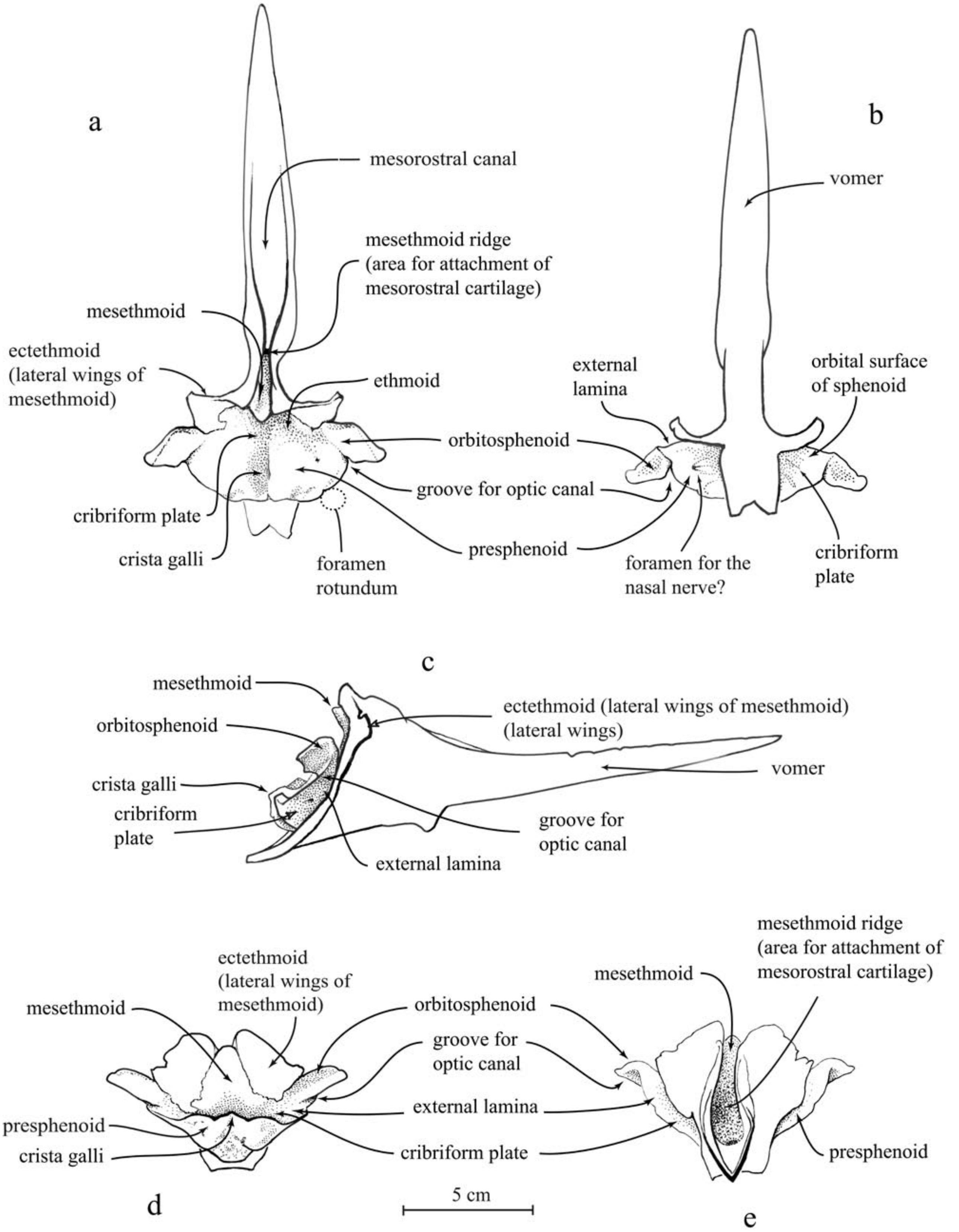


FIGURE 8. Disarticulated neonatal skull, ethmoid (USNM 504560).

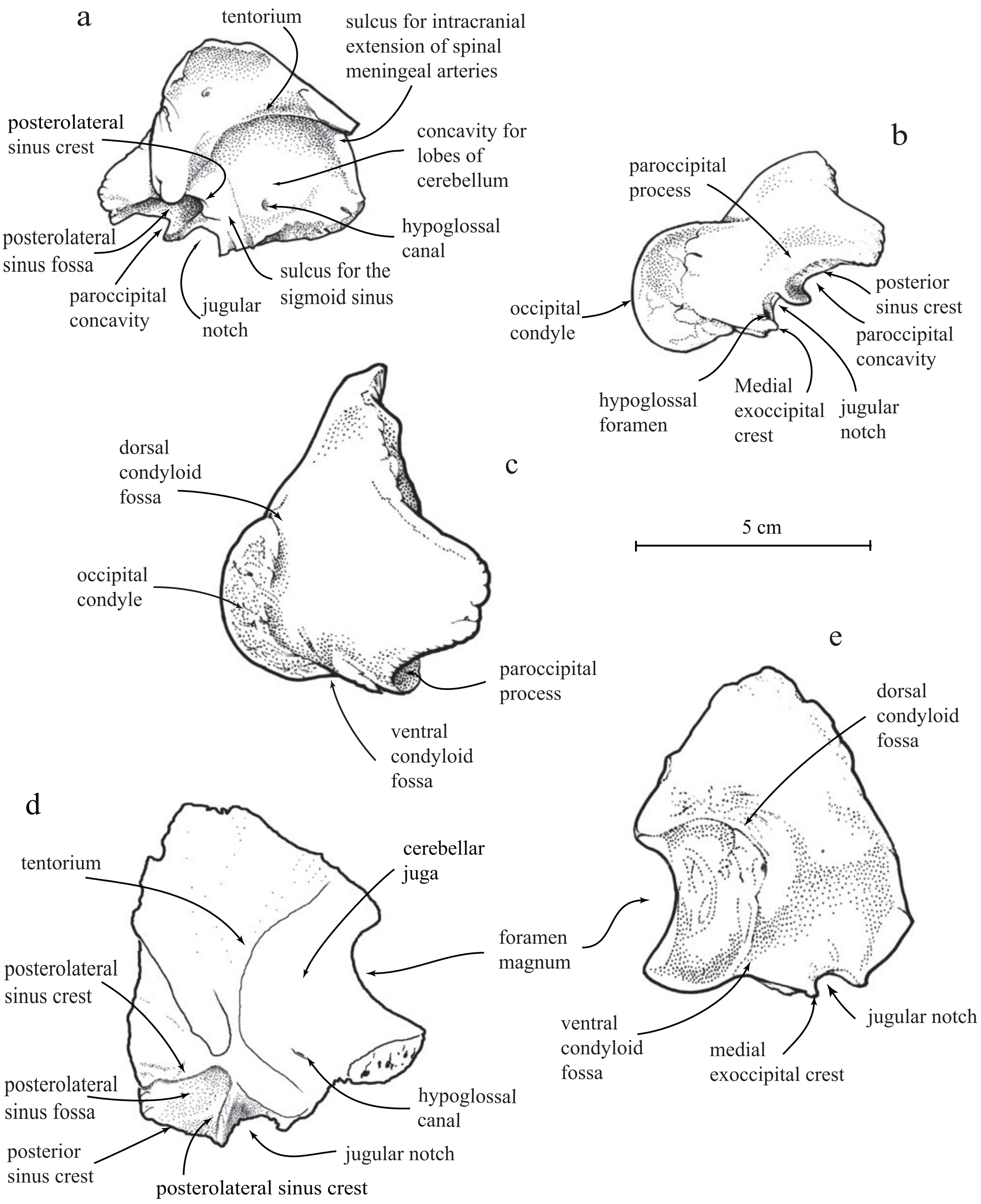


FIGURE 9. Disarticulated neonatal skull, exoccipital (USNM 504560).

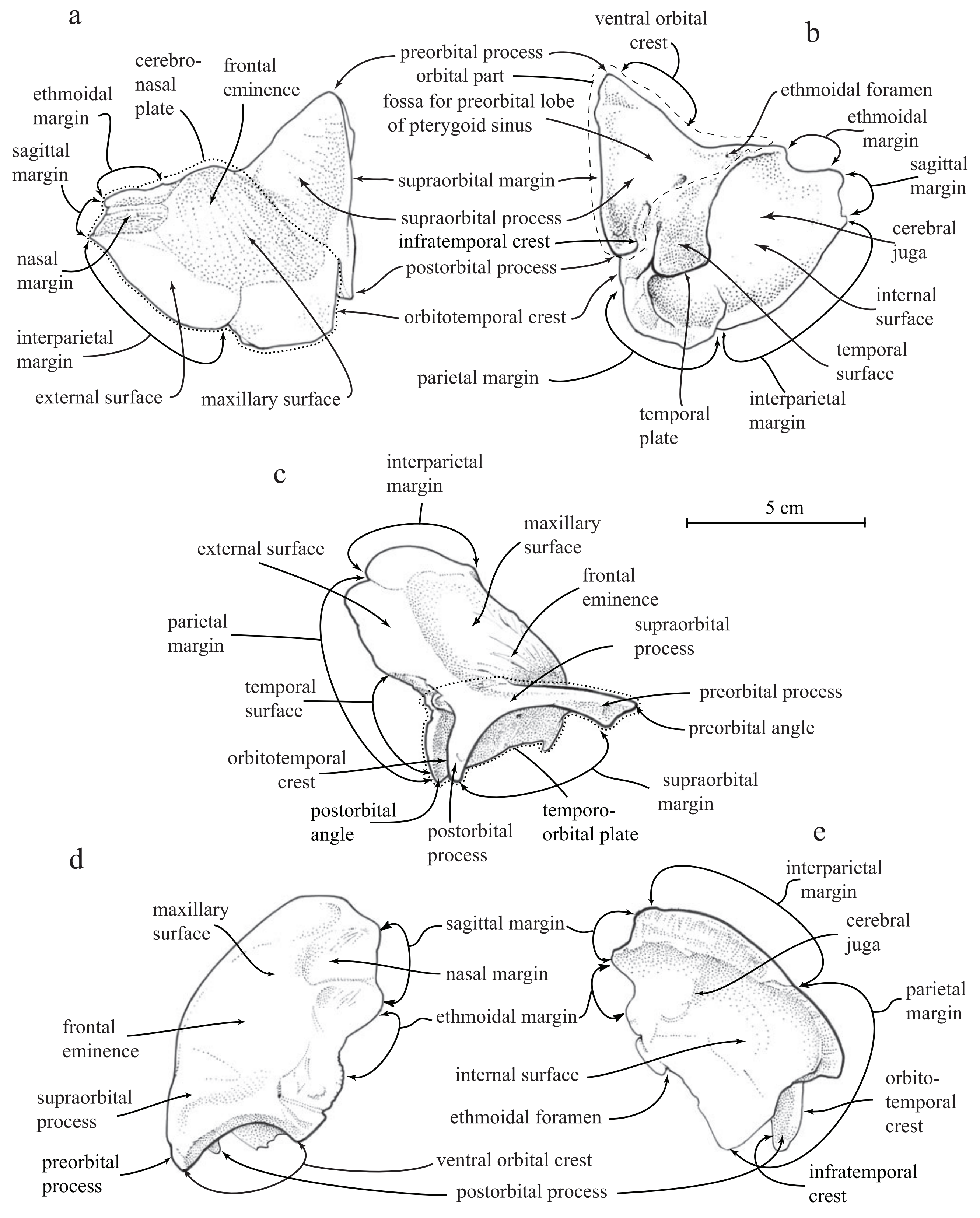


FIGURE 10. Disarticulated neonatal skull, frontal (USNM 504560).

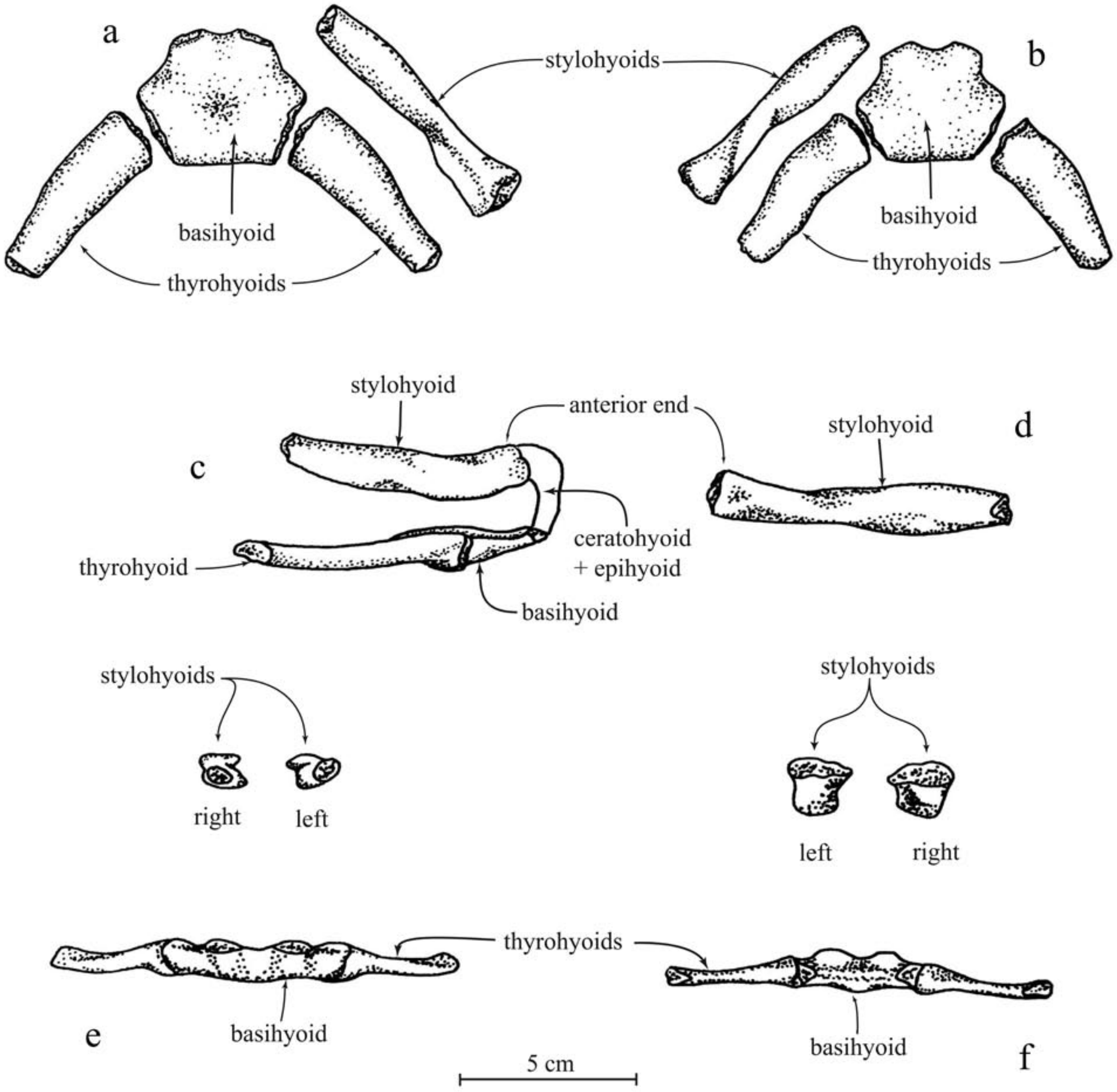


FIGURE 11. Disarticulated neonatal skull, hyoid (USNM 504560).

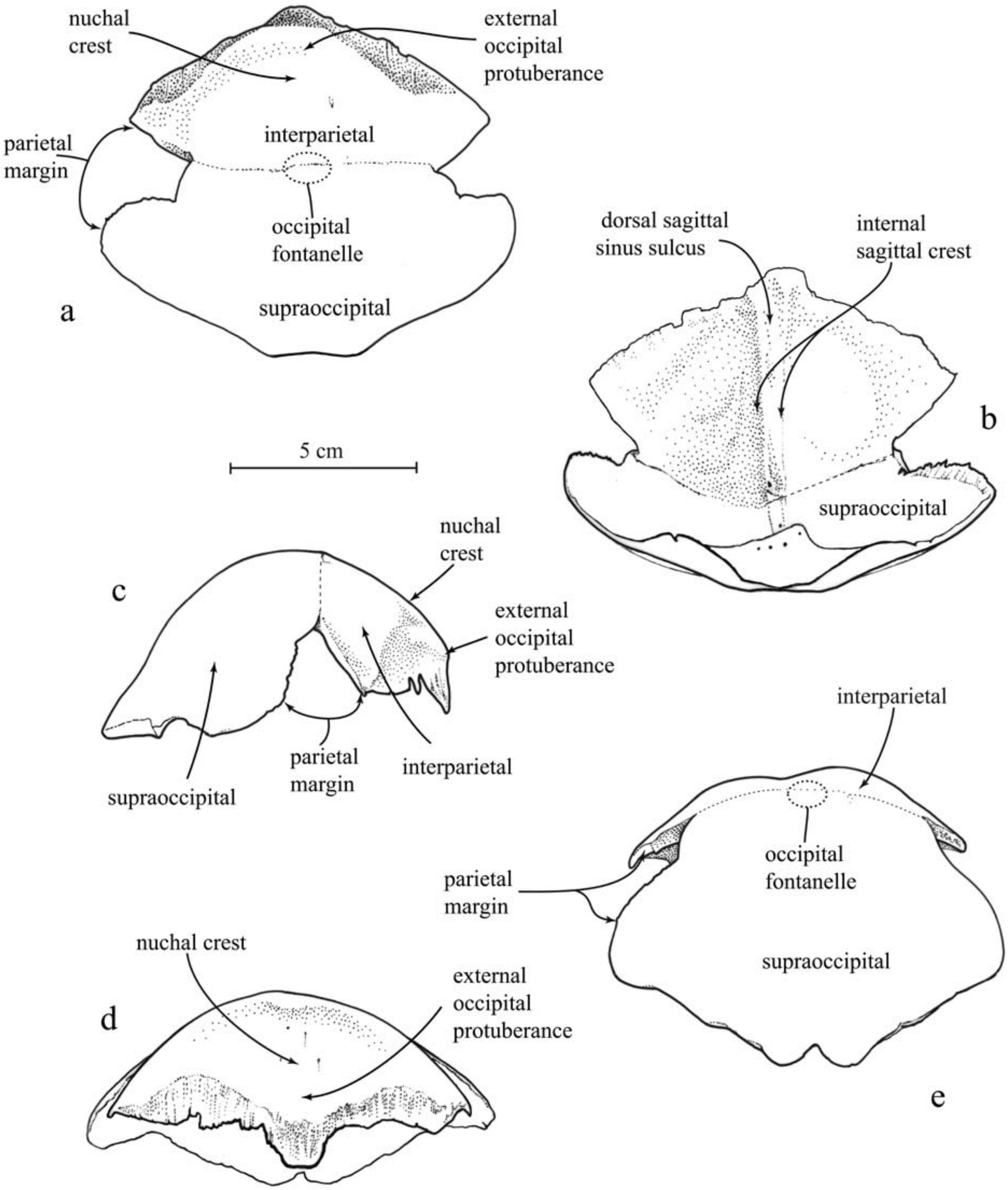


FIGURE 12. Disarticulated neonatal skull, interparietal (USNM 504560).

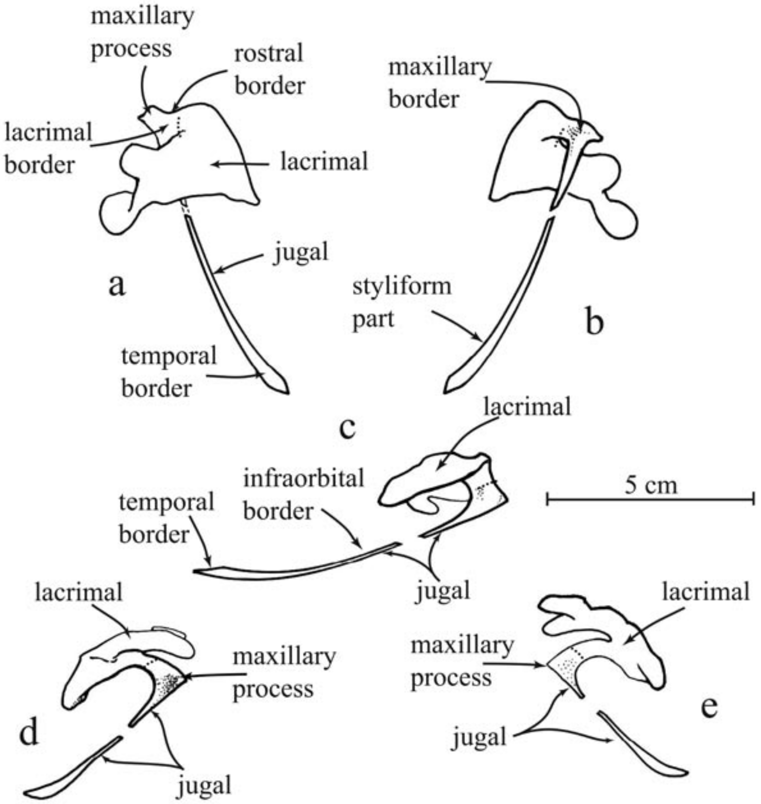


FIGURE 13. Disarticulated neonatal skull, jugal (USNM 504560).

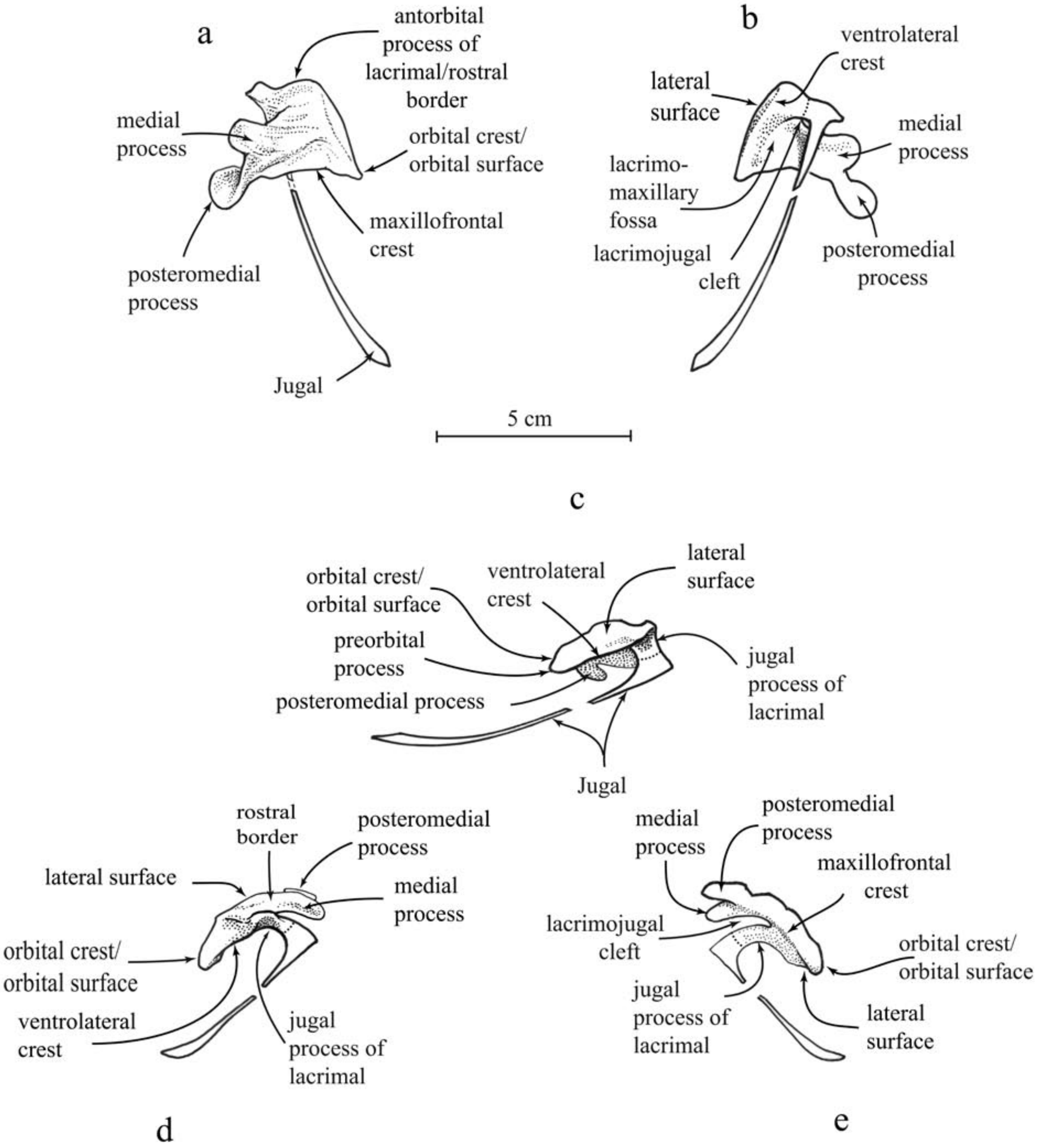


FIGURE 14. Disarticulated neonatal skull, lacrimal (USNM 504560).

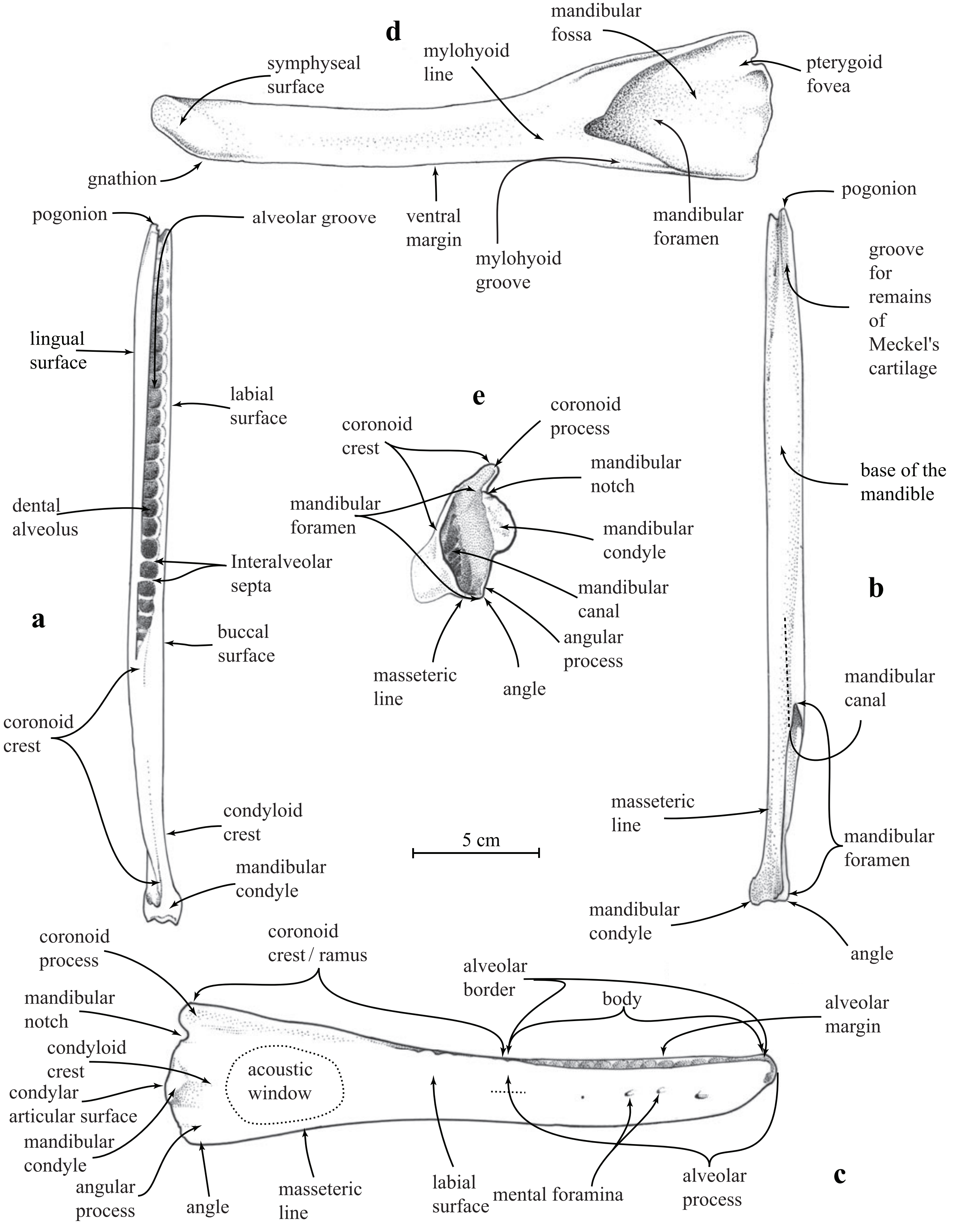


FIGURE 15. Disarticulated neonatal skull, mandible (USNM 504560).

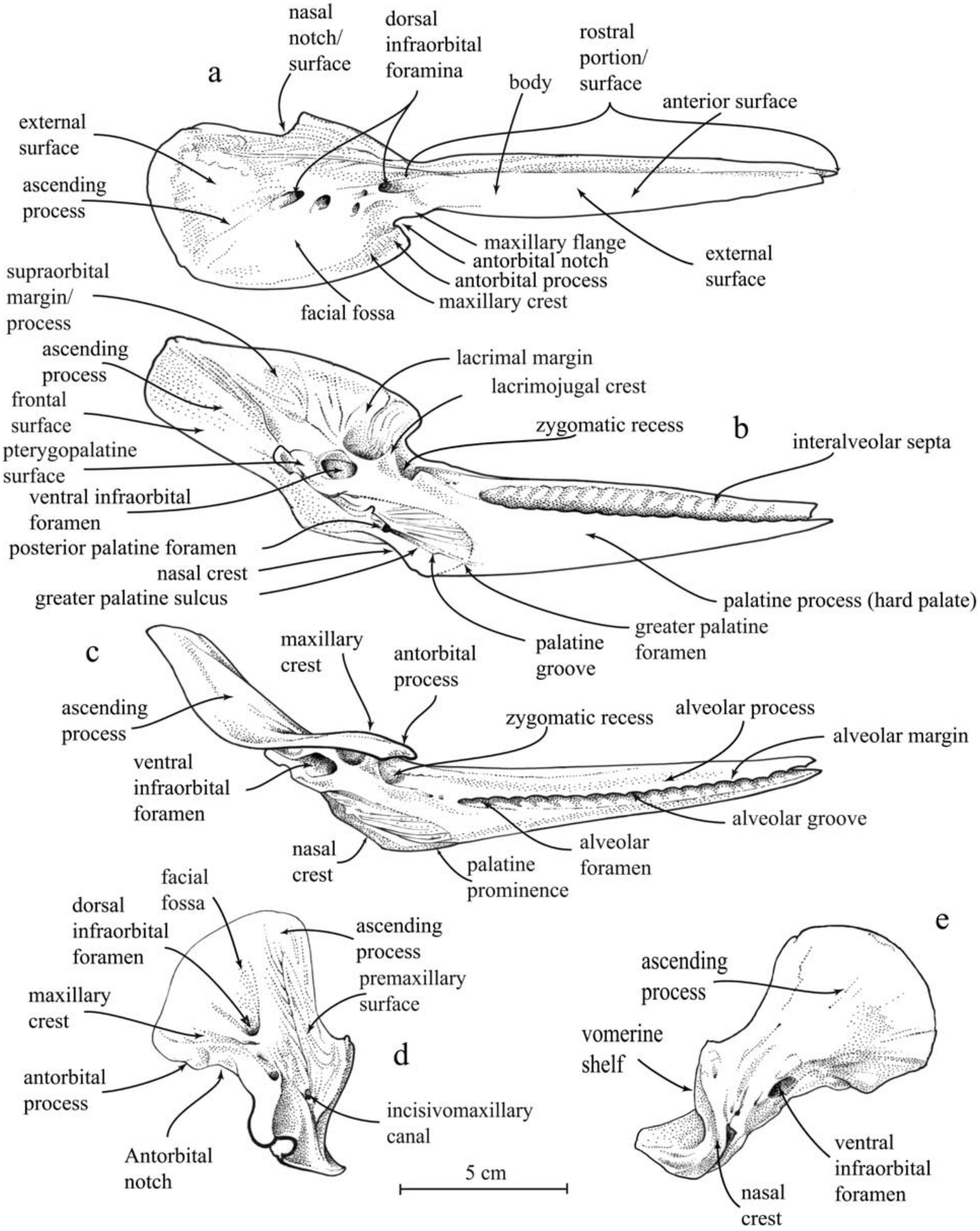


FIGURE 16. Disarticulated neonatal skull, maxilla (USNM 504560).

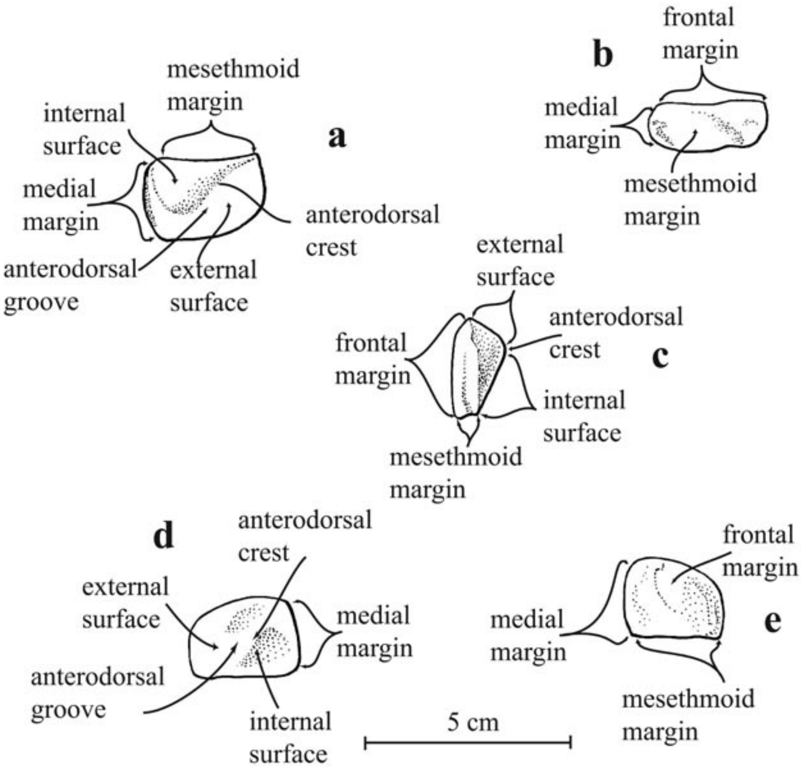


FIGURE 17. Disarticulated neonatal skull, nasal (USNM 504560).

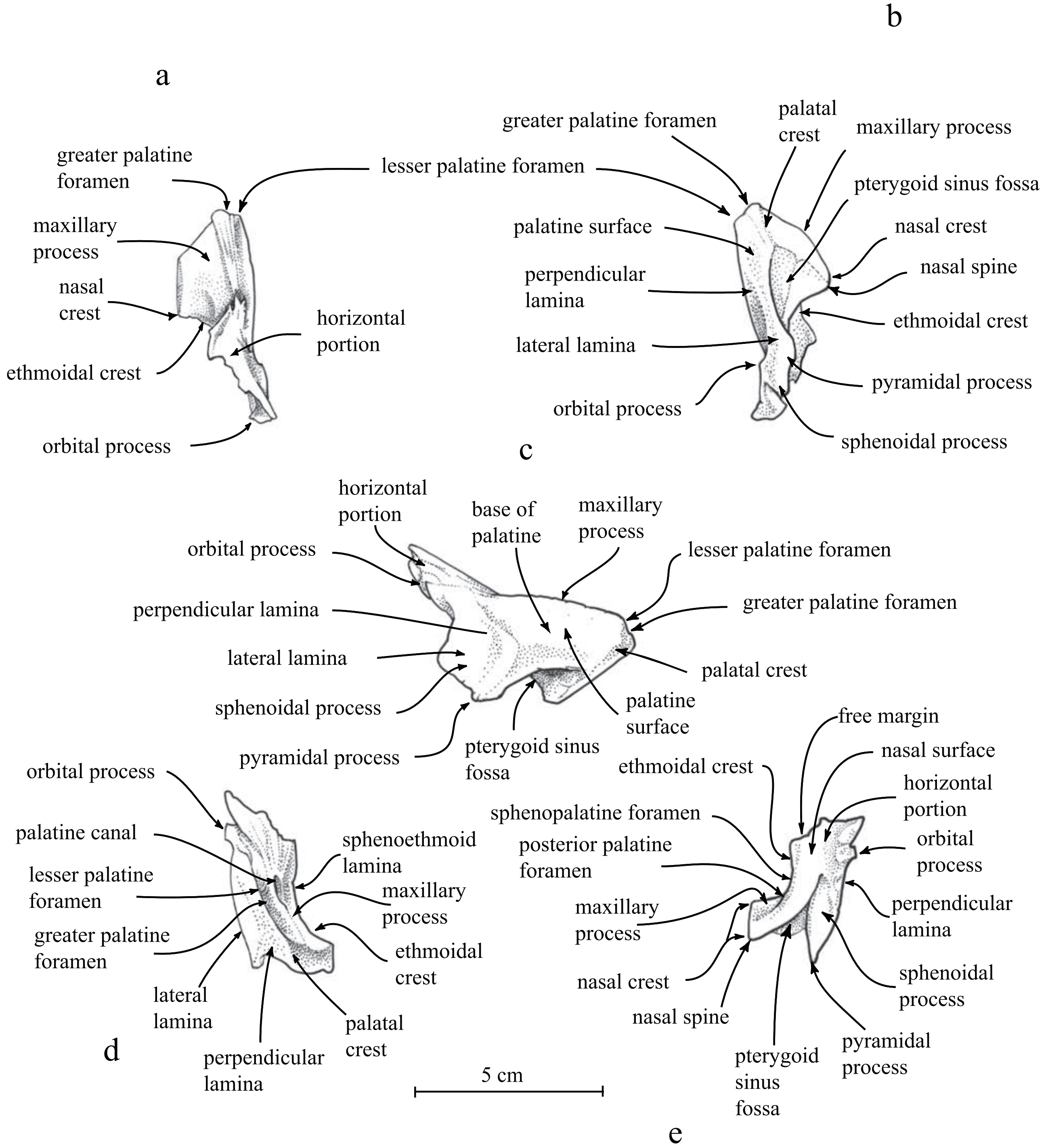


FIGURE 18. Disarticulated neonatal skull, palatine (USNM 504560).

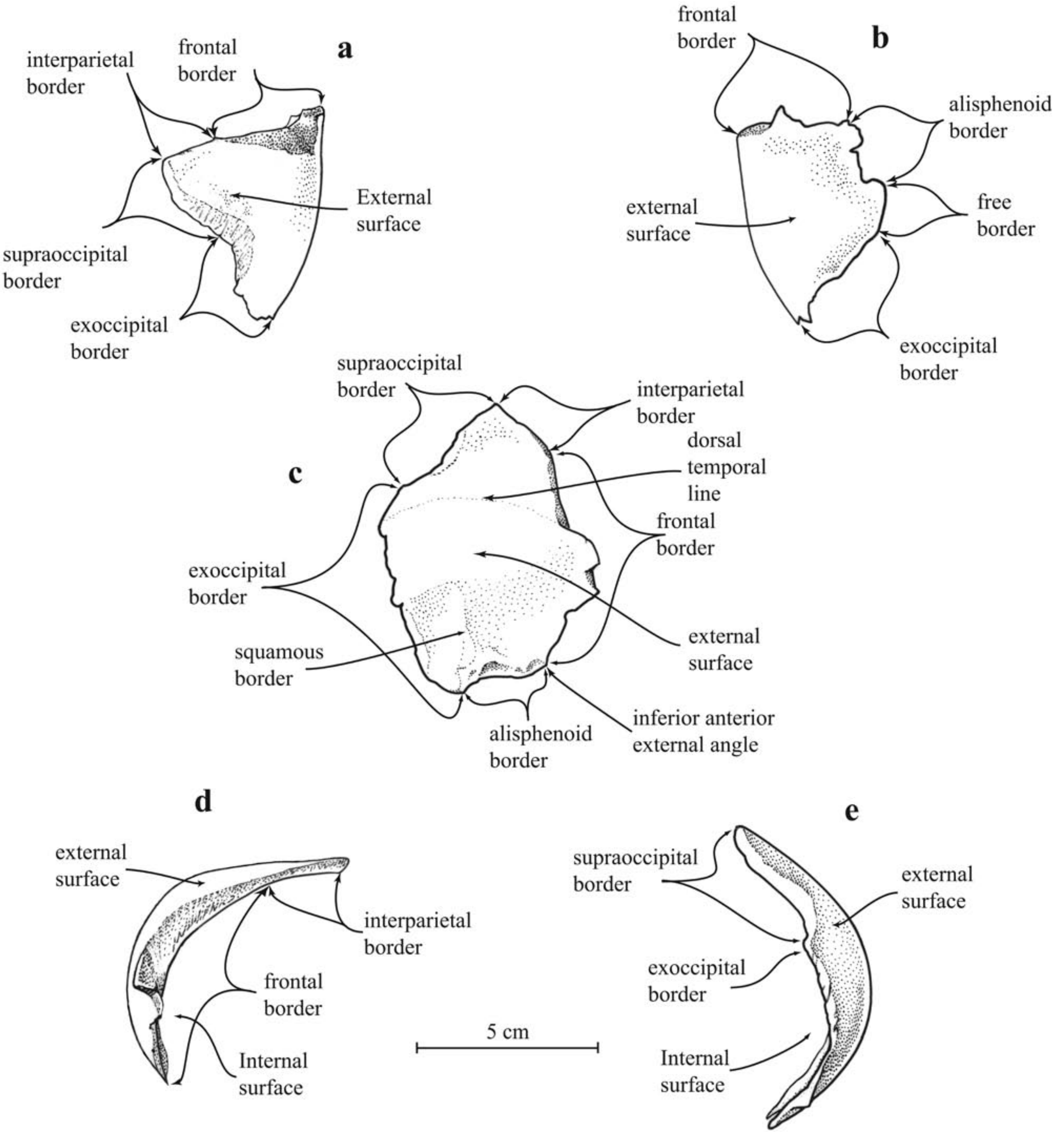


FIGURE 19. Disarticulated neonatal skull, parietal (USNM 504560).

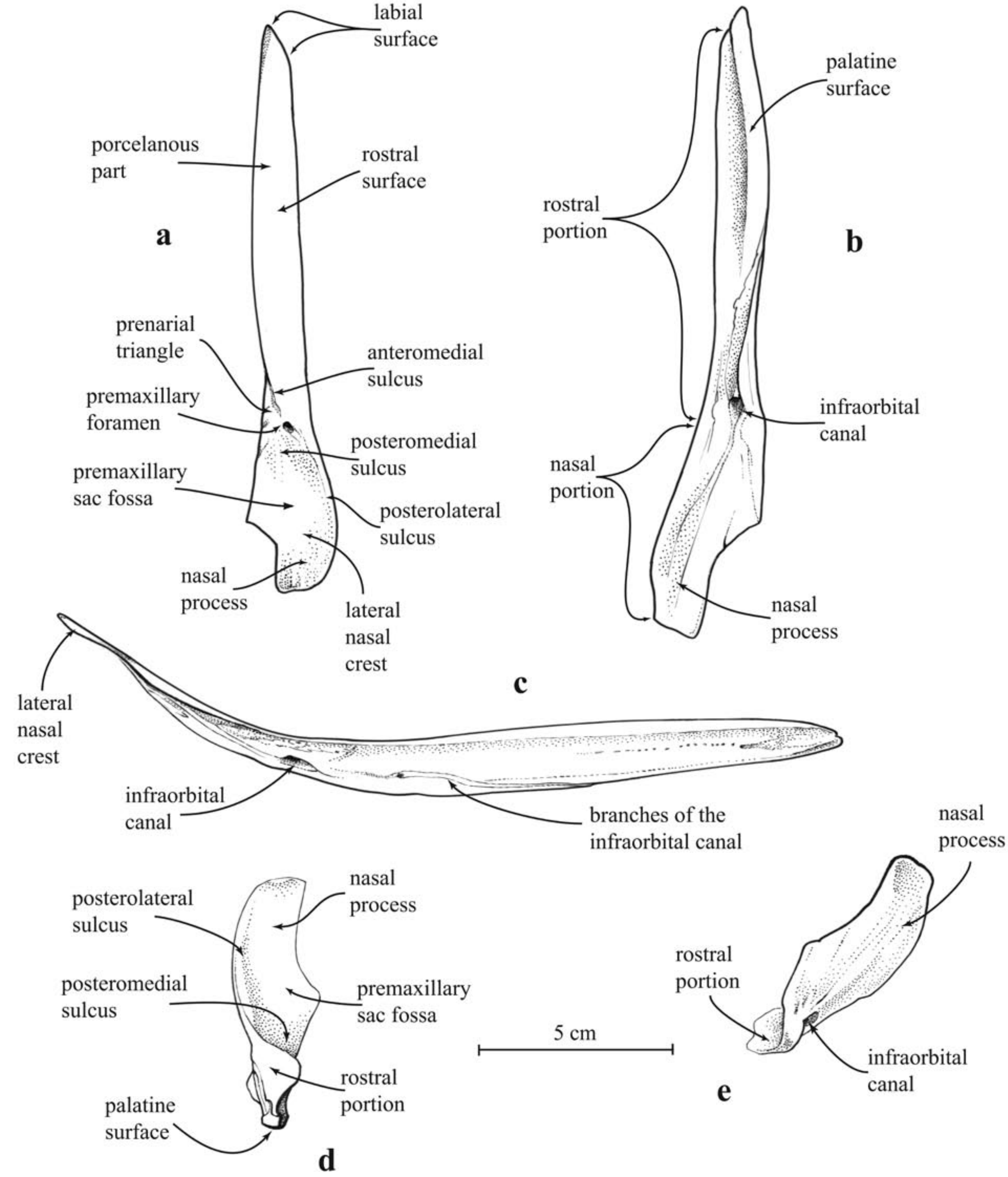


FIGURE 20. Disarticulated neonatal skull, premaxilla (USNM 504560).

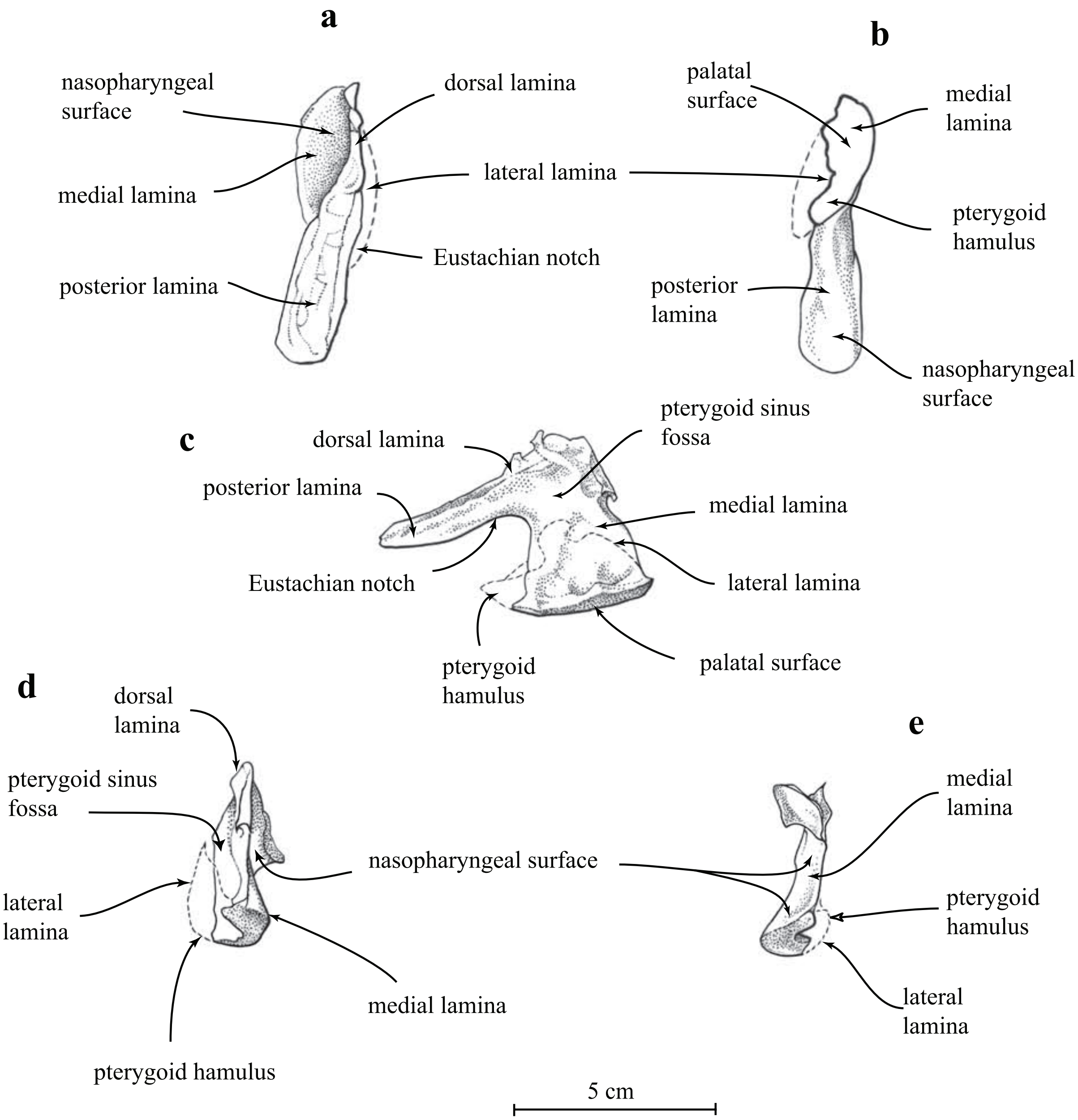


FIGURE 21. Disarticulated neonatal skull, pterygoid (USNM 504560).

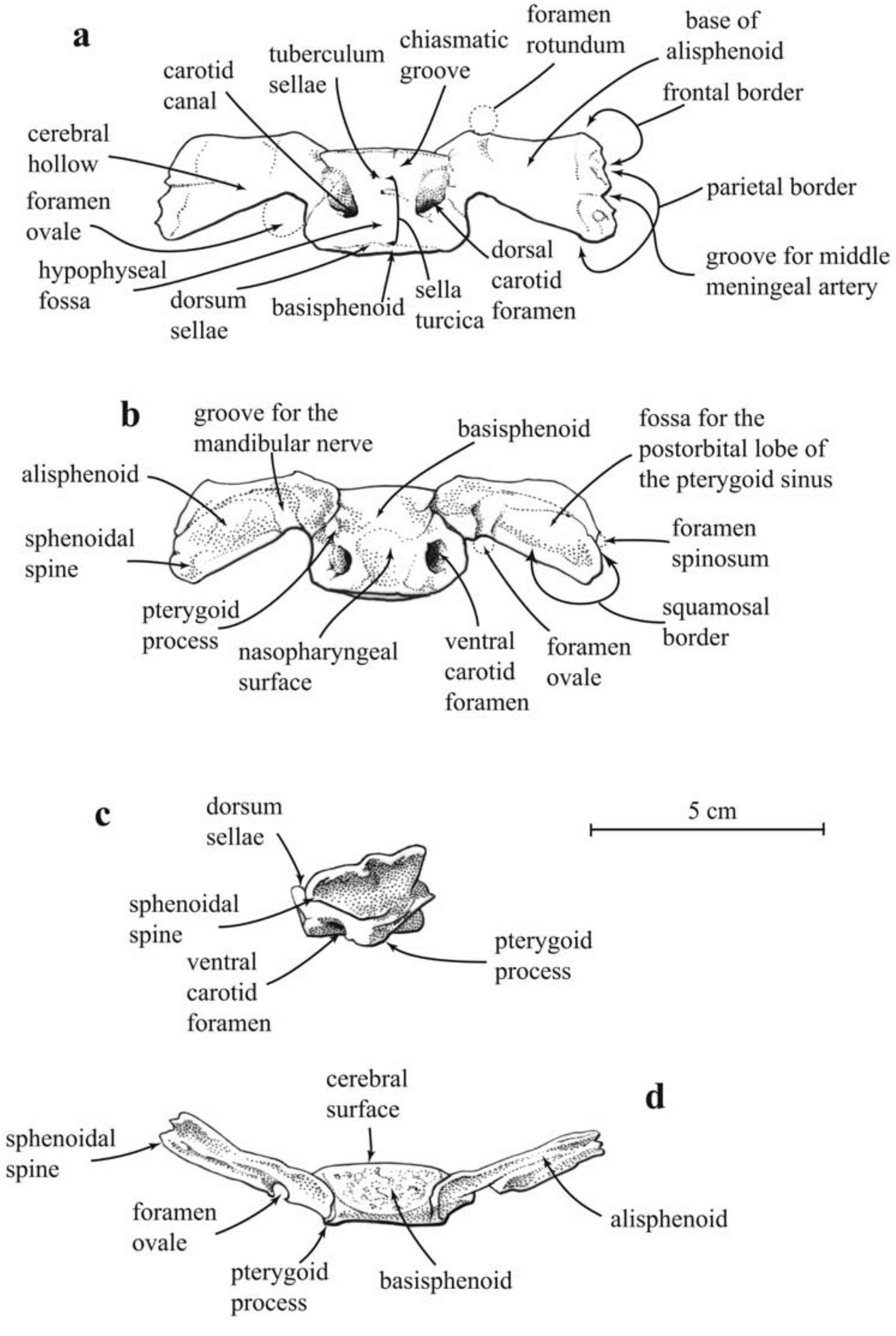


FIGURE 22. Disarticulated neonatal skull, sphenoid (USNM 504560).

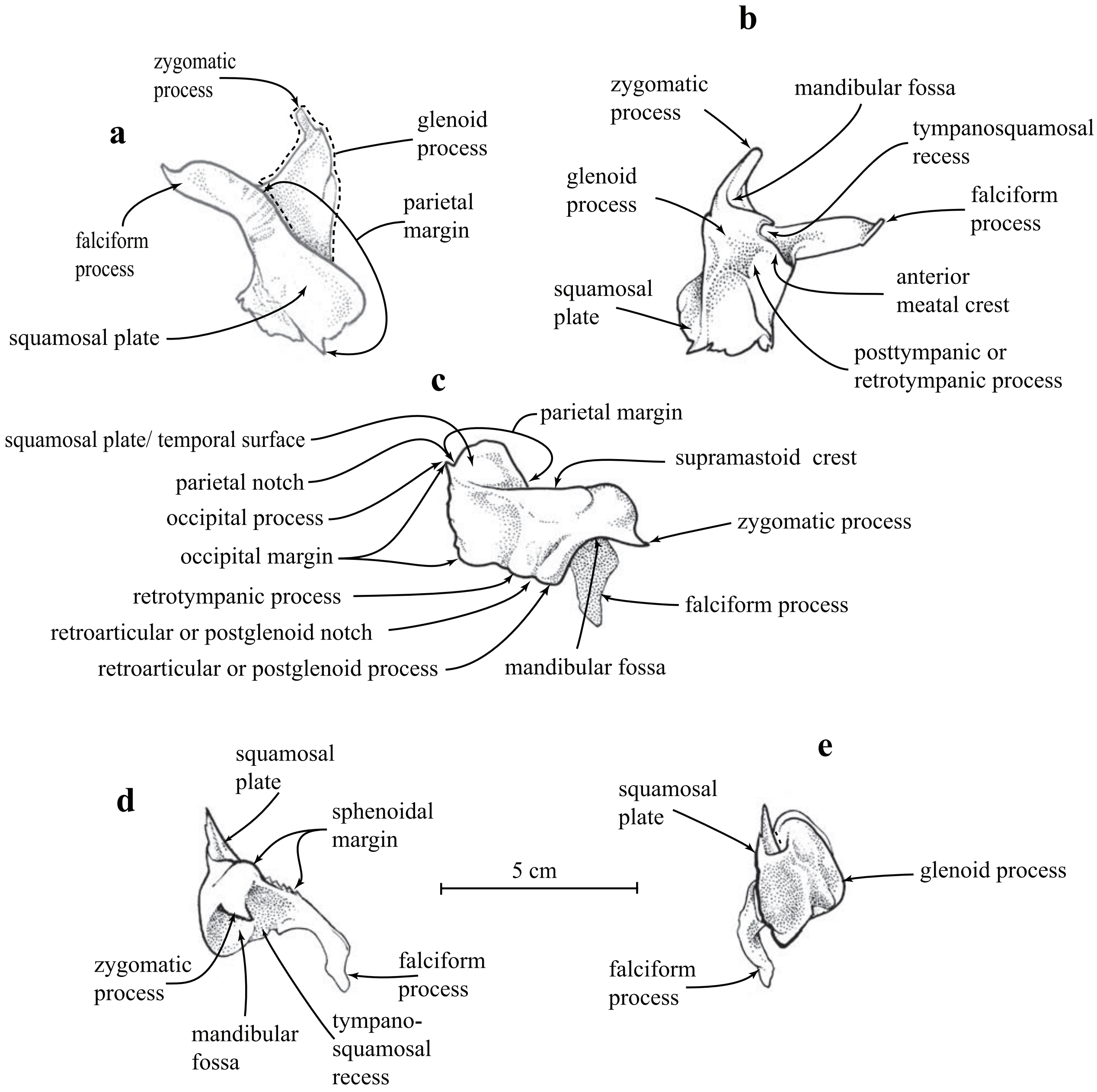


FIGURE 23. Disarticulated neonatal skull, squamosal (USNM 504560).

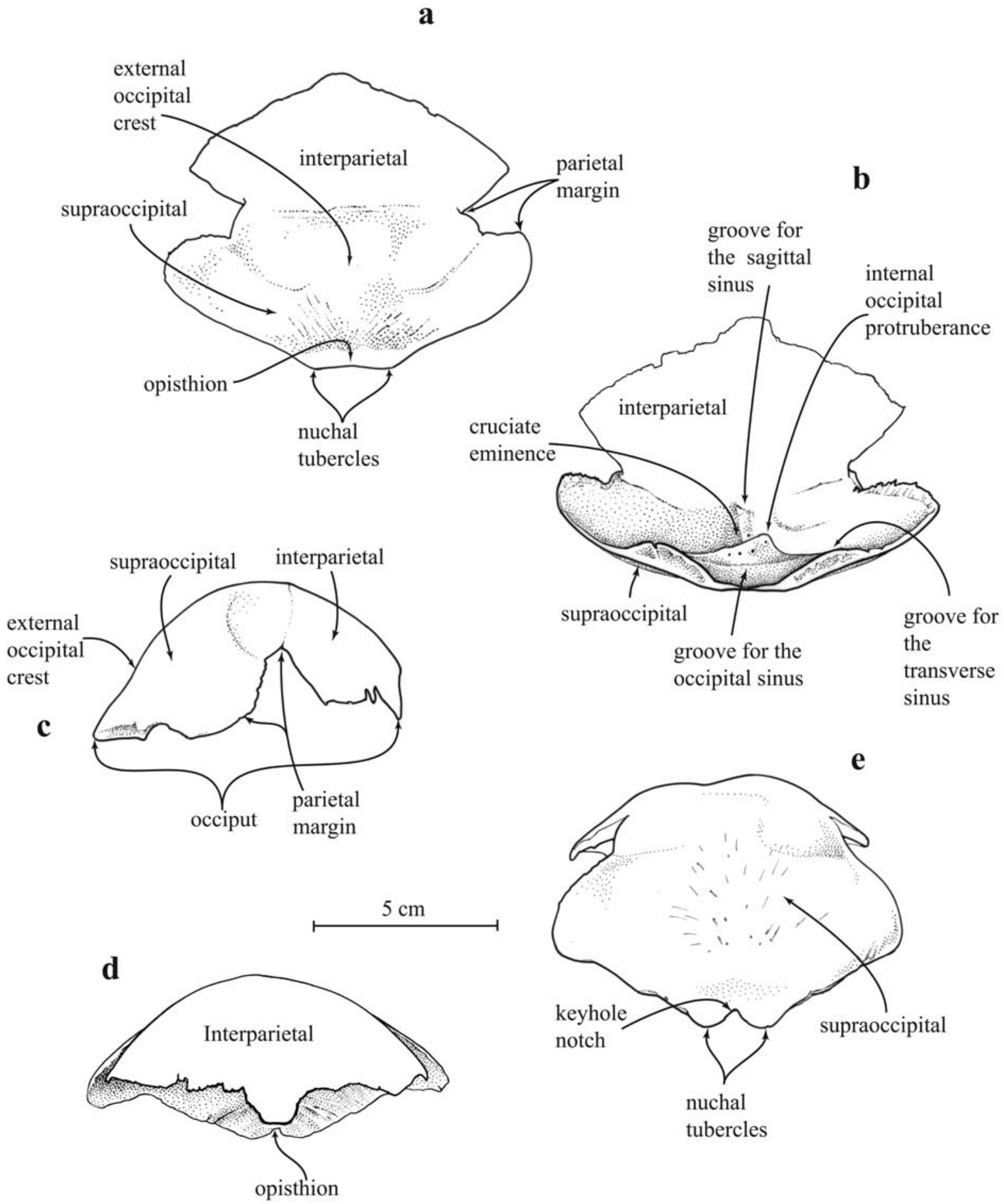


FIGURE 24. Disarticulated neonatal skull, supraoccipital (USNM 504560).

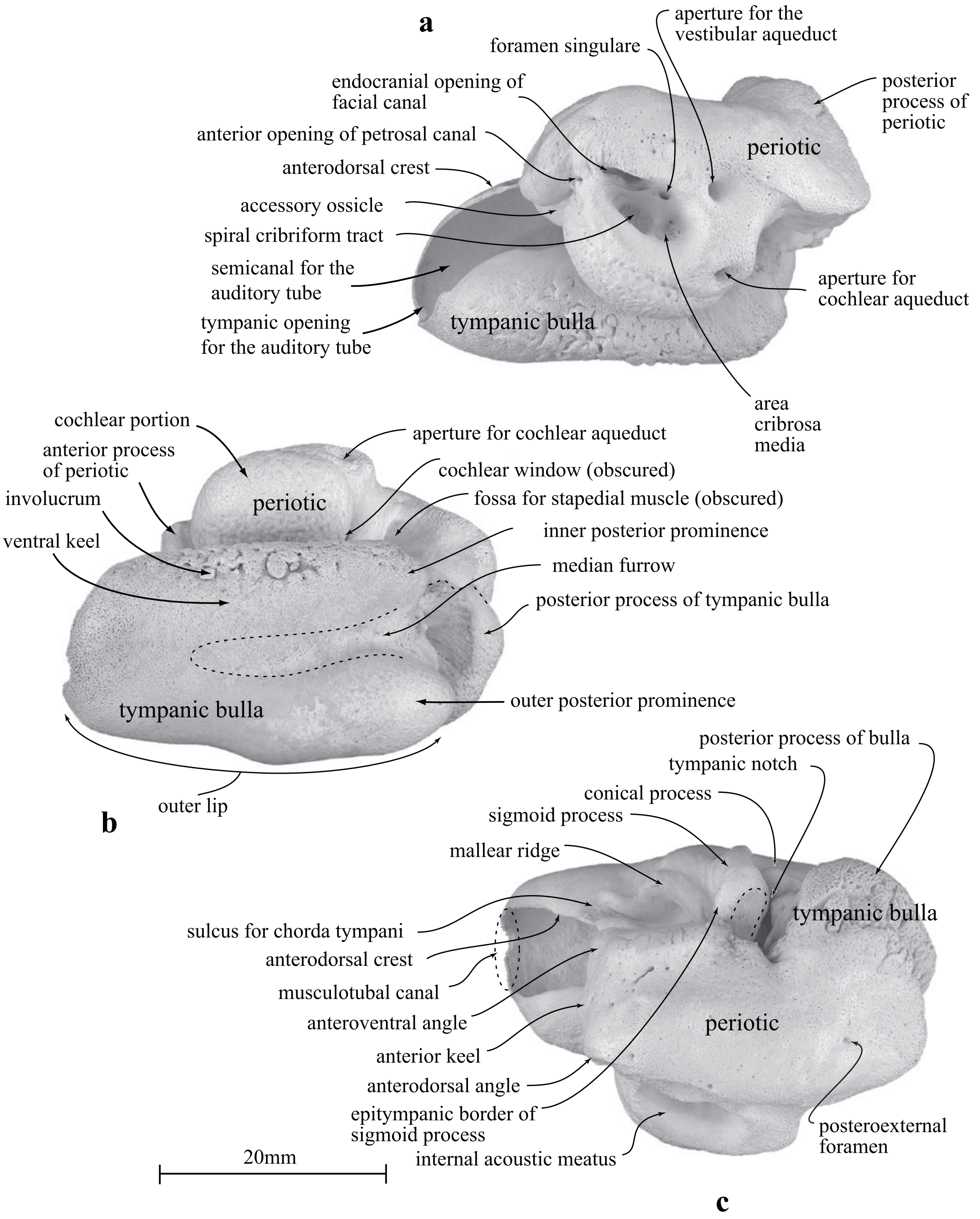


FIGURE 25a–c. Disarticulated neonatal skull, tympanoperiotic (USNM 504560).

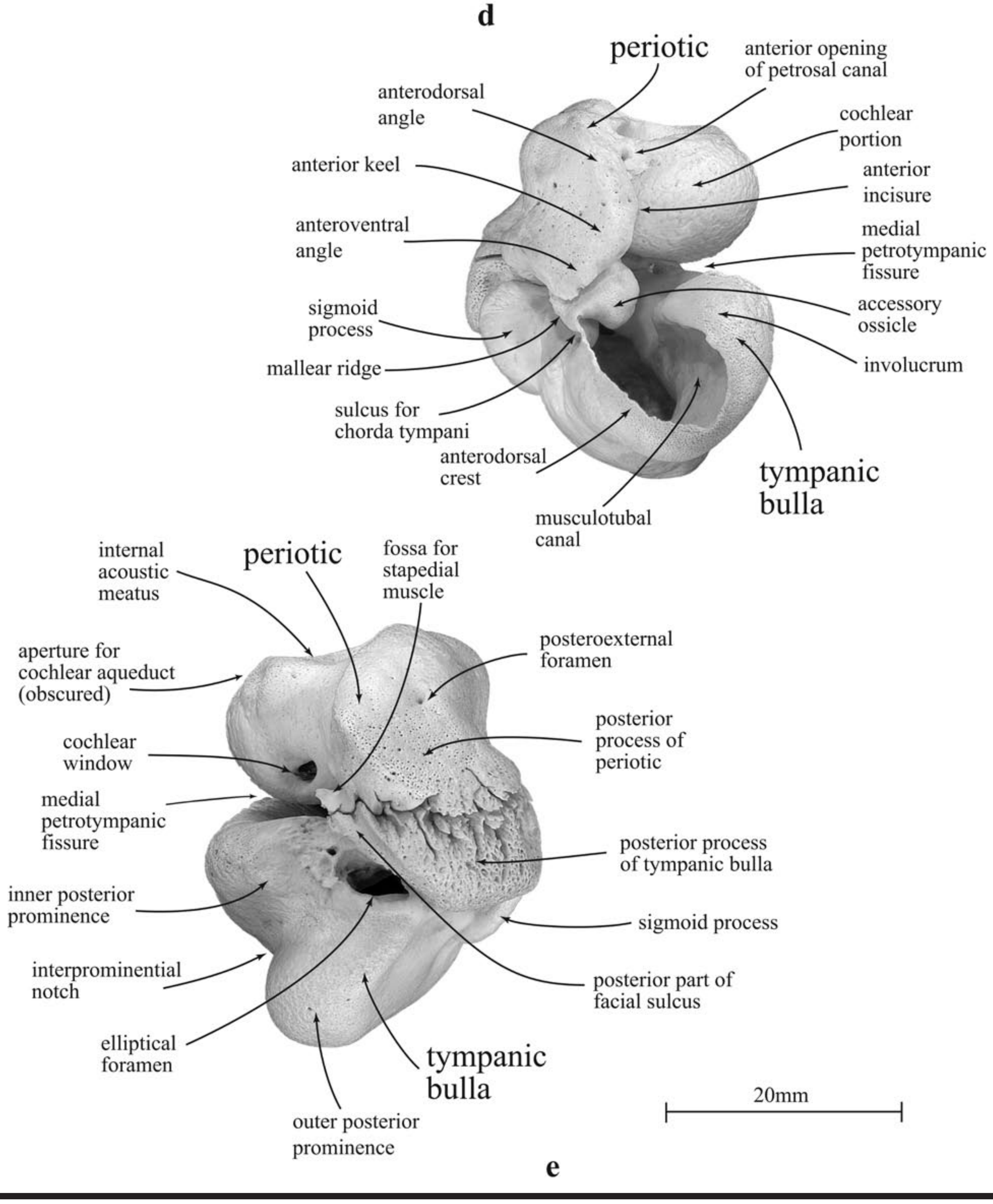


FIGURE 25d,e. Disarticulated neonatal skull, tympanic, right (USNM 504560).

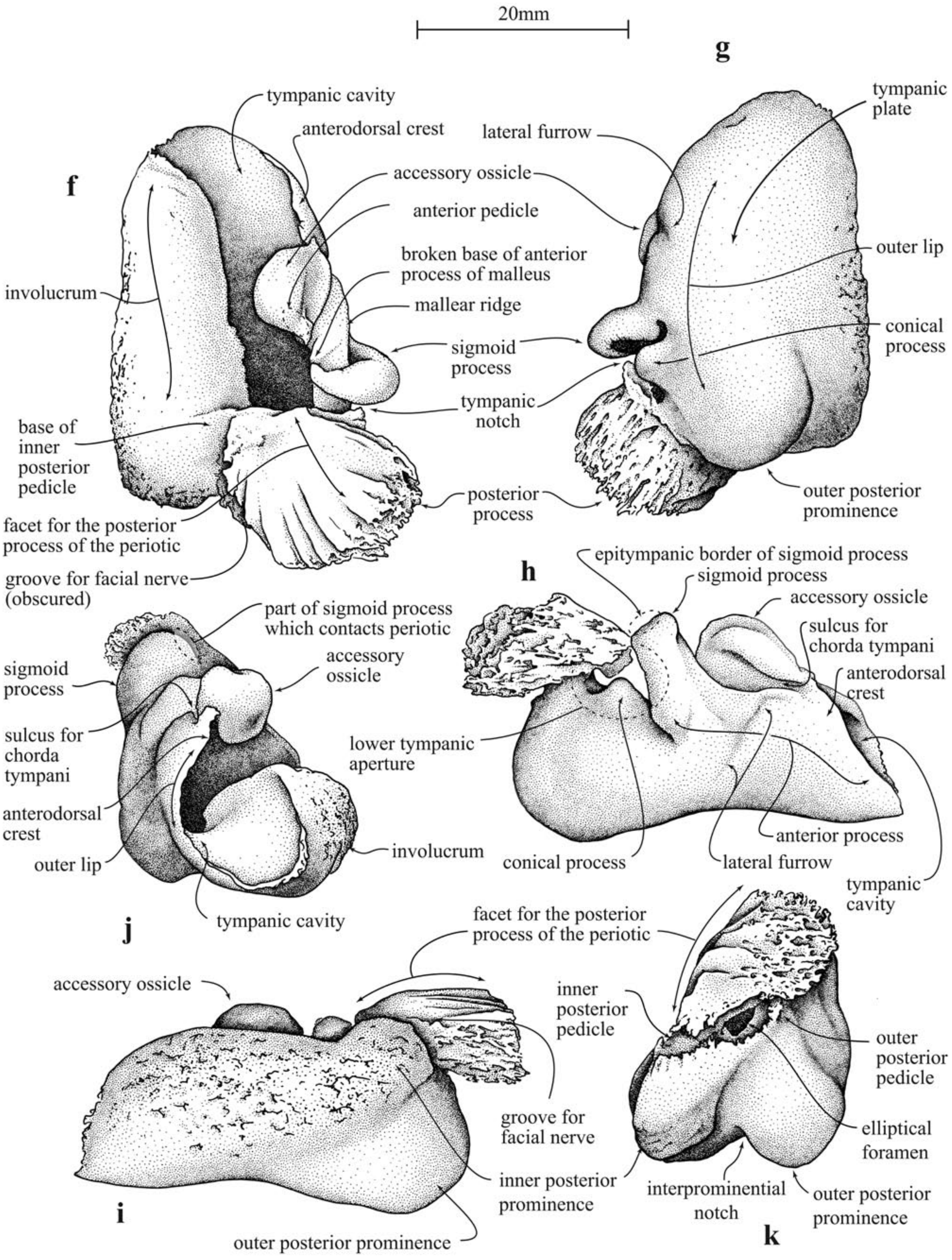


FIGURE 25f–k. Skull of adult specimen, tympanic, right (USNM 550403).

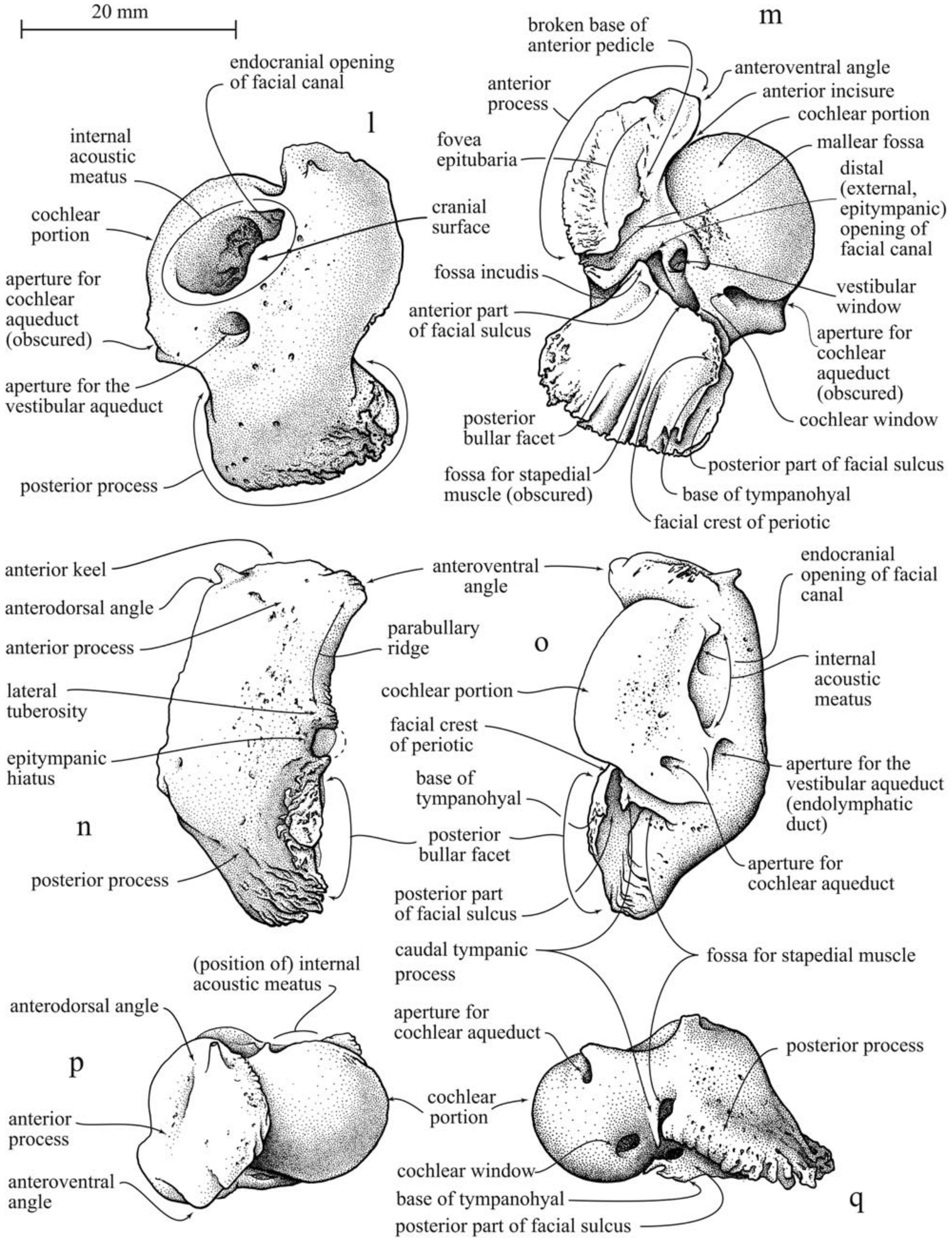


FIGURE 25l–q. Skull of adult specimen, periotic, right (USNM 550403).

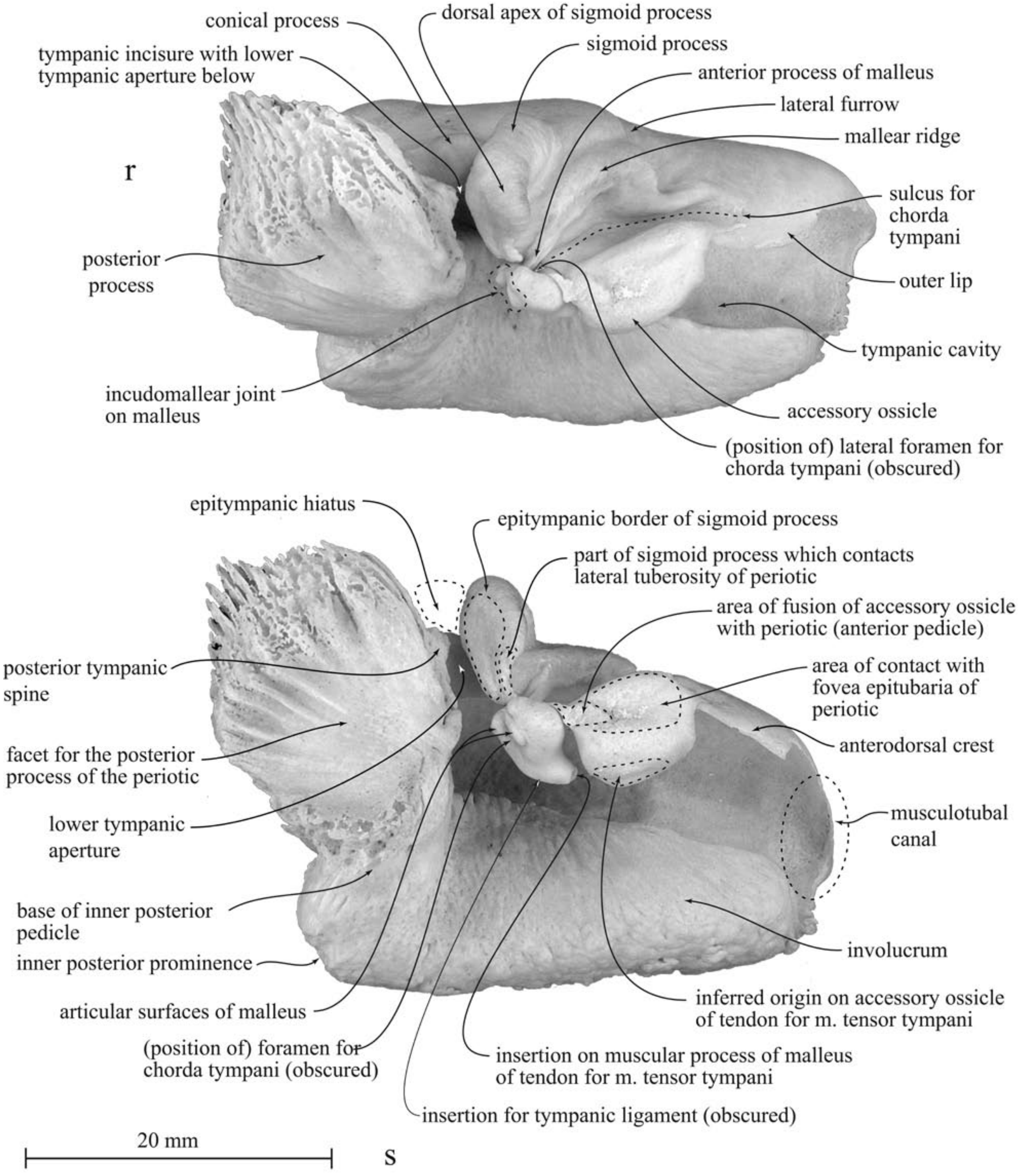


FIGURE 25r,s. Skull of adult specimen, tympanic and malleus, left (USNM 550403).

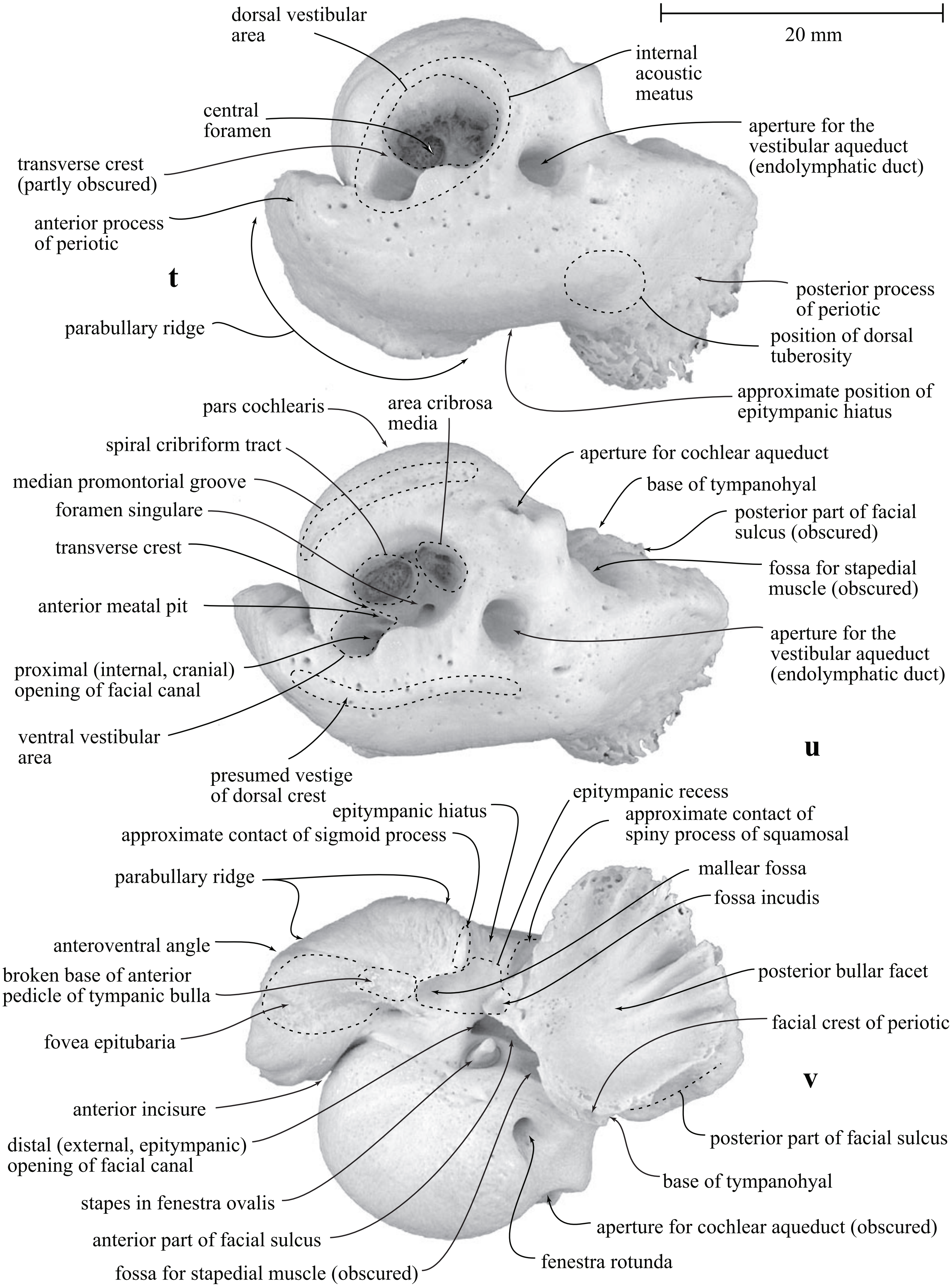


FIGURE 25t–v. Skull of adult specimen, periotic, left (USNM 550403).

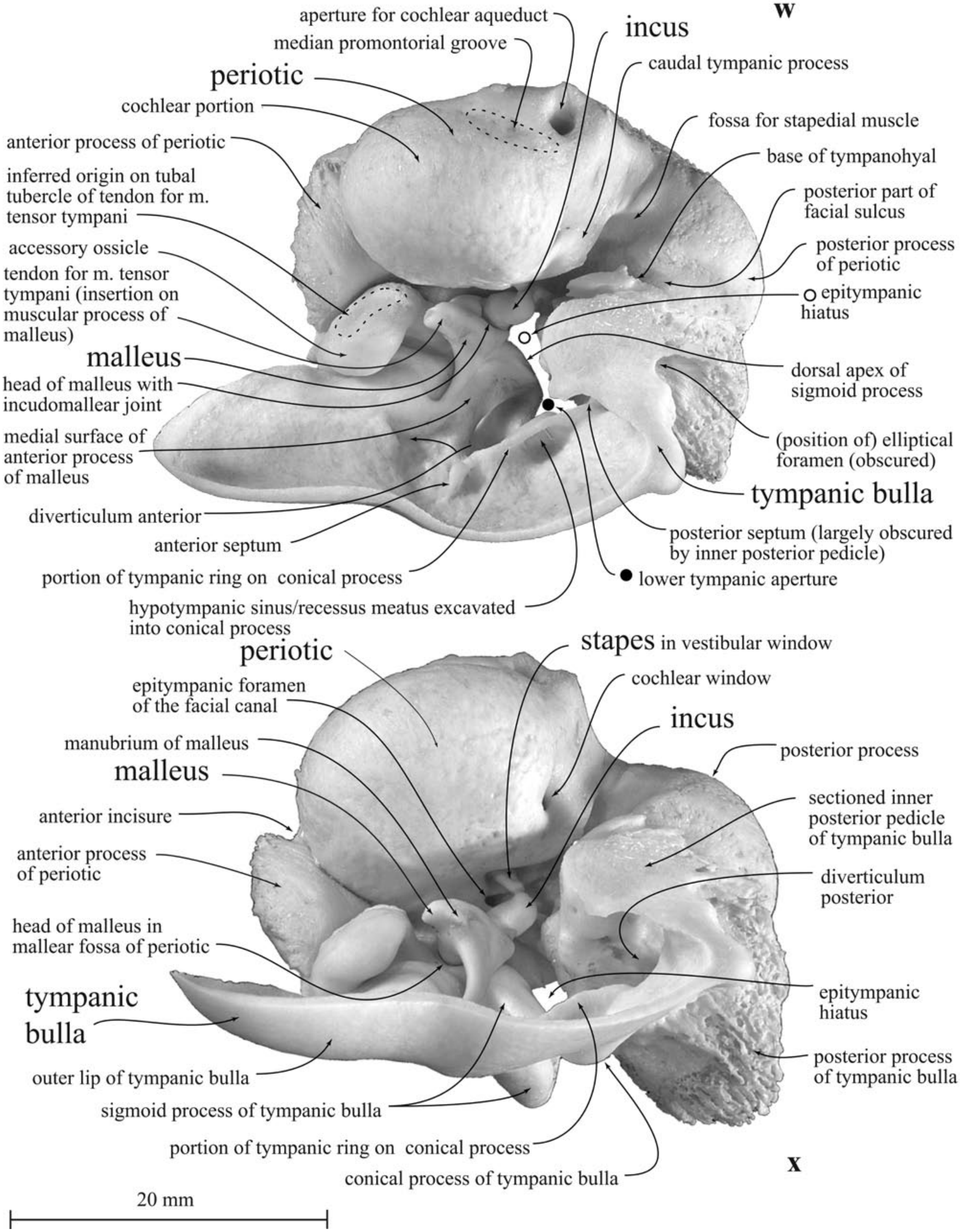


FIGURE 25w,x. Skull of adult specimen, sectioned tympanoperiotic, right (USNM 571017).

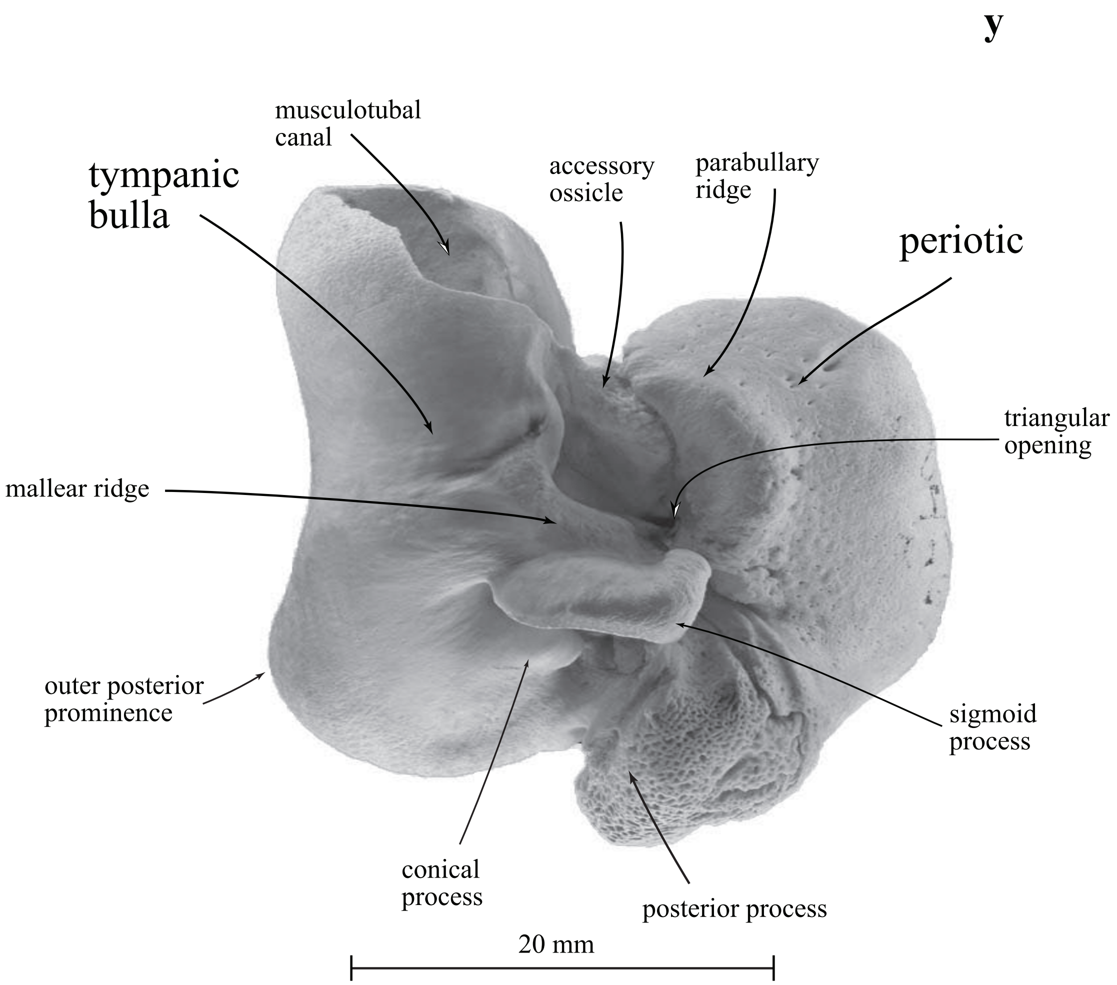


FIGURE 25y. Disarticulated neonatal skull, tympanoperiotic, left (USNM 504560).

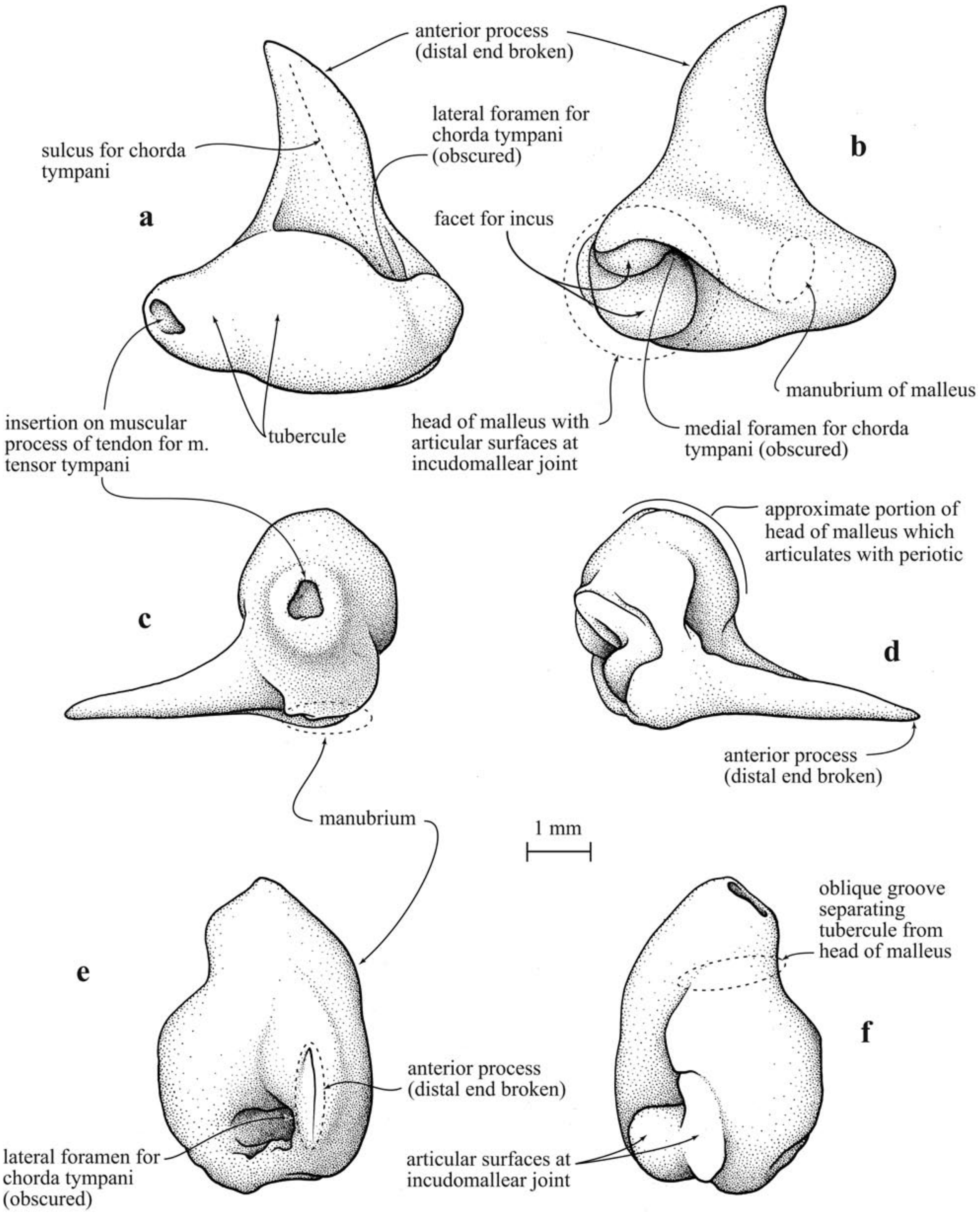


FIGURE 26a–f. Skull of juvenile specimen, malleus, right (USNM 571036).

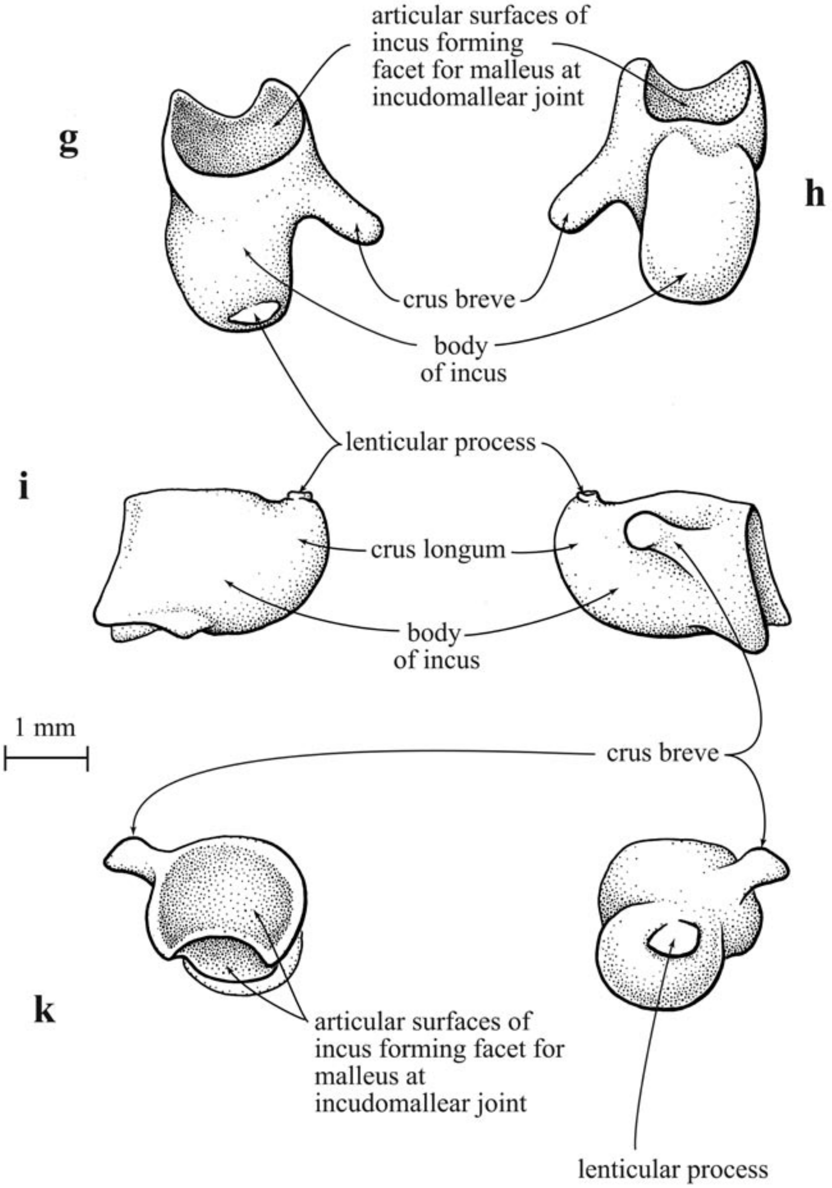


FIGURE 26g–l. Skull of juvenile specimen, incus, right (USNM 571036).

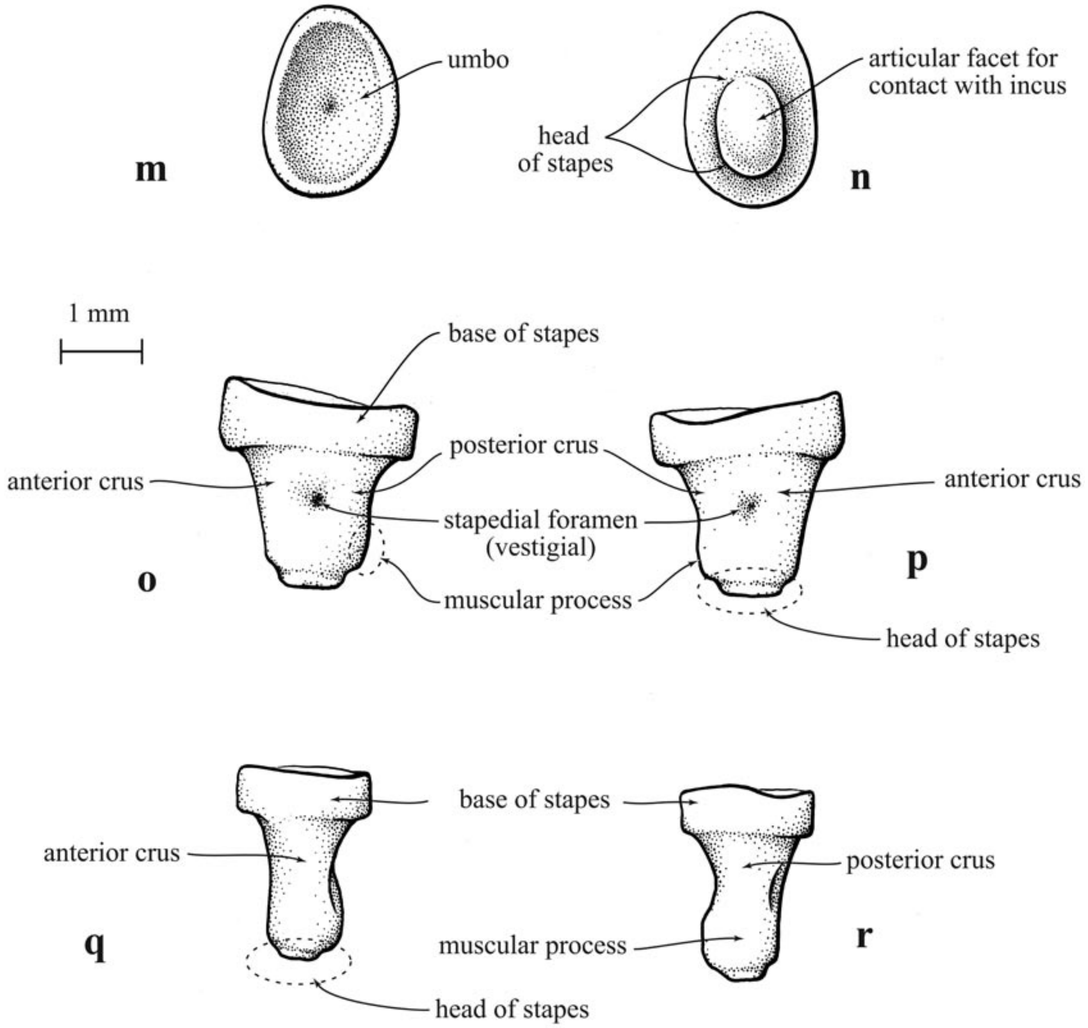


FIGURE 26m–r. Skull of juvenile specimen, stapes, right (USNM 571036).

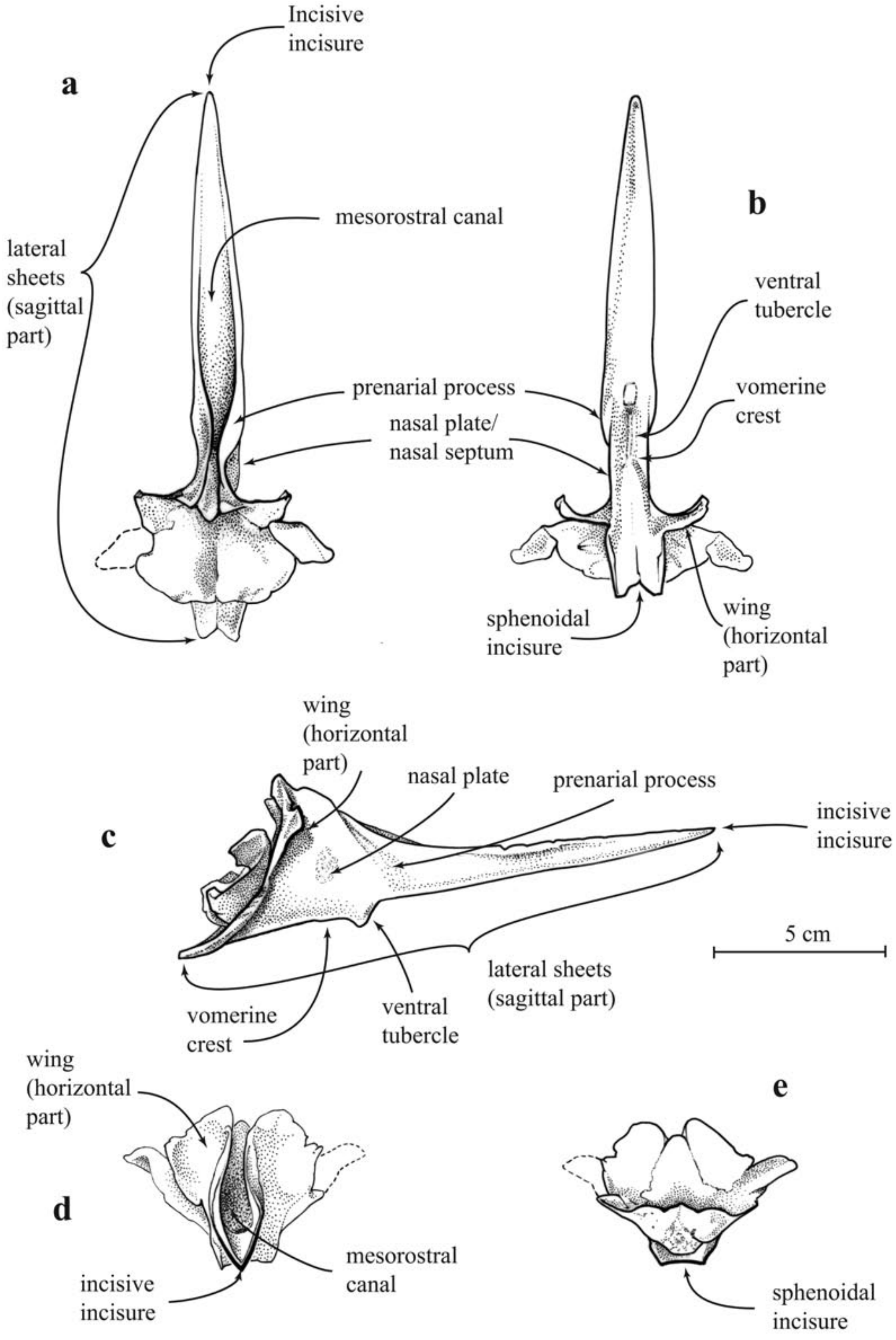


FIGURE 27. Disarticulated neonatal skull, vomer (USNM 504560).

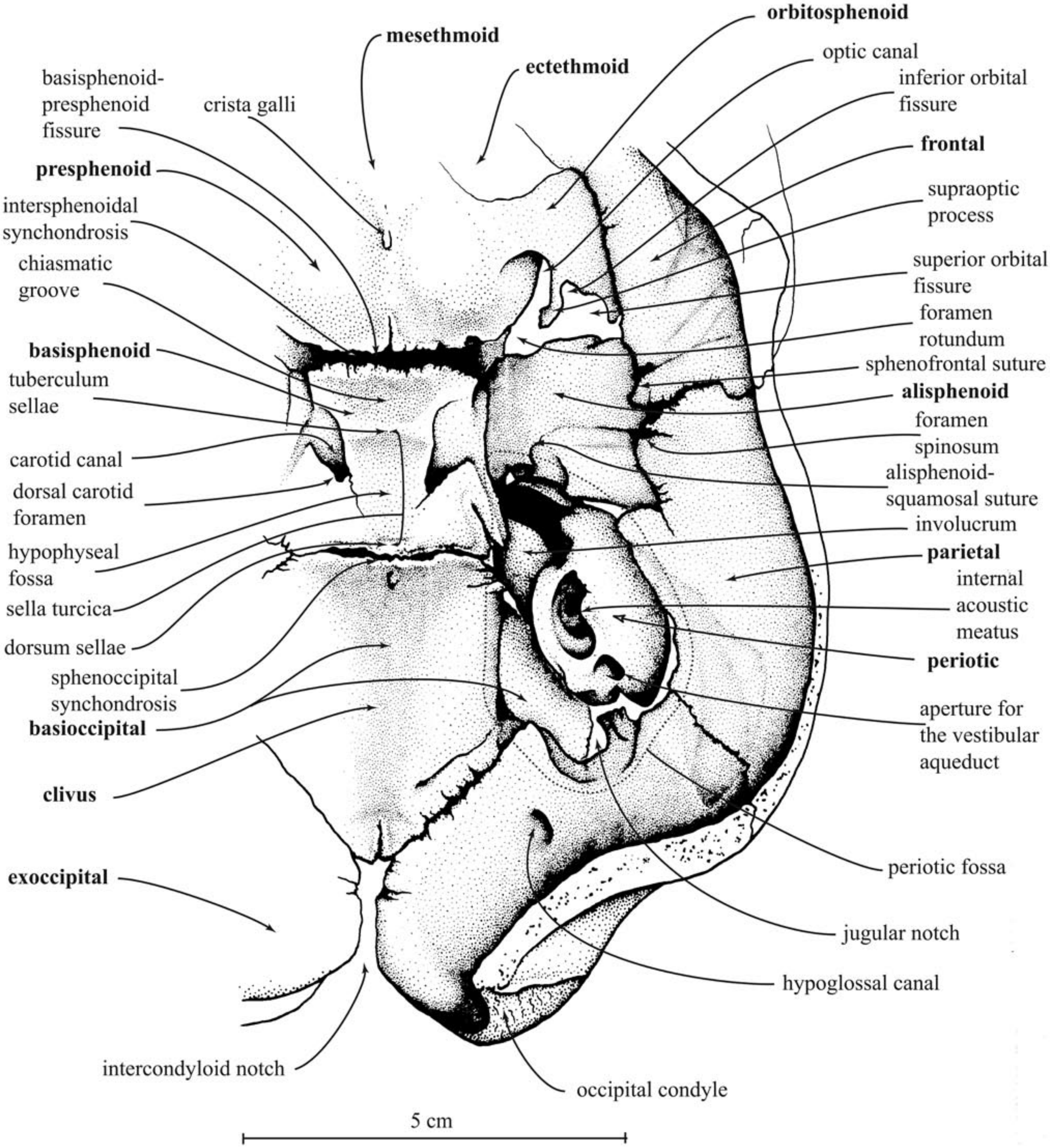


FIGURE 28. Disarticulated neonatal skull, basicranium, right, dorsal view (USNM 571622).

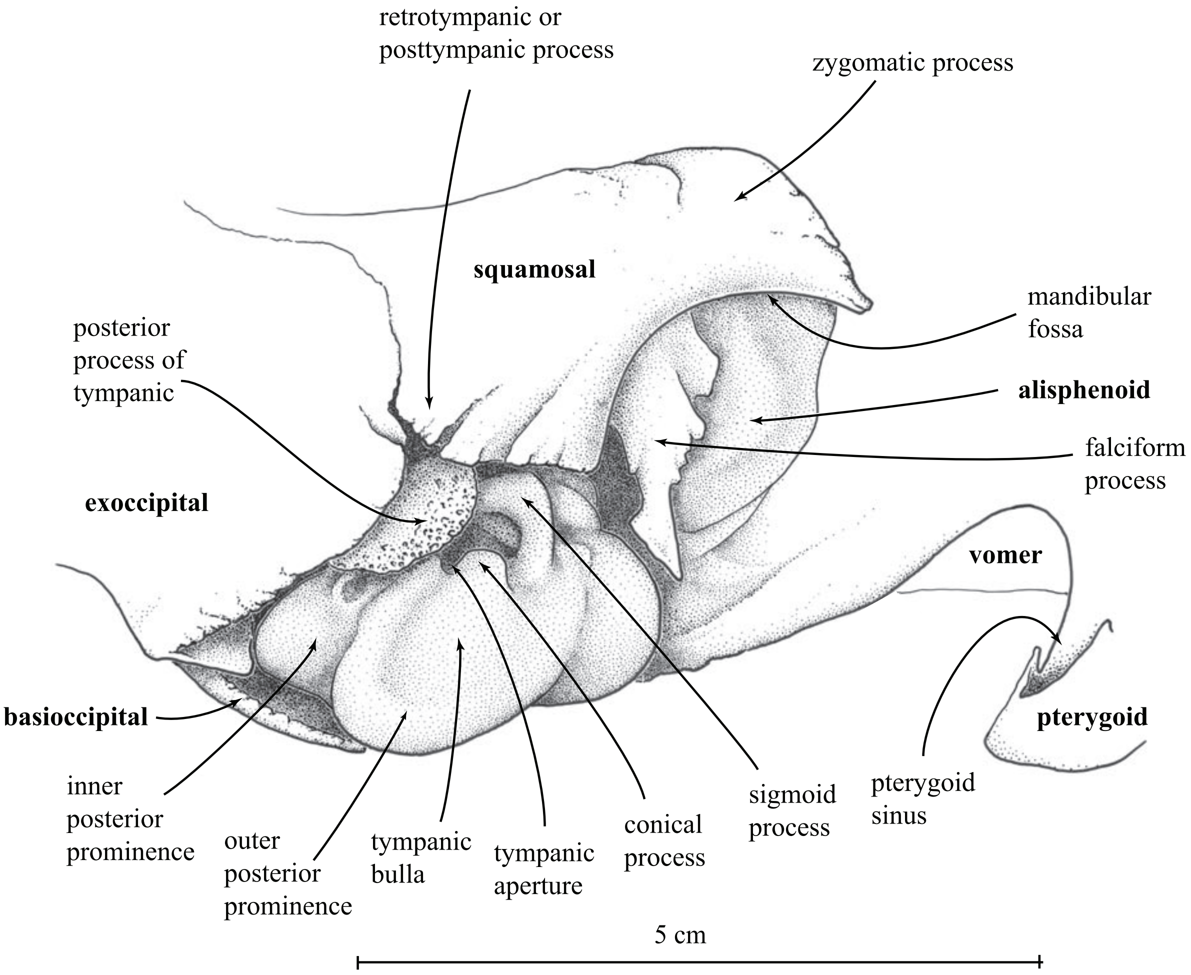


FIGURE 29. Disarticulated neonatal skull, bulla, right, ventrolateral view (USNM 571622).

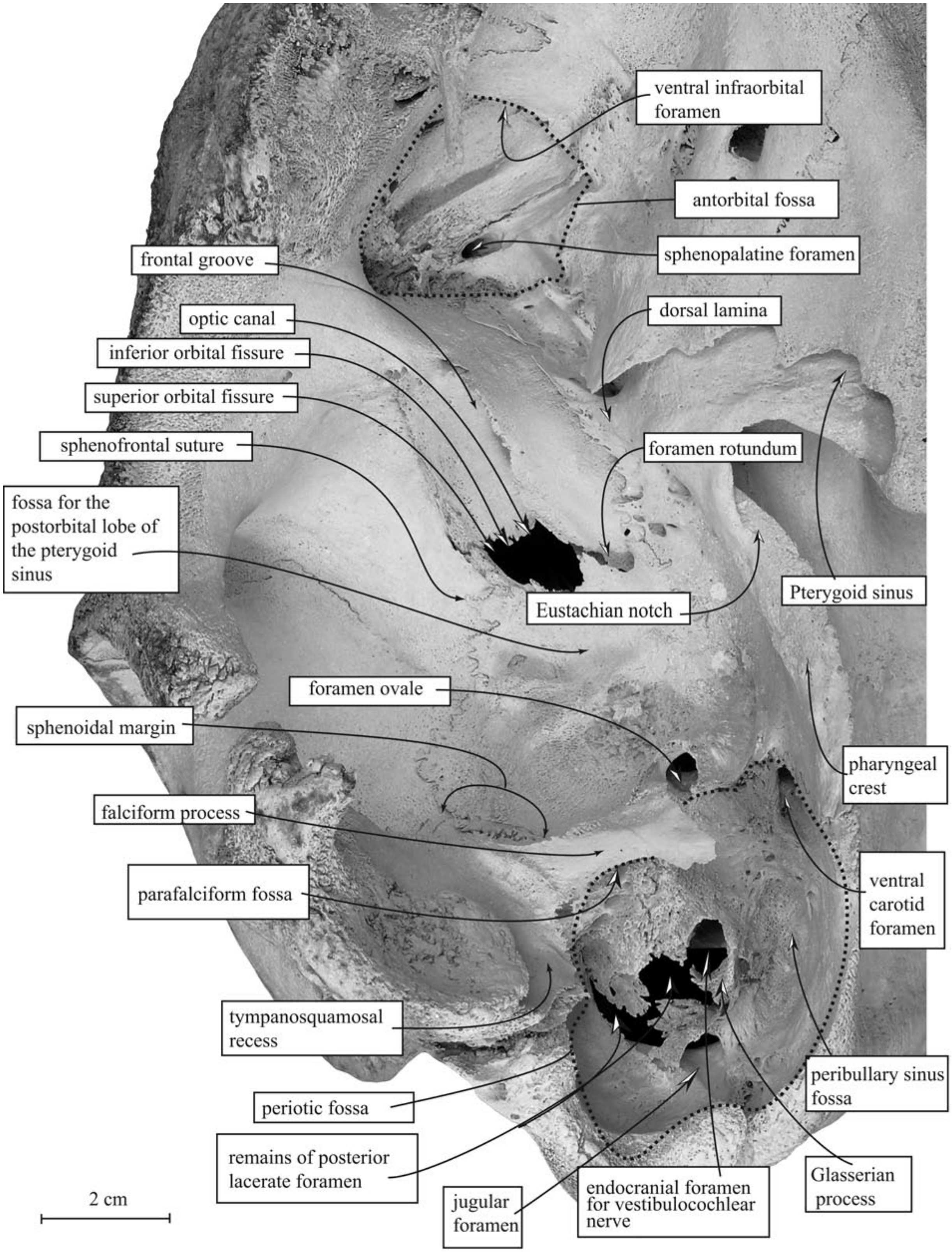


FIGURE 30. Skull of adult specimen, basicranium, right, ventrolateral view (USNM 501197).

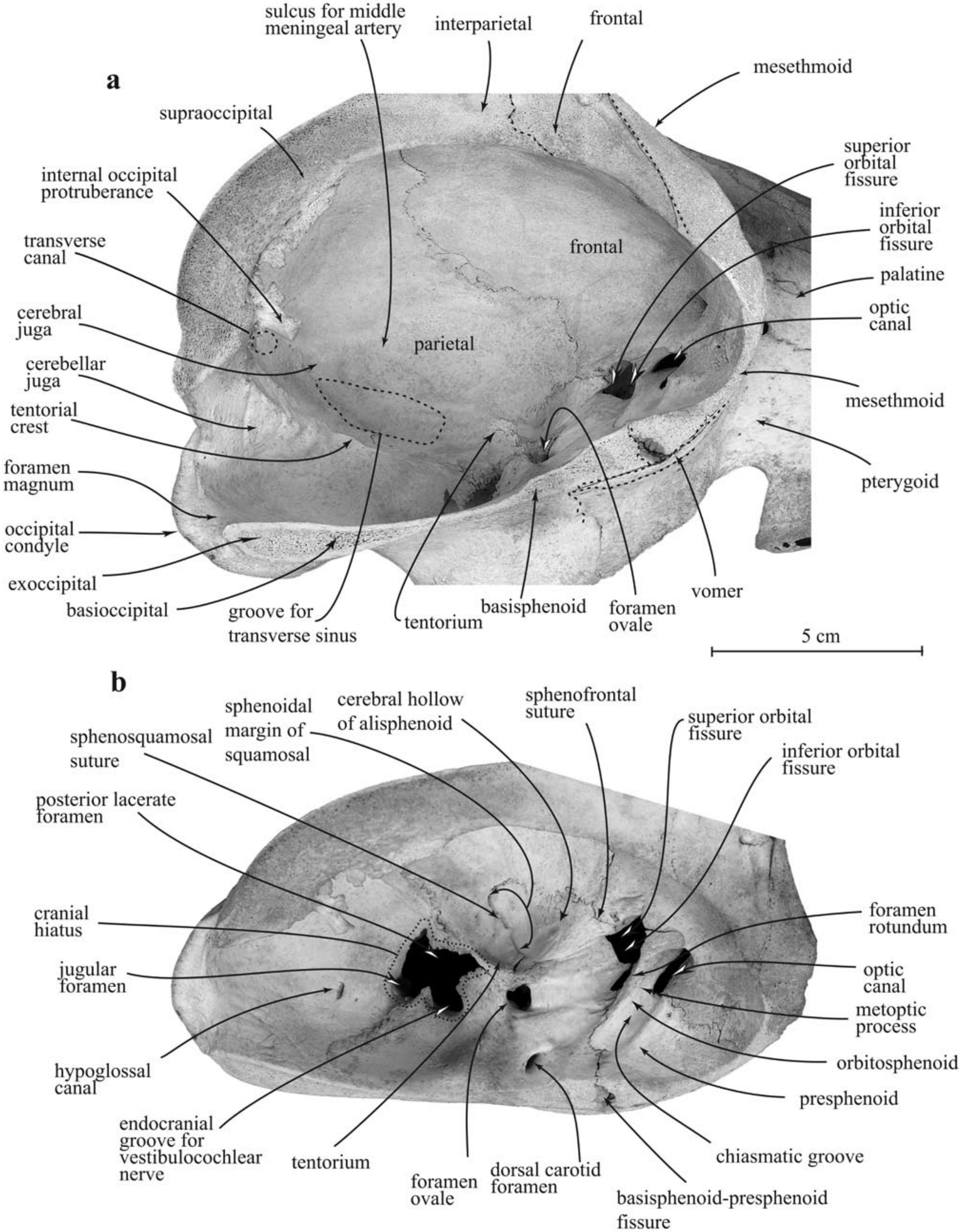


FIGURE 31. Skull of adult specimen, cranium, left, interior view; (a) medial view; (b) dorsomedial view (USNM 571695).

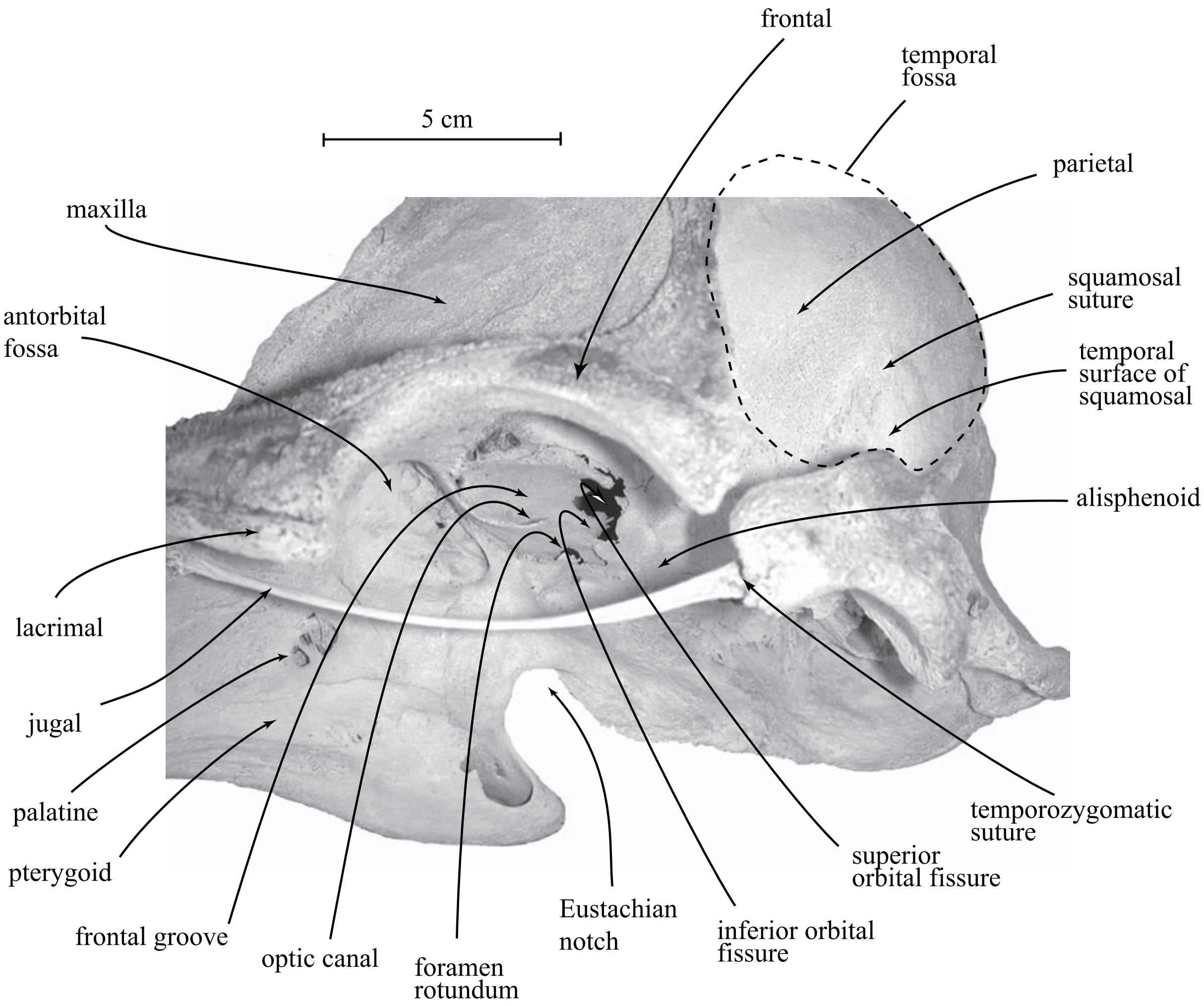


FIGURE 32. Skull of adult specimen, orbit, left, lateral view (USNM 501197).

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This project stemmed from a suggestion made in the early 1970s to the senior author by Lawrence Barnes at the Los Angeles County Museum. Barnes suggested a detailed osteological study of *Tursiops* aimed at standardizing the anatomical terms.

This work began as a volunteer project for Terrell Stoessell Henke in 1993 while she was a student at the Thomas Jefferson High School for Science and Technology in Alexandria, Virginia. Terrell scanned into the computer the cranial osteology sections of the *Nomina Anatomica* and the *Nomina Anatomica Veterinaria*, put them in a spreadsheet and then correlated the terms with material from the anatomical literature.

The success of this work depends on the illustrations and we have been extremely fortunate to obtain illustrations and photographs. Trudy Nicolson began by illustrating the adult skull (Figures 1–5), and the disarticulated neonate skull (Figures 7–10, 12–24, 27). Karolyn Darrow illustrated the tympanoperiotic, auditory ossicles, and detailed views of the sectioned skull (Figures 25f–q, 26, 28, 29). Both of these illustrators were extremely helpful in ensuring that the orientations of the material were correct. Mollie Oremland illustrated the medial view of the mandible (Figure 15d) and the hyoids (Figure 11). John Steiner photographed the tympanoperiotic and the sectioned and intact skulls (Figures 6a–f, 25a–e,r–v, 30–32). Parts g–i of Figure 6 are from Kellogg, 1928).

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The utility of a dictionary is dependent for a large part on its consistency. The authors, although they spoke the same language, were working in different dialects of it. We humbly appreciate the excellent editing that we received from the recently renovated Smithsonian Institution Scholarly Press under the able leadership of Publications Manager Ginger Strader. This work owes a lot to the hands-on editorship of Publications Specialist Meredith McQuoid and freelance copyeditor Fran Aitkens.

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Appendix A

HISTORICAL TERMINOLOGY OF THE CRANIAL NERVES

The cranial nerves are of historical and nomenclatorial significance because they have played a major role in determining the homologies and evolutionary development of the bony framework of the skull. It is helpful to review the historical nomenclature of the cranial nerves in order to understand their part in the overall naming of the bony structures surrounding them. In many cases the cranial nerves were given numbers according to their position in the longitudinal axis of the brain, and the original numbers are retained in this appendix.

Willis, Thomas. 1664. *Cerebri anatome*. Londini [London]: Tho. Roycroft for Jo. Martyn & Ja. Allestry.

1. Olfactory
2. Optic
3. Common motores oculorum
4. Pathetici
5. Trigeminal
6. Abducens
7. Facial + auditory
8. Glossopharyngeal + pneumogastric + accessory
9. Great hypo-glossal

A Society of Gentlemen in Scotland [Bell, A., C. Macfarquar, and W. Smellie]. 1771. "Anatomy." *Encyclopedia Britannica*, 1st ed., 1:145–310, pls. xiii–xxi. [Cranial nerve data extracted from pp. 248–250, pl. xviii.]

First pair: Olfactory
Second pair: Optic
Third pair: Motor oculi
Fourth pair: Pathetici
Fifth pair: [Trigeminal] (opthalmic, maxillaris superior, maxillaris inferior)
Sixth pair: [Abducens]
Seventh pair: (Portio mollis = vestibulocochlear, portio dura = facial proper)
Eighth pair: Vagus + [glossopharyngeal]
Ninth pair: [Hypoglossal]
Tenth pair: [Spinal accessory]

Handy, Washington R. 1854. "Nerves of Encephalon [Cranial Nerves]" in *A Text Book of Anatomy, and Guide in Dissections for the Use of Students of Medicine and*

Dental Surgery, pp. 420–425. Philadelphia: Lindsay & Blakiston.

First pair, or Olfactory nerves
Second pair, or Optic
Third pair, or Motores Oculorum
Fourth pair, Pathetici or Trochleares
Fifth pair, Trifacial or Trigemini [opthalmic, superior and inferior maxillary]
Sixth pair, Motores Externi or Abducens Oculi
Seventh pair, Portio Dura [facial] and Portio Mollis [auditory]
Eighth pair, Glosso Pharyngeal, Pneumogastric or par vagum, Spinal accessory.
Ninth pair, Lingual or Hypoglossal

Chaveau, A., S. Arloing, and G. Fleming (eds.). 1885. *The Comparative Anatomy of the Domesticated Animals*. 2nd ed., revised and enlarged. New York: D. Appleton and Company, trans., ed. by Fleming from the French 2nd ed. of 1872. [includes man, horse, cow, sheep, dog; Fleming omitted rabbit and dromedary.]

1. Olfactory
2. Optic
3. Common motores oculorum
4. Pathetici
5. Trigeminal
6. Abducens
7. Facial
8. Auditory
9. Glossopharyngeal
10. Pneumogastric
11. Accessory
12. Great hypo-glossal

Whitney, W. D. (ed.). 1889. *The Century Dictionary and Cyclopedia*, 2:1330. New York: The Century Co.

Olfactory
Optic
Motor oculi
Pathetic (trochlear)
Trigeminal (trifacial)
Abducent
Facial
Auditory
Glossopharyngeal
Pneumogastric
Spinal accessory
Hypoglossal

Testut, L. 1905. "Cranial Nerves" in *Traite d'Anatomie Humaine* 5th ed., 2:862–940. Paris: Octave Doin. [4 volumes: 1. Osteologie, arthrologie, myologie (vi + 1022 pp., 830 figs.); 2. Angeiologie, system nerveux central (iv + 988 pp., 836 figs.); 3. System nerveux peripherique, les organs des sens, l'appareil de la respiration et de la phonation.; 4. L'appareil de la digestion, l'appareil uro-genital, l'embryologie.]

1. Olfactif
2. Optique
3. Moteur oculaire commun
4. Pathetique
5. Trijumeau: trijumeau sensitif, trijumeau moteur
6. Moteur oculaire externe
7. Facial: nerf facial proprement dit, nerf intermediare de Wrisberg,
8. Auditif (acustique): vestibulaire, cochleaire
9. Glosso-pharyngien
10. Pneumogastrique
11. Spinal
12. Grand hypoglosse

Kingsley, J. S. 1912. *Comparative Anatomy of Vertebrates*, pp. 165–177. London: John Murray.

I. Olfactory
II. Optic
III. Oculomotorius
IV. Trochlearis
V. Trigeminal (opthalmic, maxillary, mandibular)
VI. Abducens
VII. Facial
VIII. Acustic [sic]
IX. Glossopharyngeal
X. Vagus
XI. Accessory
XII. Hypoglossal

Parsons, Frederick Gymer. 1911. "Nerve." *Encyclopedia Brittanica*, 11th ed., 19:394–400.

Olfactory
Optic
Oculomotor (motor oculi)
Trochlear (pathetic)
Trigeminal (trifacial)
Abducens
Facial
Auditory
Glosso-pharyngeal
Vagus (pneumogastric)
Spinal accessory
Hypoglossal

Hardesty, I. 1933. "The nervous system" pp. 1000–1038 in *Morris' Human Anatomy*, 9th ed., Philadelphia: P. Blakiston's Sons and Co. [ex Goss, 1959. p. 1088: Hardesty separated the masticatory nerve from the trigeminal, glossopalatine from the facial, equilabratory from the acoustic.]

Larsell, O. 1942. "The Nervous System," in J. P. Schaeffer, *Morris' Human Anatomy*, 11th ed., pp. 856–1178. Philadelphia: Blakiston Co. [Cranial nerve data is from pp. 1080–1081.]

I. Olfactorius
II. Opticus
III. Oculomotorius
IV. Trochlearis
V. Trigeminus
VI. Abducens
VII. Facialis
VIII. Acusticus
IX. Glossopharyngeus
X. Vagus
XI. Accessorius
XII. Hypoglossus

Appendix B

SKULL MEASUREMENTS FOR DELPHINIDS

One of the reasons for defining skull landmarks is to provide the ability to take consistent measurements in morphometrics analysis. Over the years we have compiled a list of the measurements that have proved of value. This list is taken primarily from Perrin (1975:9–10).

1. Condylobasal length from tip of rostrum to hindmost margin of occipital condyles.
2. Length of rostrum from tip to line across hindmost limits of antorbital notches.
3. Width of rostrum at base along line across hindmost limits of antorbital notches.
4. Width of rostrum at 60 mm anterior to line across hindmost limits of antorbital notches.
5. Width of rostrum at midlength.
6. Width of premaxillaries at midlength of rostrum.
7. Width of rostrum at 3/4 length, measured from posterior end.
8. Distance from tip of rostrum to external nares (to mesial end of anterior transverse margin of right naris).
9. Distance from tip of rostrum to internal nares (to mesial end of posterior margin of right pterygoid).
10. Greatest preorbital width.
11. Greatest postorbital width.
12. Least supraorbital width.
13. Greatest width of external flares.
14. Greatest width across zygomatic processes of squamosal.
15. Greatest width of premaxillaries.
16. Greatest parietal width, within postemporal fossae.
17. Vertical external height of braincase from midline of basisphenoid to summit of supraoccipital, but not including supraoccipital crest (not illustrated).
18. Internal length of braincase from hindmost limit of occipital condyles to foremost limit of cranial cavity along midline.
19. Greatest length of left posttemporal fossa, measured to external margin of raised suture.
20. Greatest width of left posttemporal fossa at right angles to greatest length.
21. Major diameter of left temporal fossa proper.
22. Minor diameter of left temporal fossa proper.
23. Projection of premaxillaries beyond maxillaries measured from tip of rostrum to line across foremost tips of maxillaries visible in dorsal view.

24. Distance from foremost end of junction between nasals to hindmost point of margin of supraoccipital crest.
25. Length of left orbit from apex of preorbital process of frontal to apex of postorbital process.
26. Length of antorbital process of left lacrimal.
27. Greatest width of internal flares.
28. Greatest length of left pterygoid.
29. Greatest width of anterior overhang of supraoccipital crest.
30. Greatest length of bulla of left tympanoperiotic.
31. Greatest length of periotic of left tympanoperiotic.
32. Length of upper left tooth row from hindmost margin of hindmost alveolus to tip of rostrum.
33. Number of teeth, upper left.
34. Number of teeth, upper right.
35. Number of teeth, lower left.
36. Number of teeth, lower right.
37. Length of lower left tooth row from hindmost margin of hindmost alveolus to tip of mandible.
38. Greatest length of left ramus.
39. Greatest height of left ramus at right angles to greatest length.
40. Length of left mandibular fossa, measured to mesial rim of internal surface of condyle.
41. Deviation of skull from symmetry in dorsal view, in degrees.

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