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GRADUATE STUDIES

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candidate for the MASTER OF SCIENCE IN DENTISTRY **degree.**

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Date April 29, 1982

COMPARATIVE EVALUATION OF THE CRANIOFACIAL ANATOMY OF THE BOTTLENOSE DOLPHIN (TURSIOPS TRUNCATUS)

by

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Submitted in partial fulfillment of the requirements

for the Degree of Master of Science in Dentistry

Department of Orthodontics

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COMPARATIVE EVALUATION OF THE CRANIOFACIAL ANATOMY OF THE BOTTLENOSE DOLPHIN (TURSIOPS TRUNCATUS)

Abstract

by

ELIZABETH SUSAN BUJACK

The unusual craniofacial morphology of bottlenose dolphin (Tursiops truncatus) is of interest because it relates to a "brachycephalized" cranium in conjunction with enlarged cerebral hemispheres, thus sharing a similar circumstance with the craniofacial situation seen in Homo. Unlike the human skull, however, bimaxillary reduction is not a feature in the dolphin. Furthermore, the olfactory apparatus, which is believed to play a basic role in facial design and growth in man and other mammals, is lacking altogether in the dolphin. A major re-design in the nasomaxillary components of the dolphin skull has occurred in which a nearly total disjunction between the oral and breathing parts of the face is seen. Further, fundamental, postural and environmental differences exist that markedly offset the basis for difference in facial design.

This study is a comparative evaluation of the anatomical patterns of the craniofacial complex in these two species in the light of these similarities and differences underlying facial form

and pattern. In addition, a third species is also included for comparison, the Pit Bull (Canis). The latter also has a "brachycephalized" cranium, as in both man and the dolphin. Like the human skull, the bulldog skull also has a shortened facial complex but, unlike the other two species, possesses a well developed olfactory apparatus.

The craniofacial complex of Tursiops is rearranged considerably. Repositioning of bones, and also reduction of apparently nonessential structures, has occurred. The maxilla, premaxilla, and vomer overlie one another, and their posterior parts have "rotated" superiorly and posteriorly to become nearly contiguous with the occipital bone. The latter has expanded superiorly and anteriorly to a considerable extent. The frontal bone is reduced to a narrowed crest, and the parietals have become positioned laterally, as compared to the pattern in other mammals.

These bony rearrangements relate to several functional circumstances. Existence in a marine environment has allowed the design of the skull to diverge without regard to biomechanical constraints present in terrestrial forms. The absence of olfactory tracts and bulbs has released the nasal and midfacial area from an otherwise obligatory relationship and has allowed the nasal region to rotate superoposteriorly into a vertical placement in the midface.

The unprecedented divergence of the nasal area in the dolphin has several implications. Even though there is considerable cerebral enlargement, the orbits are prevented from assuming a more anterior-projecting rotation due to the intervening overgrowth of the nasal area into the broadened interorbital region. As mentioned, the dolphin's maxilla and premaxilla have elongated posteriorly as well as anteriorly.

These composite anatomic configurations are difficult to fully explain by currently understood models of facial growth. The growth of the cranial floor itself does not seem to account for the divergence between oral and nasal areas. Also there is no nasal septum to otherwise "provide displacement" for the protruding muzzle.

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DEDICATED

TO

My parents, whose continued love, caring and support made my education possible.

TABLE OF CONTENTS

	Page
ABSTRACT	ii
ACKNOWLEDGEMENTS	v
DEDICATION	viii
LIST OF TABLES	ix
LIST OF PLATES	x
INTRODUCTION	1
LITERATURE REVIEW	4
METHODS AND MATERIALS	8
DESCRIPTION OF THE SKULL OF *TURSIOPS TRUNCATUS*	11
DISCUSSION	56
SUMMARY AND CONCLUSIONS	63
LITERATURE CITED	66

LIST OF TABLES

Table | Page

I. Age of Specimens 9

LIST OF PLATES

Plate		Page
I.	Skull of Tursiops truncatus--lateral view	13
II.	Skull of Tursiops truncatus--superior view	16
III.	Skull of Tursiops truncatus--posterior view	19
IV.	Skull of Tursiops truncatus--ventral view	22
V.	Skull of Tursiops truncatus--endocranial view	27
VI.	Mandible of Tursiops truncatus--superior view	30
VII.	Mandible of Tursiops truncatus--lateral view	32
VIII.	Lateral view of skulls	36
IX.	Superior view of skulls	41
X.	Posterior view of skulls	43
XI.	Ventral view of skulls	48
XII.	Superior view of mandibles	52
XIII.	Lateral view of mandibles	54

INTRODUCTION

As mammals, the bottlenose dolphins (Tursiops truncatus) are presumably subject to the same regulatory mechanisms common to mammals in general. However, functional existence in a marine environment, the possession of greatly enlarged cerebral hemispheres, a horizontal (piscine) body disposition, craniofacial alterations adapted to a special mode of breathing, and changed emphasis on certain of the special senses, all relate to corresponding morphologic and morphogenic changes in facial and cranial form and pattern. In regard to these adaptive anatomic adjustments, some of the controlling relationships involved in facial development also appear to have been substantially modified or even lost altogether. This study was undertaken to attempt to gain added insight into the biological basis for the nature of craniofacial relationships in light of the unusual mode of functional adaptation in this unique species.

In Tursiops, the uncommon biological events that have occurred relate directly to a series of linked changes in facial configuration. The first association, as in man, is the dolphin's possession of an unusually large cerebrum. Also Tursiops (as other Cetacea) is a large brained mammal which has strictly horizontal posture alignment. Further, several functional components

in the dolphin have been modified or deleted. In the midface, an actual disjunction of the nasal and oral regions has occurred so that the anatomic and developmental relationships between them have become substantially changed in comparison to other mammalian groups. The olfactory bulbs and nerves are essentially lacking in the dolphin and, hence, a fundamental biological association in establishing cranial form and facial design has been basically modified. Ocular function has played an important role in this species' phylogeny, and a fish-like positioning of the orbits relates to marine habitat and in turn, to facial design and development. All of these various factors are interrelated, and the composite has established the basis for the unique craniofacial composite of the dolphin.

The purpose of this study is to examine these relationships, as well as other morphologic characteristics peculiar to the craniofacial structure of Tursiops truncatus, while evaluating them in the light of currently understood functional mechanisms of mammalian facial design and morphogenesis. Craniofacial comparisons will also be made with two other species, Canis familiaris (Pit Bull) and Homo sapiens. All three species exhibit a relatively high degree of "brachycephalization" in comparison to other mammals. The dolphin and human are particularly outstanding among mammals because of their marked degree of cerebral enlargement and rounded, bulbous head form. Both the

bulldog and human are short-faced mammals in contrast to the long midfacial configuration of the dolphin. These three species exhibit a graded extent of olfaction. Tursiops, without olfactory tracts and bulbs, is apparently totally lacking in the sense of olfaction. Homo does have a functional olfactory apparatus, although it is limited in comparison to Canis, which posses the most acute and proportionately well-developed olfactory complex of the three. In essence, the dolphin, Pit Bull, and human skulls offer a varied degree of anatomic and functional development which can be compared and contrasted in the evaluation of the unusual craniofacial pattern of Tursiops truncatus.

LITERATURE REVIEW

The available investigations on the skull of Tursiops truncatus describe a "telescoping" effect in the phylogeny of the skull in this species (Miller, 1923; Kellogg, 1928). This term connotes a backward and upward rotation of the face, including the maxilla, premaxilla, and vomer, or (depending on taxonomic group) a forward and upward rotation of the posterior components of the cranium (the occipital area). Such movements have presumably occured at the expense of the mid-cranial bones, including the parietals and frontals, which have become pushed laterally. The fused frontal bones are reduced to a narrow crest. Of the two living suborders of Cetacea, each has its own predominant form produced by this telescoping effect. The Mysticeti (baleen whales) are characterized by the posterior elements coming forward, while the Odontoceti (toothed whales) are characterized by a rotation of the anterior components posteriorly (Miller, 1923). Tursiops, being a member of the suborder Odontoceti, exhibits the latter type of cranial telescoping.

Enlow (1973) points out that, among mammals in general, the neutral axis of nasomaxillary development follows an approximately perpendicular course to the olfactory bulbs. In some

families of Cetacea (the suborder Mysticeti), the olfactory apparatus is present although rudimentary (Lillie, 1910). In Tursiops truncatus, a member of the suborder Odontoceti, Langworthy (1932) could find no remnants of the olfactory nerves or bulbs. Addison (1915) also states that, while possessing the tertiary neural apparatus (paleocortical division of rhinic lobe), dolphins entirely lack olfactory tracts and bulbs. Morgane et al. (1971) concur with Addison (1915) in regard to the presence of the tertiary neural components. Thus the basis for the "olfactory-facial" relationship described by Enlow is necessarily compromised among the dolphins.

Another morphologic relationship that exists between facial configuration and neurocranial form is that of orbital position. In conjunction with enlargement of the temporal and frontal lobes of the cerebrum, the orbits are rotated into more medial positions, thus decreasing the interorbital width (Enlow, 1973). In the dolphin, however, cerebral enlargement is not accompanied by a convergence of the orbits toward the midline; they are located in a fish-like position on the sides of the head. The orbits have either rotated laterally, or were prevented from a more medial alignment by the telescoping midface.

While the intelligence of the dolphins is subject to much discussion, both in documented studies and popular narratives, it is well substantiated that Tursiops possesses one of the highest

levels of intellect in the animal kingdom (Slijer, 1962). In fact, the mental process of the dolphin is believed to rank above most anthropoids, and by many accounts is second only to Homo sapiens (Slijer, 1962). Slijer (1962) also has shown that the bottlenose of the dolphin has one of the largest brain size to body ratios of any mammal, exceeded only by man.

Lastly, another noticeable feature of the Cetacean skull which has been described in the literature (Kuckenthal, 1908; Miller, 1923) is the asymmetry of the skull about the bones associated with the nasal region. The right half of the midfacial region is noticeably larger than the left half. Specifically this involves the presphenoid, ectethmoid, premaxilla, maxilla and nasal bones. This asymmetry is not a universal finding among all Cetacea, but is pronounced in Tursiops truncatus (Kuckenthal, 1908). The reason for this dissimilarity is not known. However, several explanations have been advanced to clarify this occurrence. Lillie (1910) postulated that the asymmetry in Odontoceti allowed the swallowing of large prey. The epiglottis, arytenoid cartilages, and laryngeal muscles in members of this group, all lie left of center, forming a larger swallowing area on the right. This pattern continues anteriorly to include the facial bones. Thompson (1942) maintained that the asymmetry was due to uneven hydropressure resulting from the rotary action of the tail

while swimming. However, Slijer (1962) found that the tail of the dolphin moves in a vertical plane while swimming and is not accompanied by any rotary motion. Still a third hypothesis is put forth by Evans and Prescott (1962). These investigators state that the asymmetry is a consequence of unequal nasal pressure involved in sound production.

METHODS AND MATERIALS

This investigation utilized nine skulls, not including mandibles, of Tursiops truncatus obtained from the Smithsonian Institutes, Washington, D.C. The ages of the skulls (Table I) were estimated (by Smithsonian) according to dental characteristics.

Division into five growth stages was used:

1. Infant; less than one year post natal
2. Approximately 1/3 active growth completed
3. Approximately 1/2 active growth completed
4. Approximately 2/3 active growth completed
5. Adult; active growth completed.

Analyses

An anatomic description will be made for each of the principal bones of the skull. The relationships of all the bones to each other as a functional composite will then be presented. These anatomic descriptions were made from gross examination of the dried skulls as well as radiographic headfilms of the same specimens.

Radiographic Method

A standard cephalometer was used to radiograph the dry skulls. The specimens were positioned on a flat board with the muzzle supported during exposure. All skulls were radiographed in two planes, lateral (right to left) and ventral to dorsal.

TABLE I

AGE OF SPECIMENS

Specimen Code Numbers	Age (years)
1	1
2	1
3	1.5
4	2
5	3
6	4
7	4
8	12
9	18

Exposure times were determined by a series of trials with a dry skull. The radiographs were taken on 14" x 17" film (Kodak XRP-1 film, Eastman Kodak Company, Rochester, New York) at 0.25 seconds, 15 milliamperes and 85 kilovolts. A standard chest x-ray cassette was used for film exposure. The source-to-film distance was held constant at 5 feet. All films were developed with an automatic processor.

The measurements were taken directly from radiographs. Due to the lack of actual morphogenic evidence (vital dyes, use of implants) providing information on directional growth fields, all growth relationships are with respect to anatomic pattern and not actual morphogenic process. As will be evaluated in the discussion, the essentially total lack of the knowledge of the dynamics of growth in the dolphin would make interpretation of conventional cephalometric analyses questionable.

DESCRIPTION OF THE SKULL OF TURSIOPS TRUNCATUS

The skull of the bottlenose dolphin shows one of the most extreme forms of cranial "telescoping" among all the Cetacea (Miller, 1923). The vomer premaxilla, maxilla, and nasal bones have become shifted, in relative position, superiorly and posteriorly over the "frontal" area to a position nearly contiguous with the occipital, and the frontal bone itself is reduced to a narrow ribbon across the calvaria (Plate I). Indeed, even the brain of Tursiops truncatus has rotated into a position overlying the anterior end of the vertebral column. Especially evident is a rotation of the forebrain ventrally under the cerebrum. As previously noted, among most large-brained species, the growth of the cerebrum relates to an anterior rotation of the orbits toward the midline. However, with the nasal and midfacial regions positioned as far posteriorly as the constraints of the cranial boundaries appear to allow, the orbits have been prevented from a medial direction of realignment. The orbits have seemingly been "squeezed" laterally.

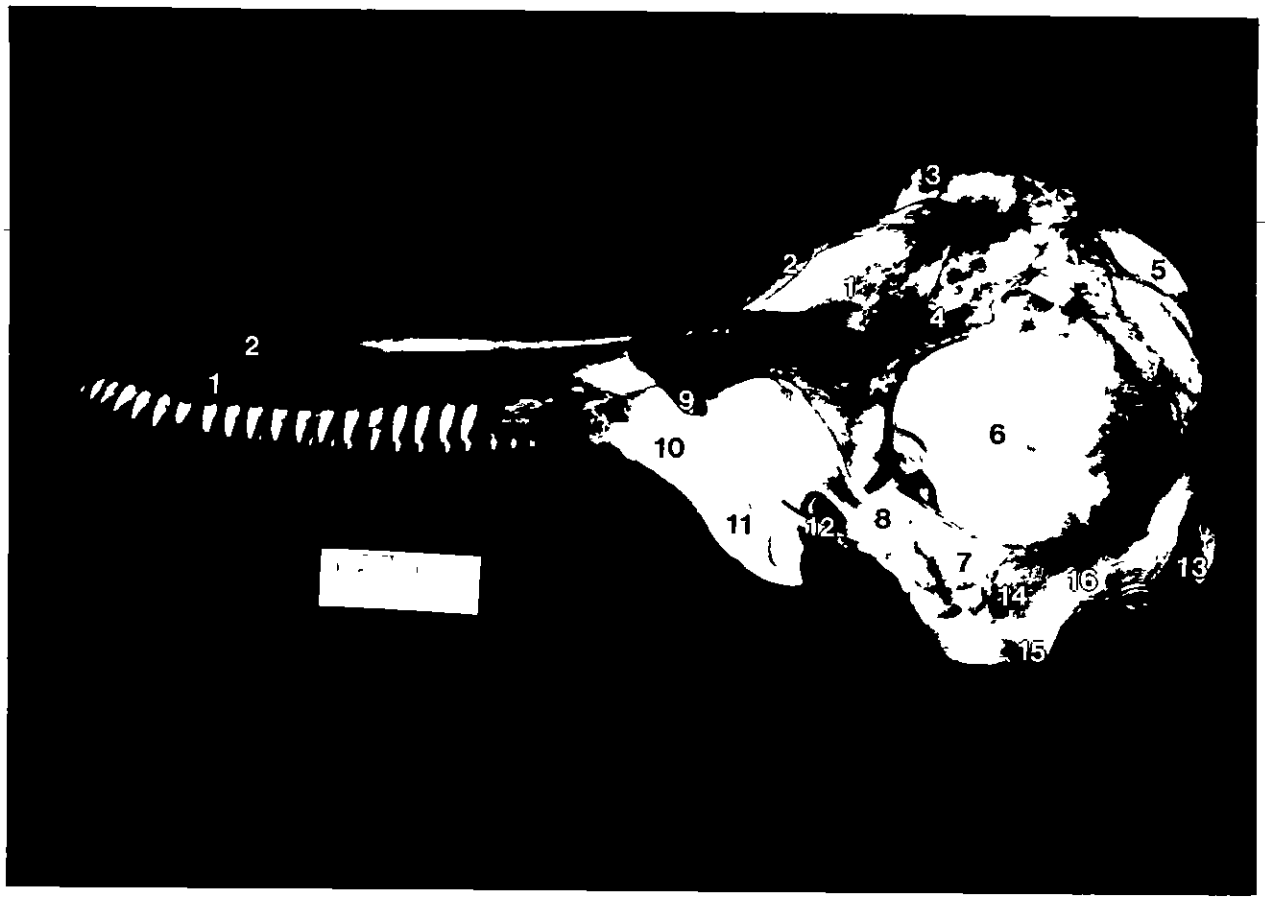
Spreading posteriorly over the frontal bone, the maxilla also becomes flattened laterally to overlay a pronounced supraorbital crest. The premaxilla is not, as in other mammals, restricted merely to an anterior facial position, but rather ex-

PLATE I

SKULL OF TURSIOPS TRUNCATUS

LATERAL VIEW

1. Maxilla
2. Premaxilla
3. Nasal
4. Frontal
5. Occipital
6. Parietal
7. Squamosal
8. Zygoma
9. Lacrimal
10. Palatine
11. Pterygoid
12. Jugal
13. Occipital Condyle
14. Groove for External Auditory Meatus
15. Lamboid Crest
16. Exoccipital


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tends along with, and dorsal to, the maxilla. The vomer is a long, conical bone which not only divides the nasal chamber into two halves, but continues along anteriorly to lie "sandwiched" between the two maxillae.

The nasal passages have become rotated superiorly and posteriorly to a point nearly perpendicular to the jaws. What appears to be a snout overlying the palate no longer functions as an actual nasal passageway. It is, rather, a sinus. The small paired nasal bones are positioned caudal to the nasal opening, which is located dorsally nearly at the vertex of the skull. Rectangular, blade-like extensions of the premaxilla flank the nasal apertures on either side.

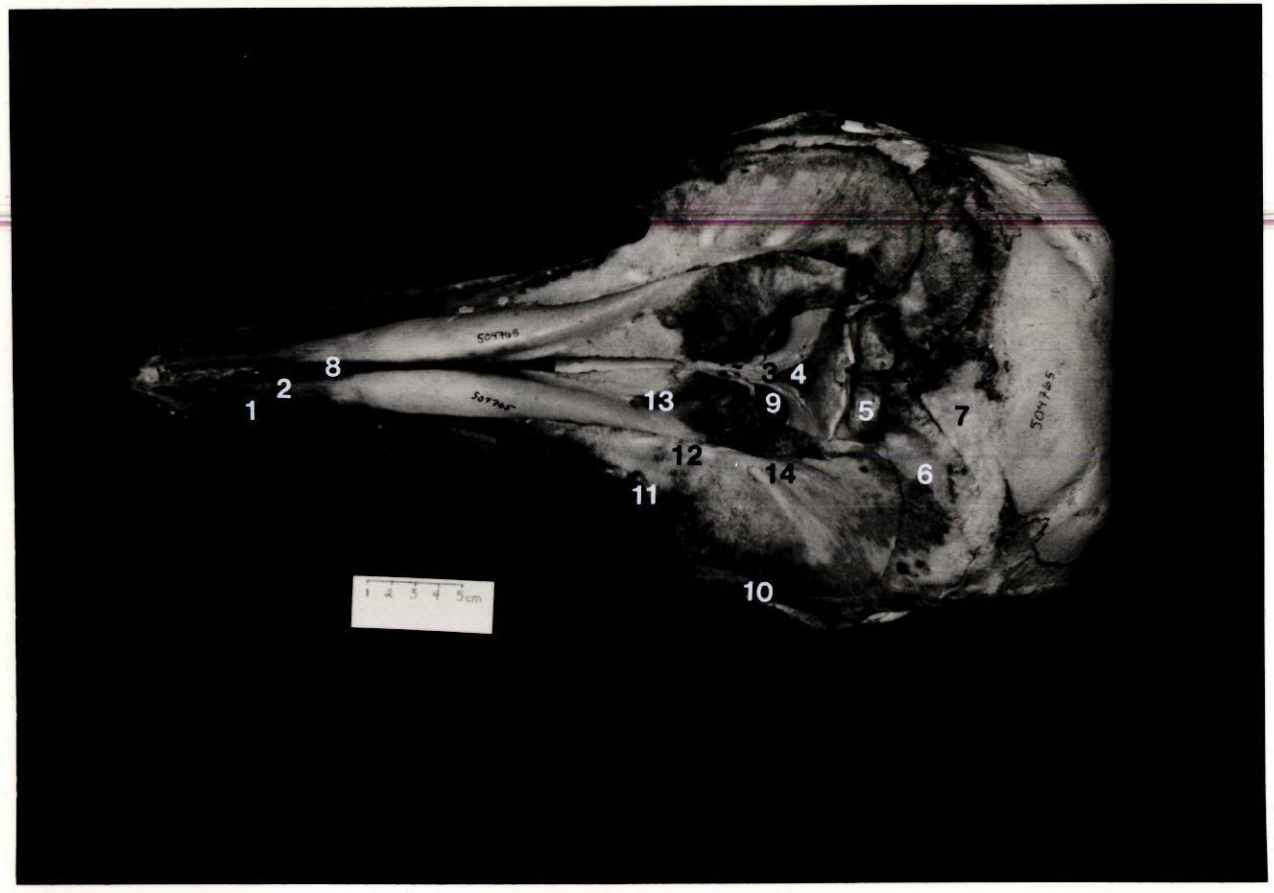
From the superior surface of the skull (Plate II), the vomer, presphenoid, and ectethmoid can be seen extending up the nasal midline and rising to meet the nasal bones. When viewed from the superior aspect, a striking feature of the dolphin skull is the roughly triangular shape formed by the long, protruding, seemingly fragile "rostrum" (muzzle) offset against a wide, rounded, and robust cranium. The maxilla and premaxilla are also roughly triangular in shape and fan out at their proximal aspects upon the underlying frontal bone. A narrow sutural line, the mesiorostral groove, is interposed between the maxillary and premaxillary halves and terminates at the narial openings. Just medial to the supraorbital crest is a pronounced antorbital notch

PLATE II

SKULL OF TURSIOPS TRUNCATUS

SUPERIOR VIEW

1. Maxilla
2. Premaxilla
3. Vomer
4. Ectethmoid
5. Nasal
6. Frontal
7. Occipital
8. Mesiorostral groove
9. Nares
10. Supraorbital crest
11. Antorbital notch
12. Infraorbital foramen
13. Premaxillary foramen
14. Posterior maxillary foramen


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(Rankin, 1956), formed by the maxilla and frontal bone. Medial to the antorbital notch, on each maxillary and premaxillary half, are several foramina. The most anterior and medial of these is the premaxillary foramen. Lateral to this is the infraorbital foramen. Some smaller, irregularly placed foramina lie posterior, continuing to the most prominent one, the posterior maxillary foramen. The occipital bone is not merely confined to the ventro-posterior boundaries but slopes superiorly to meet the substantially narrowed, bow-shaped frontal bone. Curving inferiorly and laterally, the frontal bone underlies the maxilla and forms the most lateral portion of the supraorbital crest.

When the skull of Tursiops truncatus is viewed from a superior aspect, it is then that the definite asymmetry of the skull becomes noticed. At approximately two-thirds the distance from the tip of the snout, the mesiorostral groove begins a cant to the left. This deviation from the midline is also evident in the vomer, presphenoid, ectethmoid, and nasal bones. The resultant asymmetry produces right-halfed bones which are larger than their left counterparts.

From the posterior aspect of the skull (Plate III), a prominent feature is the broad and rugged expanse of the cranium as a whole. The rounded, brachycephalic nature of the skull is most apparent when considered separately from the long, slender muzzle. Again, the occipital bone is positioned so as to

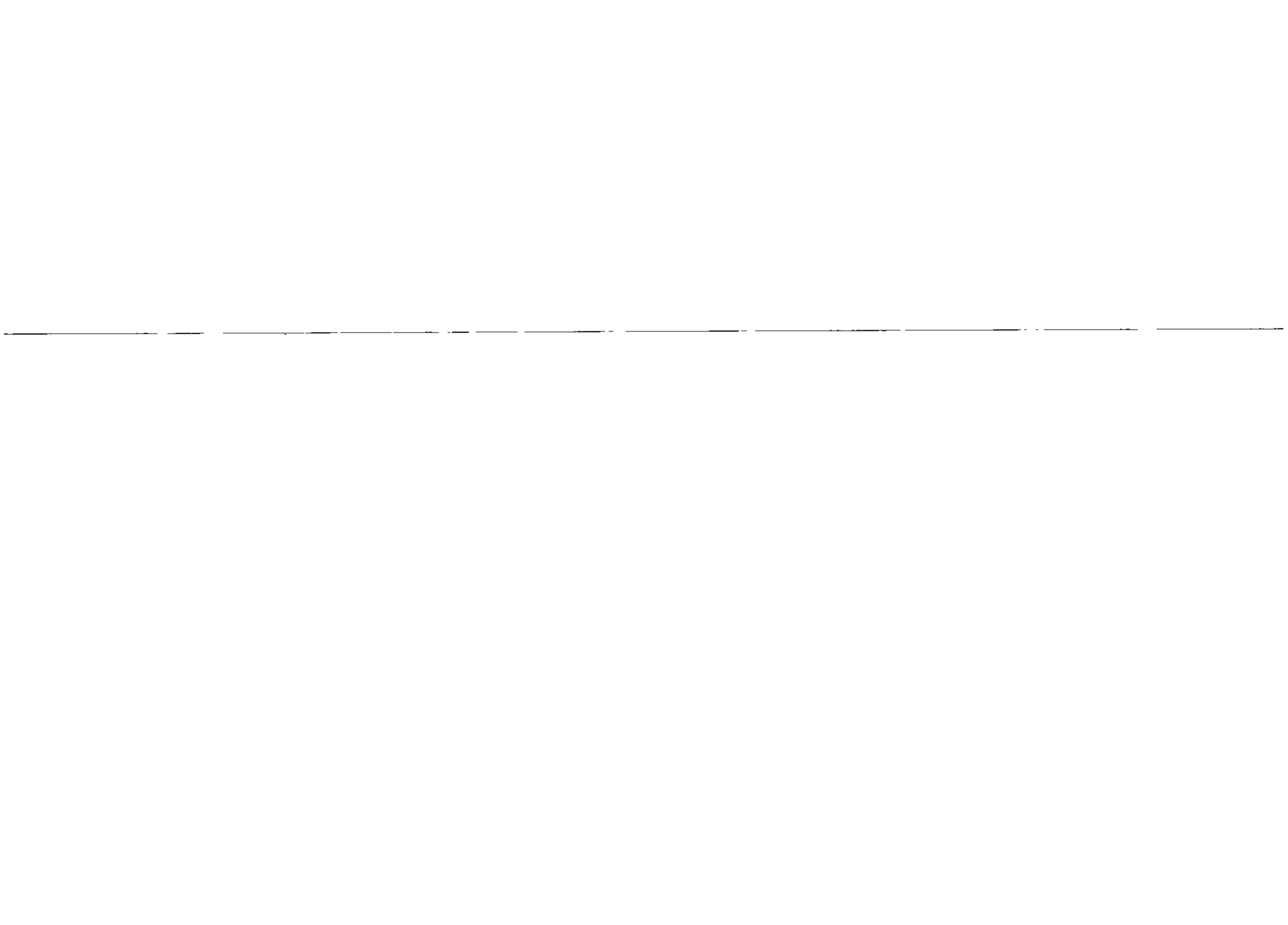
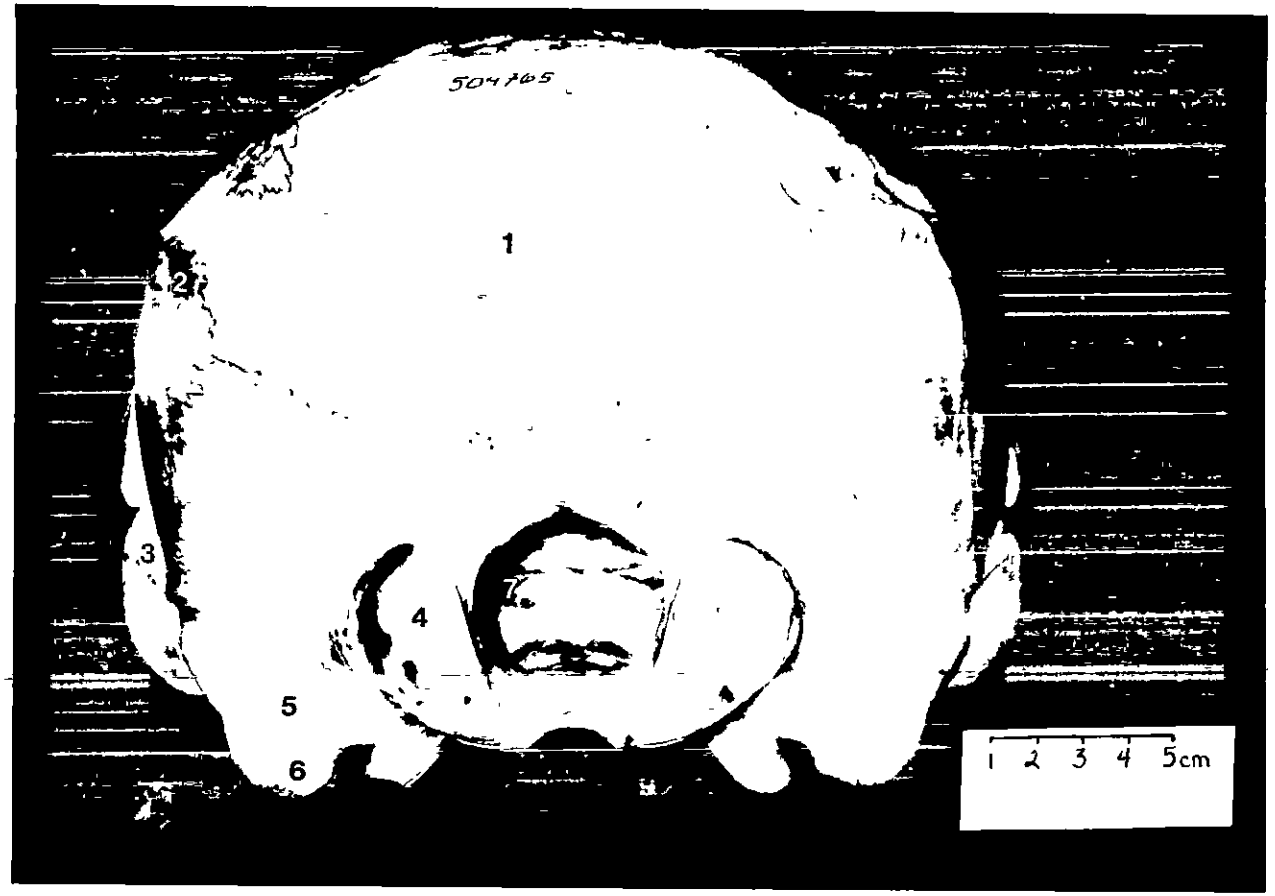


PLATE III

SKULL OF TURSIOPS TRUNCATUS

POSTERIOR VIEW

1. Occipital
2. Parietal
3. Zygoma
4. Occipital condyle
5. Paraoccipital process
6. Lamboid crest
7. Foramen magnum


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overlay nearly the entire posterior of the skull to the vertex. The parietals, meanwhile, are placed laterally and have come to occupy a relatively unobtrusive portion of the skull. The paraoccipital process of the occipital, along with the zygomatic process of the squamosal, curve laterally and anteriorly to form the broadest expanse of the skull. Flanking the foramen magnum, are the ovoid occipital condyles, and lying lateral and inferior to each is the exoccipital area continuing and terminating in the curved lamboidal crest of the paraoccipital process (Rankin, 1956)

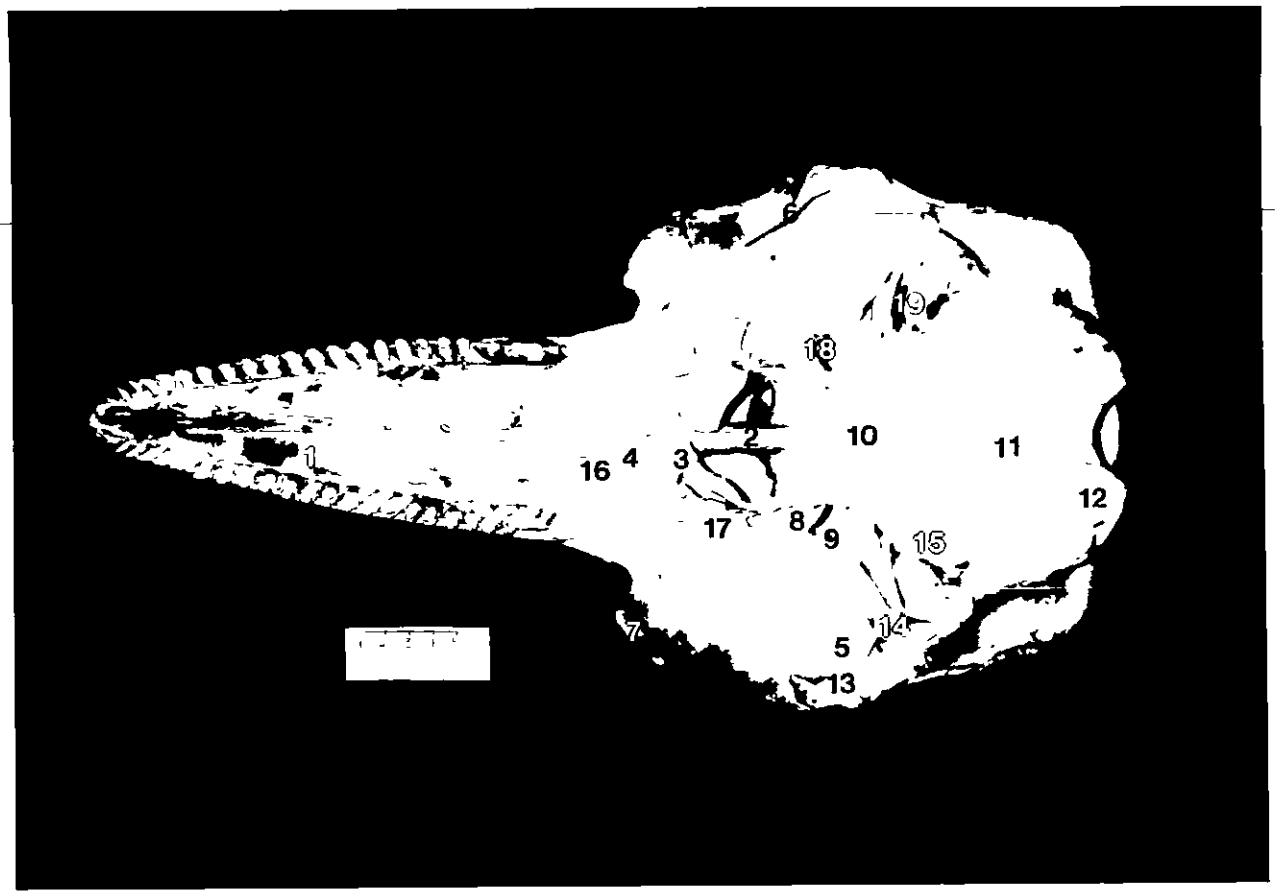
The ventral surface (Plate IV) is characterized by numerous fossae, foramina, crests, and ridges in comparison with the other, relatively smooth areas of the skull. From the occipital condyles, the occipital bone then flattens to its junction with the basioccipital which extends along the midline of the skull to the basisphenoid portion of the sphenoidal complex. Laterally, the basioccipital curves ventrally to form the falcate process of the basioccipital. Again, at the midline one encounters the basisphenoid and its sutural attachments with the vomer and pterygoid bones. The pharyngeal opening to the nasal chambers are visible from this view, with the vomer forming the dividing septum. The sinus-filled corpus of the pterygoid bone lies ventral to the vomer, and the medial walls of the pterygoid, which are shelf-like extensions, rise laterally. Continuing dorsally on

PLATE IV

SKULL OF TURSIOPS TRUNCATUS

VENTRAL VIEW

1. Maxilla
2. Vomer
3. Pterygoid
4. Palatine
5. Frontal
6. Jugal
7. Lacrimal
8. Orbitosphenoid
9. Alisphenoid
10. Basisphenoid
11. Basioccipital
12. Occipital condyle
13. Glenoid fossa
14. Falciform process
15. Falcate process
16. Palatine foramen
17. Antorbital foramen
18. Optic foramen
19. Composite foramen
    - Foramen ovale
    - Stylomastoid foramen
    - Posterior glenoid foramen
    - Posterior lacerated foramen
    - Orifice for eustachian tube


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the medial wall of the pterygoid are the paried palatine bones which project rostrally to contact the paired maxillae. At their dorsal borders, the palatine bones also contact the maxillae, and at their dorsoposterior border adjoin the orbital roof of the frontal. The inner surface of the orbital roof is lined with numerous undulating concavities and is pierced by several foramina. The most anterior and most prominent is the antorbital fossa, which is a collecting area for numerous small foramina. Through the anterior wall of this fossa pass the infraorbital and maxillary branches of the trigeminal nerve. The posterior wall of the fossa transmits small nerves which enter into the nasal chamber. The dorsal roof of the antorbital fossa opens onto the dorsal surface of the maxilla as a series of smaller foramina.

Posterior to the antorbital fossa is the optic foramen, through which passes the corresponding nerve. The optic foramen is bordered anteriorly by the orbitosphenoid process and posteriorly by the alisphenoid which articulates with the parietal bone. The alisphenoid contacts in its laterosposterior aspect the falciform process of the squamosal which continues laterally to join the oval-shaped, and scalloped glenoid fossa, the articulation for the mandibular condyle. The glenoid fossa curves anteriorly and from a lateral projection, gives rise to the slender jugal. The jugal forms, in essence, the only bony floor to the orbit and has its anterior articulation on the medial aspect of the lacrimal bone.

Posterior and medial to the glenoid fossa is the falciform process of the squamosal. This thin projection of bone, depending on specimen variation, overlies either one large composite foramen, or a cluster of smaller foramina. This composite is comprised of the foramen ovale, stylomastoid foramen, the orifice of the eustachian tube, and the posterior glenoid and posterior lacerated foramina. Just caudal to this network is the rather inconspicuous condylar foramen. The foramen rotundum is located anterior and medial to this network and lies in the posterior aspect of the alisphenoid. Curving behind the glenoid fossa is the scallop-shaped lamboid crest, between which lies the groove for the passage of the eustachian tube.

On the ventral aspect of the facial complex can be seen the paired palatal surfaces of the maxillae. Again the two maxillary halves are long, slender, and roughly triangular in configuration. In portions of the mid-palatal suture, the vertex of the vomer can be seen. At the juncture of the maxilla and the palatine bone, several small palatine foramina are positioned throughout the bone. Each quadrant in the dental arch houses between twenty and twenty-three teeth, depending on the individual specimen. The teeth are all cone-shaped, and other than some variation in size, there are no distinguishing structural characteristics among them.

The neurocranium has a distinctive, rounded, "brachycephalized" configuration (Plate V). The cranial vault is wide and relatively short in its anteroposterior dimension. Indeed, even the brain appears to have undergone "telescoping" by rotation of the forebrain ventrally. However, whether this is an actual physical rotation, or is a rotational effect produced by differential growth, has not been experimentally or histologically verified. No olfactory fossae exist, and the endocranial surface of the fused and flattened ethmoids reveals no patent foramina for passage of olfactory nerves.

The lesser wing of each sphenoid bone articulates with the ethmoid, and located posterior to this is the furrow for the optic chiasm. The hypophyseal fossa is quite broad transversly, corresponding in shape to the pituitary gland (Jacobs and Morgane, 1972). Just posterior and lateral are the paired foramina rotundum and from here the greater wing of the sphenoid articulates with the parietal to form the broadened fossa for lateral parts of the cerebrum. According to Morgane and Jacobs (1972), the trigeminal nerve contains more nerve fibers than any other neural tract in members of the Cetacea. Accordingly, the depressions for the paired semilunar ganglia are pronounced.

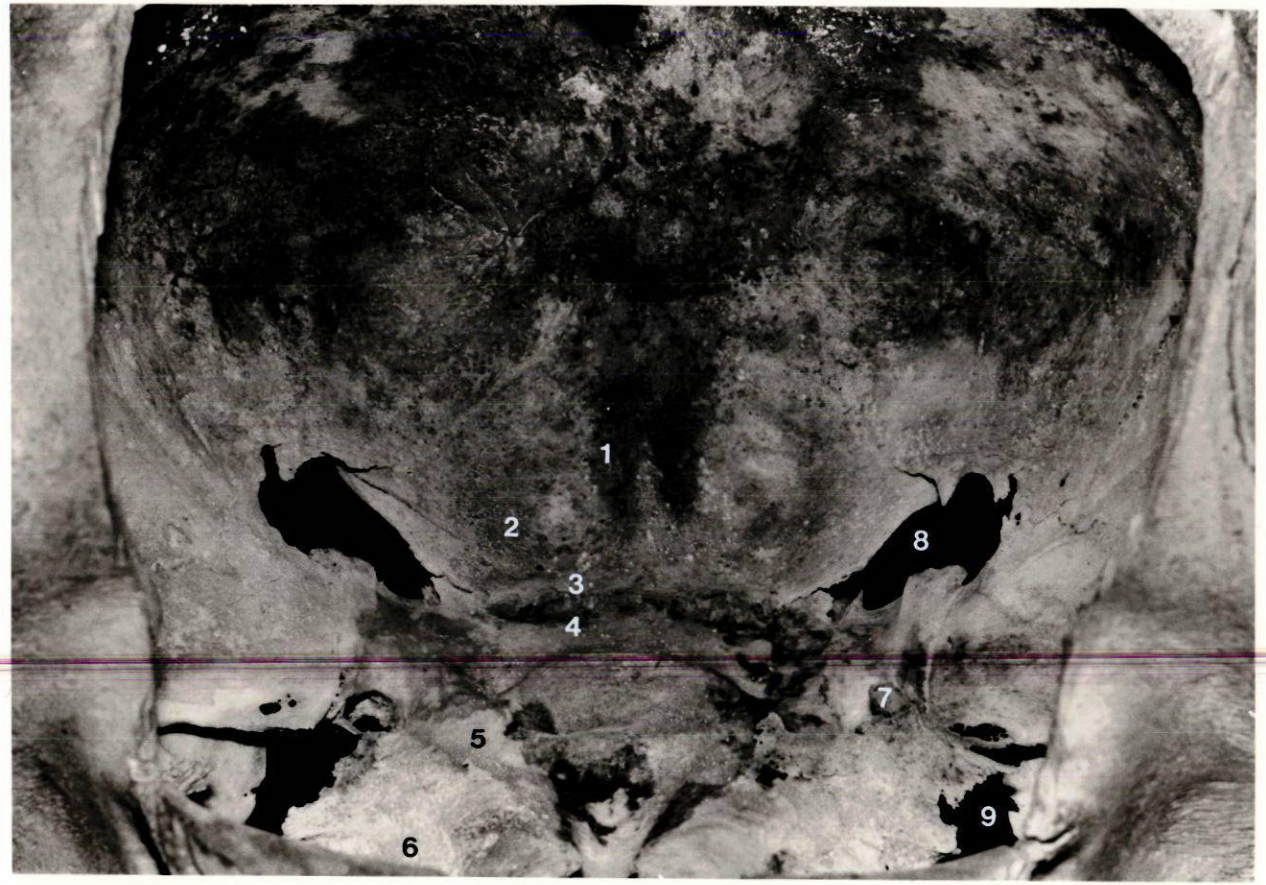
The borders of the composite foramen ovale, stylomastoid foramen, eustachian orifice, and the posterior glenoid and posterior lacerated foramina are formed by the basisphenoid and

PLATE V

SKULL OF TURSIOPS TRUNCATUS

ENDOCRANIAL VIEW

1. Ethmoid
2. Sphenoid
3. Optic chiasm
4. Hypophyseal fossa
5. Trigeminal fossa
6. Occipital fossa
7. Foramen rotundum
8. Optic foramen
9. Composite foramen
   - Foramen ovale
   - Stylomastoid foramen
   - Posterior glenoid foramen
   - Posterior lacerated foramen
   - Orifice for eustachian tube


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basioccipital bones. This location is at the anterior boundary of the posterior cranial fossa. This general area, for the cerebellum, medulla oblongata, and pons, is broad and expansive. Laterally, the deep occipital fossae rise and fan out posteriorly. Perpendicular to the long axis of the skull is the foramen magnum. Rising above the foramen magnum, on the endocranial surface, is an internal longitudinal occipital crest which serves to separate the right and left cerebellar fossae. This crest contains an occipital sinus.

The mandible of the dolphin (Plate VI), is roughly "V" shaped as seen from a superior aspect. The two mandibular halves are not fused but are joined by a midline connective tissue symphysis. The corpus of the mandible is ovoid in cross-section in the anterior region but posteriorly its cortex becomes distinctly "C" shaped in cross-section. The posterior third of the mandible is reduced to an exceptionally thinned sheet of cortical bone. As viewed from the lateral aspect (Plate VII), the mandible is triangular in shape with the symphyseal region forming a rather distinct apex and gradually widening toward the condylar region. There is no distinct differentiation between the corpus and ramal portions of the mandible, in contrast to the human and dog mandibles. In fact, there is no gonial angle at all, and the long axis of the dolphin's mandible is more or less straight from the symphysis to the condyle. The condyle itself is situated at the

PLATE VI

MANDIBLE OF TURSIOPS TRUNCATUS

SUPERIOR VIEW

1. Symphysis
2. Pan bone
3. Condyle

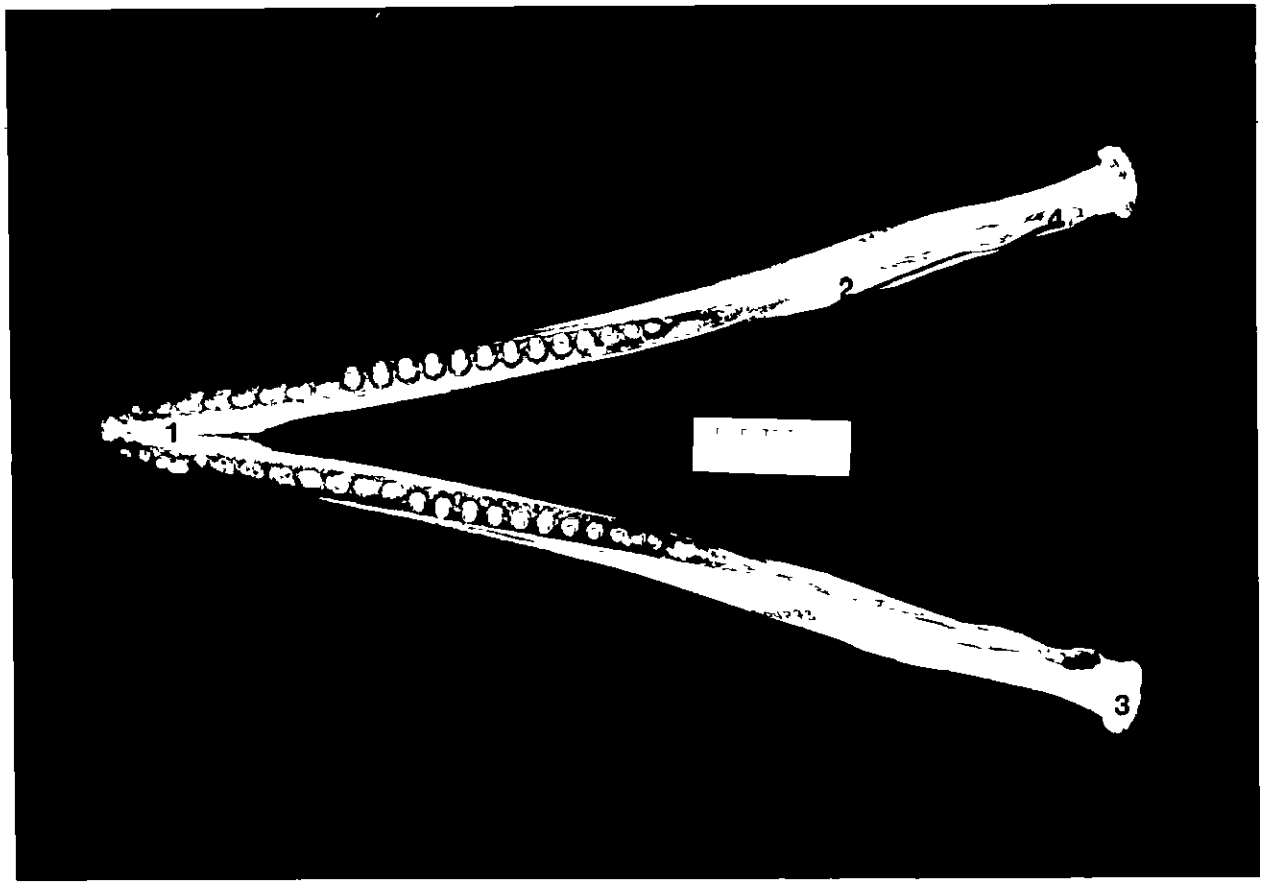
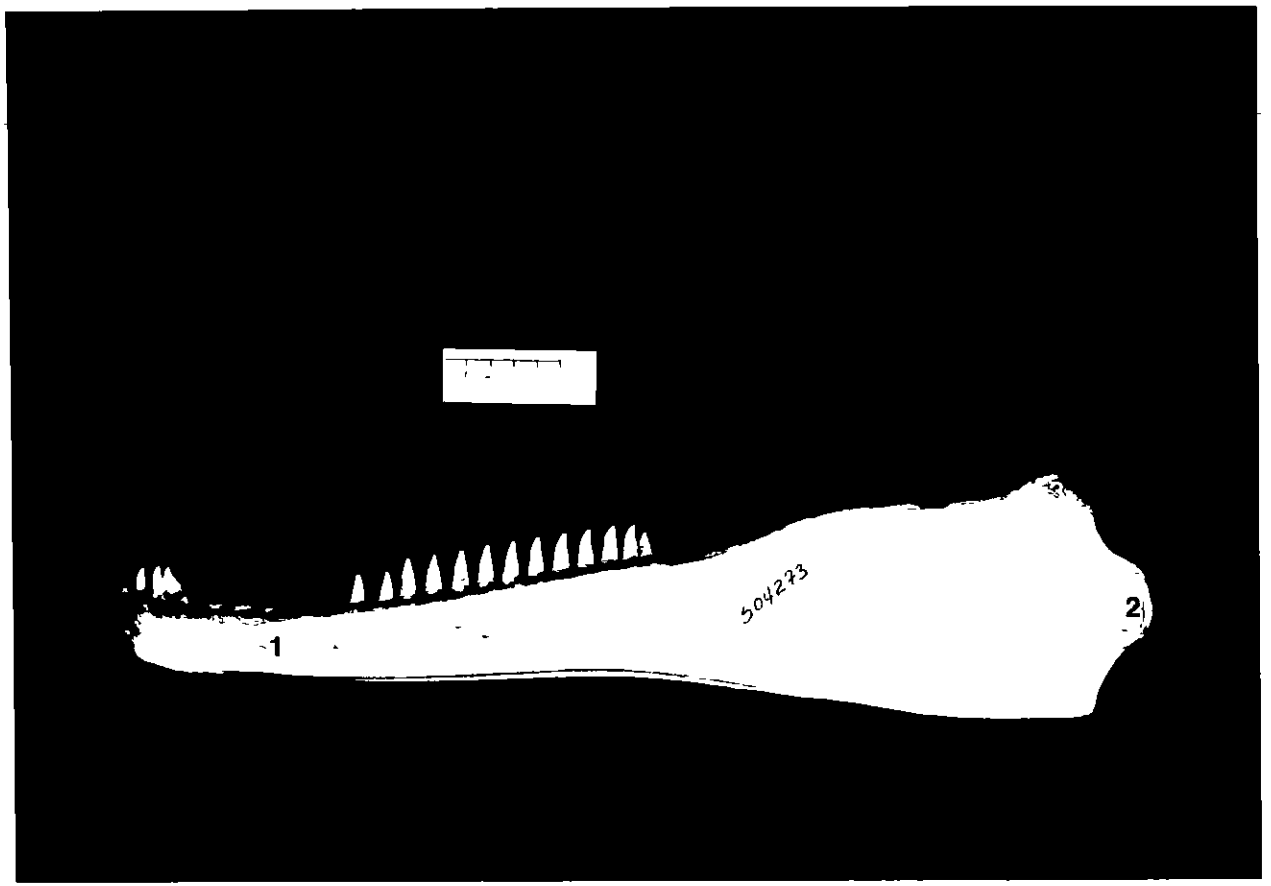

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PLATE VII

MANDIBLE OF TURSIOPS TRUNCATUS

LATERAL VIEW

1. Mental foramen
2. Condyle
3. Coronoid process


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2
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most posterior portion of the mandible, approximately mid-way between the superior and inferior borders of the mandible.

As viewed from the posterior aspect of the mandible, the dolphin's condyle is roughly diamond-shaped with the long axis angling superiorly and posteriorly. The articular surface of the condyle is somewhat flat or slightly convex.

As mentioned above, the mid region of the mandible is "C" shaped in cross-section and becomes exceedingly thin toward the posterior. This "C" shaped area has been termed the pan bone for this reason (Norris, 1964). Mesial to this distinctive area, the mandibular corpus becomes "hollow" in the medullary region for most of the anterior remainder of the mandible. Norris believes that this hollow, pan bone region acts as a sensory area providing sound wave reception. Thus, angular movements of the mandible could presumably serve as a receiving system to allow fine discrimination of sound waves contacting the bony surface.

Comparison of Skulls

Comparisons of the craniofacial pattern characterizing Tursiops truncatus, Canis familiaris, and Homo sapiens are made for several reasons. First, both the bottlenose dolphin and man are unique in that they possess usually large cerebral hemispheres, and both also have a distinctively widened cranial form. The most obvious difference between the skull of Tursiops and

Homo is the presence of a conspicuously protruding midfacial region in the dolphin. Tursiops also differs from Homo (and most other mammals) in that a total absence of the olfactory tracts and bulbs exists. A specific breed of dog (the Pit Bull) was selected for comparison because it possesses a "brachycephalized" cranial form but with this breed (as in the human) a shortened facial pattern. The dog also possesses a large, well-developed olfactory apparatus, in contrast to the human and the anosmic dolphin.

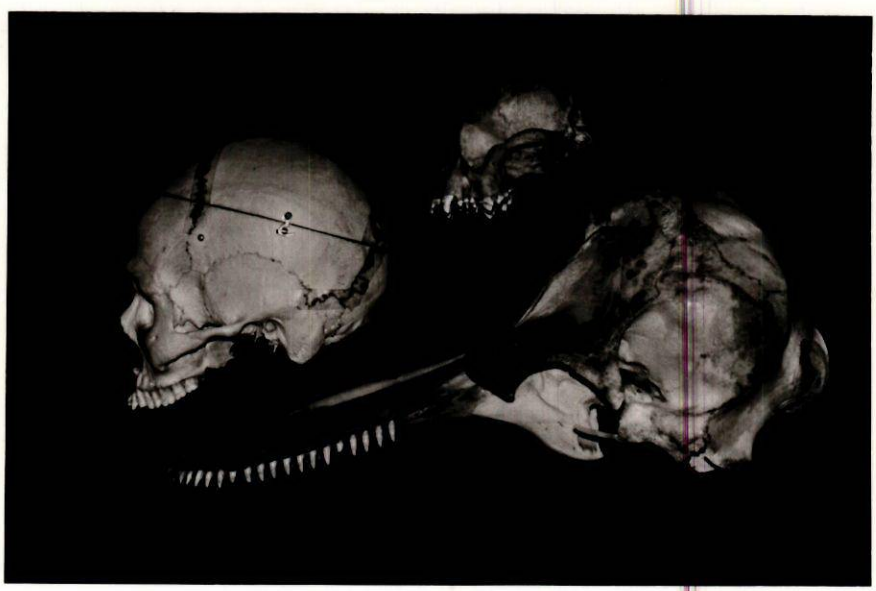
In the lateral view (Plate VIII), a striking feature of the dolphin skull is a long, protruding muzzle. Not only does the upper jaw project considerably anterior to the cranium, but it also extends posteriorly and dorsally. The maxilla is able to attain such distinguished length by virtue of two conditions, the buoyancy of the water and a broad midfacial base. In other brachycephalized species, such as man and the bulldog, the facial complex is considerably reduced in horizontal length but possesses an increased width, thereby maintaining a roughly equivalent airway capacity. A more protrusive snout requires a correspondingly wider interorbital base to support it.

Even though mammalian species having a brachycephalized cranial pattern are usually typified by a flattened midface (Enlow, 1973), the dolphin differs in that it is characterized by an elongate, protruding muzzle. Also, the dolphin's maxilla and premaxilla extend posteriorly beyond the usual cranial boundary

PLATE VIII

LATERAL VIEW OF SKULLS

Homo sapiens--upper left
Canis familiaris--upper right
Tursiops truncatus--lower



and overlaps the anterodorsal wall of the neurocranium. These midfacial bones are nearly twice the span of the cranial length. The dolphin's midface does not rotate in a ventroposterior fashion as in Canis and Homo but, as mentioned previously, has proceeded in an unusual dorsoposterior direction. In the dolphin, further, the premaxilla is not confined to the anterior of the muzzle as in the dog and man, but traverses nearly the entire length of the maxilla. In the human, the maxilla provides significant portions of the orbital floor. In the short-faced bulldog, the maxilla composes much of the orbital shelf. In the dolphin, however, the involvement of the maxilla in the orbit is restricted to a narrow portion of the anterior orbital roof. In all three species, the roof of the orbit is formed primarily by the frontal bone, although Tursiops is unique with its pronounced supraorbital crest. In the dolphin, the lacrimal bone does not form part of the medial wall of the orbital cavity, but forms the most lateral extent of the orbital roof. Extending medially and inferiorly from the lacrimal bone is the long, slender jugal, which is the sole bony component of the orbital floor. Unlike the skulls of the dog and the human, there is no continuous zygomatic arch in the dolphin, and the zygomatic bone does not articulate with the maxilla but rather connects with the squamous. In both Canis and Homo, the molar teeth are positioned beneath the heavy malar buttresses on the anterior part of the zygomatic arch, but

in Tursiops, no teeth are present on the posterior portion of the maxilla or in any area of supplementary bony reinforcement.

In a lateral view of the human and dog skulls, with the occlusal plane parallel to the horizontal, the alveolar process is the most inferior portion of the maxillocranial composite. However, when the dolphin is positioned such, portions of the palatine bones, pterygoid, and vomer dip below the occlusal plane. Therefore parts of the nasal cavity actually extend beneath the level of the maxilla. As emphasized previously, a striking characteristic of Tursiops is the disjunction of the nasal and oral regions. The nasal chambers have rotated in a dorsoposterior direction to become aligned nearly perpendicular to the horizontal axis of the midface. In the human and short-faced dog, conversely, the nasal and oral regions are closely aligned, according to standard mammalian pattern, and the floor of the nasal chambers serve also as the roof of the oral cavity.

In Tursiops, with enlargement of the cerebral hemispheres, the parietal bone has been considerably narrowed in relative size and configuration. In man and the dog, the vertex of the skull is formed by the expansive parietals, but in the dolphin, the occipital bone extends superiorly onto the vertex, thereby reducing the relative growth field occupied by the parietals. In man and the short-faced dog, the temporalis attachment and the superior and inferior temporal lines are noticeable,

but relatively faint, muscle crests. In the dolphin, these lines are much more prominent and actually form an oval-shaped, bony peak.

From a superior view of the three skulls (Plate IX), the contrast between the vertical-faced human, the moderately protrusive face of the Pit Bull, and the elongate facial complex of the dolphin is most evident. Likewise, the orientation of the orbits follows a graded continuum. In the human, the eyes have rotated toward the midline so that the neutral orbital axes are aligned directly anteriorly. In the Pit Bull, the eyes are also rotated forward, although the extent of convergence toward the midline is not as extreme, and orbital alignment is obliquely anterior and superior. However, in the dolphin, the eyes are in extreme lateral positions. In fact, each infraorbital foramen is actually located superior to its orbit. In essence, it is not that the infraorbital foramen is superior, but that the orbit itself remains inferior relative to the foramen. In all three species, the foramen is situated in the approximately same area of the maxilla. The infraorbital foramen of the dolphin is actually located in a "conventional" anatomic position, and the seemingly contradictory terminology in the dolphin is due to the orbits being relocated below the body of the maxilla.

From a posterior view of the three skulls (Plate X), the most evident characteristic for all three species is the marked

PLATE IX

SUPERIOR VIEW OF SKULLS

Tursiops truncatus--upper
Homo sapiens--lower left
Canis familiaris--lower right

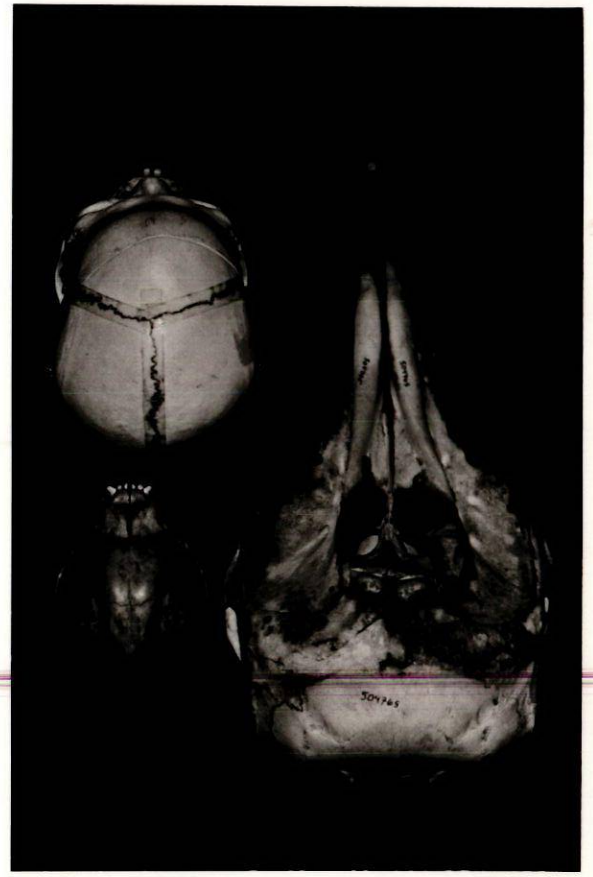


PLATE X

POSTERIOR VIEW OF SKULLS
LEFT TO RIGHT

Homo sapiens
Tursiops truncatus
Canis familiaris



breadth of the cranium, although the narrowest relative span of these three species is seen in the dog skull. The bulldog's cranial extent is nonetheless widened in comparison to the long, narrow headform of other canine breeds. An illusion of even more lateral fullness in the short-faced dog skull is given by the very wide, protruding zygomatic arches. In the human, the exceedingly widened cranial configuration tends to dominate the appearance of the zygomatic region and its size relative to the proportionately smaller masticatory muscles attached to it. In the dolphin, which has the widest relative expanse of cranial bone, the zygoma is quite evident, from the dorsal view, as it bows laterally to a considerable degree in conjunction with relatively large masticatory muscles associated with the sizable mandible. In the dog, the occipital bone is a relatively small component of the cranium surrounding the foramen magnum with just a thin lip of bone extending superiorly between the parietals. In both the human and dolphin, the relative expanse of the occipital bone is far more consequential, proportionately, and in both species, it not only forms the base of the skull but extends across the entire posterior border of the cranium as well. Again, in Tursiops, the occipital extends more superiorly than in Homo. The positioning and alignment of the foramen magnum corresponds to the posture of the species and the alignment of the basicranium relative to the vertebral column. For the upright posture of the human, the

foramen magnum is located at the most inferior position relative to the other two species. With the quadrapedal stance of the dog, the foramen has rotated to an obliquely more superior position. In the dolphin, with its horizontal postural alignment, the foramen magnum is positioned so the aperture is perpendicular to the long axis of the skull.

From a posterior view, the base of the skull formed by the occipital bone is straight to slightly convex. In the dolphin, however, the cranial base has a marked concave outline. This shape is formed by the pronounced occipital extensions of the falcate and paraoccipital processes. All the processes and extensions of the occipital are more extreme in the dolphin. The groove for the occipital artery is a shallow furrow in the human and dog skull, but it becomes a deep crevice in the dolphin.

As contrasted to most external surfaces throughout the dolphin's skull, with their smooth texture and generally gentle contours, the occipital bone displays numerous scalloped crests, deep irregularities and furrows for muscle attachments, and multiple foramina. The occipital bone in both the bulldog and human is seemingly more topographically coarse than the other bones of the skull, but only in the dolphin does this element possess such pronounced irregularities. The occipital has developed into a broadened "strategic" area of postural support and hydropressure adaptation. It is here that the anterior tele-

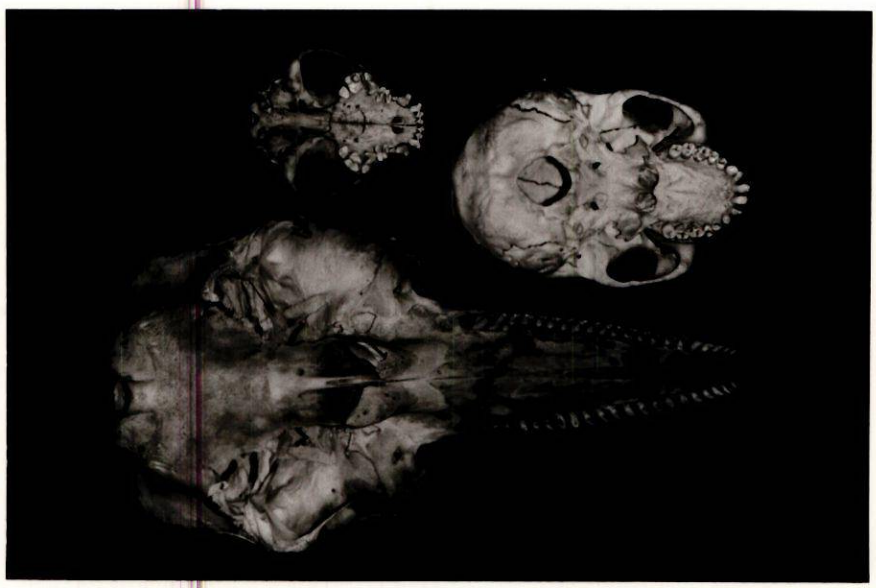
scoping occurrences and configurational rearrangements are apparently counterbalanced and receive compensatory support. Although enlargement of the cerebral hemispheres has not brought about orbital convergence due to the spatial encroachment of the midface, brachycephalization has allowed the occipital to widen and lengthen with less restrictions. Therefore, the broadened occipital bone serves as a foundation for the overlying midfacial base and prominent supraorbital crests.

In viewing the ventral surface of the skull (Plate XI), even though the three species are brachycephalized relative to other mammals, the contrast of their respective maxillary arch forms is most evident. In the human skull, the arch form is horseshoe-shaped, the widest transpalatal dimension being the posterior of the maxilla. In the short-faced dog, the posterior of the widened and shortened dental arch displays a definite constriction, and the anterior form of the arch is somewhat more "V" shaped compared to the human. The dolphin also has a tapered arch form, and unlike the dog and human specimens, no teeth are present in the posterior "buttressed" portion of the maxilla. The teeth are intended primarily for catching and not grinding or chewing. In all three species, the pterygoid plate of the sphenoid articulates with the palatine bone. However, in Tursiops the palatine bone is superior to the pterygoid, as opposed to an anterior location as in Homo, and Canis. In the latter two skulls,

PLATE XI

VENTRAL VIEW OF SKULLS

Tursiops truncatus--upper
Homo sapiens--lower left
Canis familiaris--lower right



the horizontal plate of the palatine is a continuation of the maxilla to form the dental arch. In the dolphin, this is not the case. Its palatine bone is somewhat removed from the dental arch and, in fact, there is no horizontal plate of the palatine bone at all in the dolphin. This bone assumes a strictly vertical position and by its juncture with the pterygoid, forms the outer wall for a sinus. The palatine bone then ascends into the maxilla to form the anterior wall of the nasal chamber.

In all three skulls, the vomer can be seen as a midline septum of the nasal passage. In the dog and human, the medial pterygoid plate forms the bony wall of the pharyngeal space, and the palate is on roughly the same axis as the base of the skull. In the canine, the anteroposterior dimension is lengthened as the pharynx has a long axis more closely aligned to the nasal passages and hence, the base of the skull. In the human, the pharynx joins the nasal region at a more perpendicular position, both to the palate and to the basicranium, in conjunction with the basicranial flexure, bipedal posture, and facial and palatal rotation. Hence, the medial pterygoid plate does not continue posteriorly to such an extent as in the dog. In the dolphin, however, disjunction of the nasal and oral regions have brought about compensations in the base of the skull. Even though the nasal chamber is uniquely perpendicular to the base of the neurocranium, the walls of the pharynx are parallel with the cranial

base, and as such, are continued along the ventrum of the skull by osseous extensions. The bony pharyngeal wall is formed not only by the medial pterygoid plate, but by a similar continuation of the occipital.

In comparing the mandibles of Tursiops, Canis and Homo (Plates XII and XIII), a noticeable feature of course is the presence of symphyseal fusion in man. The human mandible is a broad, continuous, horseshow-shaped arch. Both the dolphin and dog possess relatively elongate, tapering, "V" shaped dental arches. However, only the dolphin has a "pan bone" configuration in a part of the mandible. The human mandible is unique because of its distinctive mental protuberance, and the gonial angle is prominent. Neither the dog nor the dolphin has a pronounced flexure from the corpus to the ramus of the mandible, the dolphin possessing none at all. Although the inferior border of the dog mandible is "rocker" shaped, this border in the dolphin is nearly flat. All three species have a coronoid process, the most distinctive being possessed by the mandible in Canis; In Tursiops it is barely discernible. The dolphin's mandible is also without a sigmoid notch as the coronoid process slopes gradually to give rise to the condyle. All three skulls exhibit mental foramina, the dog and the dolphin having three and four per side, respectively, but lacking altogether in the dolphin. Instead, the mandible of Tursiops is characterized by a long, hollow area in this area.

PLATE XII

SUPERIOR VIEW OF MANDIBLES

Homo sapiens--upper left
Canis familiaris--upper right
Tursiops truncatus--lower

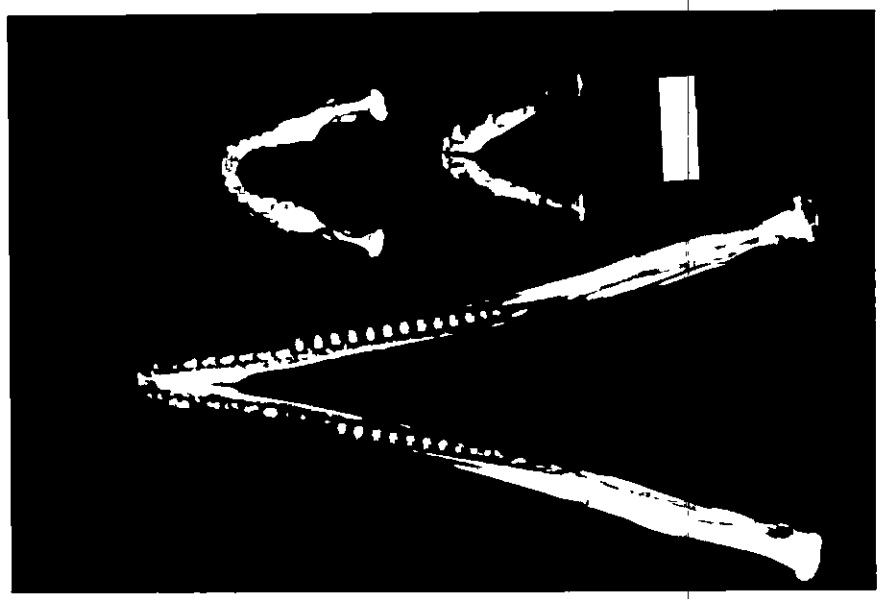
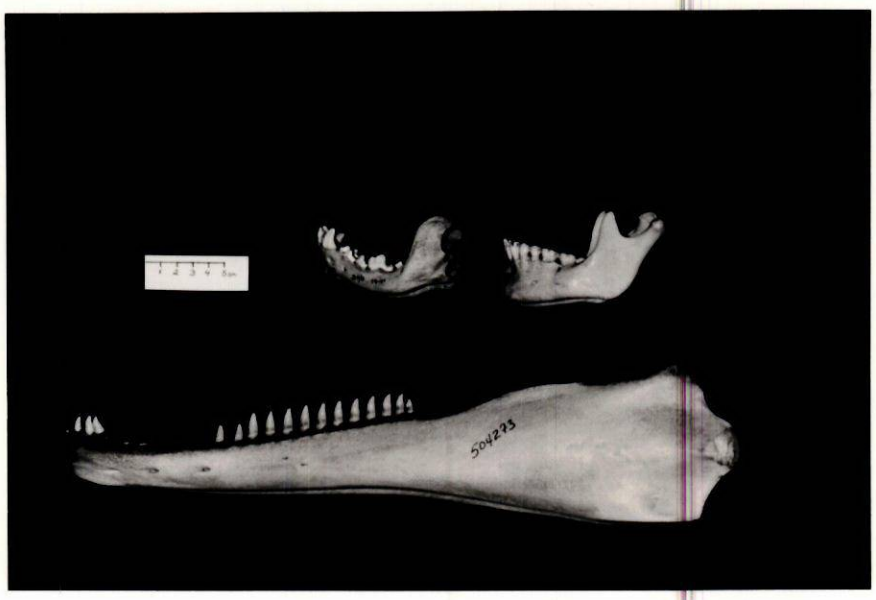


PLATE XIII

LATERAL VIEW OF MANDIBLES

Canis familiaris--upper left
Homo sapiens--upper right
Tursiops truncatus--lower


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As in most other regions of the dolphin's skull, the mandible lacks most of the relatively well-defined muscle crests that occur on the mandibles of the dog and human. However, when viewed in relation to the dentition, this is not surprising. The homodont dentition of the dolphin is intended mainly for grasping and not incising or crushing, in contrast to the other two species. Also, the restriction of dental units to the more anterior portion of the jaws in Tursiops would be basically inconsistent with the possession of powerful jaw musculature, as force magnitude would be insufficient for any large biting pressures to be generated in the anterior portion of the jaws.

DISCUSSION

The bottlenose dolphin, Tursiops truncatus, is unique within the animal kingdom as a representative whose overall craniofacial form differs substantially from other mammals in general, and also among those other forms having unusually large brain size and/or a significant degree of brachycephalization. Not only do the overall shapes and proportions of many of the individual bones differ, but the geometric nature of the contacts of contiguous bones and the relative positioning among them have become altered extensively in comparison to other large-brained mammals. Furthermore, beyond modification of existing anatomic features is the reduction, virtual elimination, or marked alteration of craniofacial components related to existence in a marine environment.

In many ways, the unique craniofacial pattern of Tursiops is only possible due to its marine-habitat existence. The dolphin has been freed from certain biomechanical and functional relationships by its watery environment. Buoyancy has provided an opportunity for the skull to develop and rearrange within conditions quite different from factors associated with terrestrial gravity, air environment, locomotor system, feeding manner, sensory requirements, and postural disposition. Also, some

investigators have maintained that the combination of the water pressure against the forward projection of the body encountered while swimming actually enhanced the phylogenetic "telescoping" of the Cetacean skull (Miller, 1923; Kellogg, 1928).

In essence, no part of the cranium is unaltered in terms of "standard" mammalian form. Among the noticeable features is an overlapping of the maxilla upon the vomer, and the premaxilla upon the maxilla. The anteriorly and superiorly directed growth of the occipital has reduced the frontal bone to a narrow, bow-shaped crest. Unlike other species, cerebral expansion has not related to a rotation of the orbits toward the midline or a shortened midface. Rather, a "pushing" of the parietals laterally has occurred. Overgrowth of the midface upon the cranium has maintained the orbits in a lateral, fish-like position. Although the frontal bone has been reduced posteroanteriorly, it has spread laterally to form its pronounced supraorbital crest. The lacrimal bone has also been laterally positioned to become the most lateral projection of the roof of the bony orbit.

In Tursiops there has been a reduction of the buttressing portions of the face made less necessary because of water buoyancy. The zygomatic arch is not a continuous structure, and no zygomatic process of the frontal bone exists. Again, not only are these structures less functional or even unnecessary, but they would have compromised the adaptive potential of the dolphin skull that has provided for its phylogenic adjustments.

One of the key morphologic arrangements that has occurred in the craniofacial pattern of Tursiops is that associated with the nasal region. The dolphin is anosmic, that is, lacking the sense of olfaction, and an absence of the olfactory tracts and bulbs exists. Although the nasal area is still utilized for breathing, the facial respiratory components have been released from the fundamental olfactory positional relationships found in other mammals. The nasal area has actually become disjoined from its conventional palatomaxillary relationships and has "rotated away" from the remainder of the midface.

In the human skull, the nasal region does not prevent biorbital convergence, and the marked expansion of the anterior and middle endocranial fossae relate to rotations of the orbits medially, rather than laterally as in the dolphin.

In the bulldog skull "brachycephalization" relates to an anteroposteriorly foreshortened basicranium associated with its achondroplastic condition. The short anterior cranial fossae, which establish the template for nasomaxillary development, relates to the resultant short midface.

In the human skull, an unusual olfactory relationship also occurs (downward-rotated bulbs in association with the greatly enlarged cerebrum), and the nasal complex has also been accompanied by a corresponding rotation. However, the rotational direction in the human is inferoposteriorly, in contrast to superoposteriorly in the olfactory-lacking dolphin.

There presently are two established theories attempting to account for the growth "displacement" of the nasomaxillary complex during the morphogenesis of the mammalian face. One of these, proposed by Scott (1954), is the nasal septum theory, and the other, the functional matrix theory, was developed largely by Moss (1969). Evaluation of the craniofacial pattern in Tursiops truncatus, with reference to these concepts for other mammals, does not shed much illumination on the possible manner of craniofacial morphogenesis in the dolphin. Regarding the septal theory, it is held that expansion of the nasal septal cartilage provides a mechanical force which produces the anteriorly and inferiorly directed displacement of the contiguous midfacial components. However, the nasal region of Tursiops is separated from the remainder of the midfacial composite. Therefore, it would not be tenable to attribute the growth displacement of its elongate, protruding midface to a presumed pace-making region that has become functionally and anatomically disjoined.

With regard to the functional matrix theory, the forward and downward displacement of the nasomaxillary complex is generally explained as a function of the soft tissue growth and its "carry effect" on the contiguous bones. The factor of disjunction between the nasal and oral components in the dolphin thereby precludes a nasal expansion effect from contributing to the displacement of the noncontiguous upper jaw. The extent to which

this might compromise the functional matrix displacement theory cannot presently be evaluated. The maxilla, premaxilla and oral cavity do have associated soft tissues, and whether or not these tissues provide pacemaking growth control for the maxilla in the dolphin is presently not known.

The unusual facial configuration and anosmic nature of Tursiops is of interest when evaluated in reference to a group of congenital defects known as holoprosencephaly (arhinencephaly). The pathogenesis involves a failure of the cleavage of the prosencephalon resulting in the absence of olfactory bulbs (Cohen, 1974). In the human, agenesis of the olfactory bulbs results in a shortened midfacial pattern and closely-spaced (hypoteloric) orbits. However, in the dolphin, absence of the olfactory apparatus relates to a quite opposite pattern, that of a protruding midface and a markedly broadened interorbital dimension.

For evaluation of the cephalometric radiographs, a difficulty exists regarding use of traditional methods of analysis. The standard cephalometric landmarks (sella, nasion, porion, A and B point, etc.) are either non-existent or indiscernible in headfilms of Tursiops truncatus. Other landmarks were used, such as the inferior and superior points of foramen magnum, and also the most anterior and posterior point on the jugal outline to represent the floor of the orbit. However, comparisons of the cephalometric tracings of the various age categories did not yield

any consistent findings regarding anatomic positional variations with age. For example, when superimposed on the basicranial and orbital landmarks, the maxilla would show apparent rotation inferiorly in some specimens, and in others, superiorly. The difficulties encountered could most likely be surmounted if application of valid morphologic and morphogenic landmarks could be developed.

Any discussion of the growth and development of the bottlenose dolphin at this time must deal only with relative changes and displacements. There presently exists virtually no actual morphogenic information derived from studies utilizing vital dyes, implants, and histologic analyses to reveal actual patterns of growth in the dolphins. An investigation employing such growth-revealing methods would be required as a basis for meaningful cephalometric analytic interpretations. Without knowledge of the dynamics and kinematics of the dolphin's craniofacial growth process, cephalometric analyses would lead to questionable and, likely, incorrect conclusions.

A detailed account of the growth and development of the craniofacial complex of the dolphin utilizing radiographic markers for serial evaluation and vital dyes for histogenic analysis, does not presently exist. This will be needed in order to document the histogenic basis for the presumed rotations that occur, as well as the developmental processes in general, underlying the

unusual structural and functional relationships seen in this anatomically unusual species.

SUMMARY AND CONCLUSIONS

The unusual craniofacial morphology of bottlenose dolphin (Tursiops truncatus) is of interest because it relates to a "brachycephalized" cranium in conjunction with enlarged cerebral hemispheres, thus sharing a similar circumstance with the craniofacial situation seen in Homo. Unlike the human skull, however, bimaxillary reduction is not a feature in the dolphin. Furthermore, the olfactory apparatus, which is believed to play a basic role in facial design and growth in man and other mammals, is lacking altogether in the dolphin. A major re-design in the nasomaxillary components of the dolphin skull has occurred in which a nearly total disjunction between the oral and breathing parts of the face is seen. Further, fundamental, postural and environmental differences exist that markedly offset the basis for difference in facial design.

This study is a comparative evaluation of the anatomical patterns of the craniofacial complex in these two species in the light of these similarities and differences underlying facial form and pattern. In addition, a third species is also included for comparison, the Pit Bull (Canis). The latter also has a "brachycephalized" cranium, as in both man and the dolphin. Like the human skull, the bulldog skull also has a shortened facial

complex but, unlike the other two species, possesses a well developed olfactory apparatus.

The craniofacial complex of Tursiops is rearranged considerably. Repositioning of bones, and also reduction of apparently nonessential structures, has occurred. The maxilla, premaxilla, and vomer overlie one another, and their posterior parts have "rotated" superiorly and posteriorly to become nearly contiguous with the occipital bone. The latter has expanded superiorly and anteriorly to a considerable extent. The frontal bone is reduced to a narrowed crest, and the parietals have become positioned laterally, as compared to the pattern in other mammals.

These bony rearrangements relate to several functional circumstances. Existence in a marine environment has allowed the design of the skull to diverge without regard to biomechanical constraints present in terrestrial forms. The absence of olfactory tracts and bulbs has released the nasal and midfacial area from an otherwise obligatory relationship and has allowed the nasal region to rotate superoposteriorly into a vertical placement in the midface.

The unprecedented divergence of the nasal area in the dolphin has several implications. Even though there is considerable cerebral enlargement, the orbits are prevented from assuming a more anterior-projecting rotation due to the intervening over-

growth of the nasal area into the broadened interorbital region. As mentioned, the dolphin's maxilla and premaxilla have elongated posteriorly as well as anteriorly.

These composite anatomic configurations are difficult to fully explain by currently understood models of facial growth. The growth of the cranial floor itself does not seem to account for the divergence between oral and nasal areas. Also there is no nasal septum to otherwise "provide displacement" for the protruding muzzle.

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