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Evolution and the pathology of deep diving in the Bottle-nosed Dolphin, *Tursiops truncatus* (Montagu, 1821) (Notes on Cetacea, Delphinoidea V)

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ABSTRACT

Cadenat (1959) and Rancurel (1964) produced strong indirect evidence that off the west coast of Africa, the Bottle-nosed Dolphin, *Tursiops truncatus*, is in the habit of diving very deeply, possibly down to 600 m. Examination of the skulls of fully adult specimens of *Tursiops* taken off Dakar and St. Helena revealed marked distension and fenestration of bones associated with the accessory air sinuses of the middle ear.

The condition suggests a pathological enhancement of the normal processes of evolution of these bones in order to adjust to excessive middle ear pressure sustained intermittently over a long period.

In the collections of the British Museum (Natural History) there is a series of ten skulls of Bottle-nosed Dolphins, *Tursiops truncatus*, which had been harpooned by fishermen off the coast of St. Helena at various times during 1959. Two juvenile skulls and four sub-adults show the normal condition found in fully adult specimens collected in shallow waters in various parts of the world (fig. 1). The remaining four, fully adult skulls from St. Helena show marked distension and fenestration of the bones associated with the accessory air sinuses of the middle ear (fig. 2), a condition very similar to that observed in other skulls of this species collected off Dakar. As the rest of the bones and teeth appeared perfectly healthy it seemed to us that the condition indicated some abnormality in the diving behaviour.

In 1959, Cadenat postulated, from evidence of otoliths of bathypelagic fish found in the stomachs of *Tursiops truncatus* taken off the Senegal coast, that the animals may have been capable of diving to a depth of over 200 metres. Rancurel (1964) found undamaged bathypelagic fish in the oesopha-

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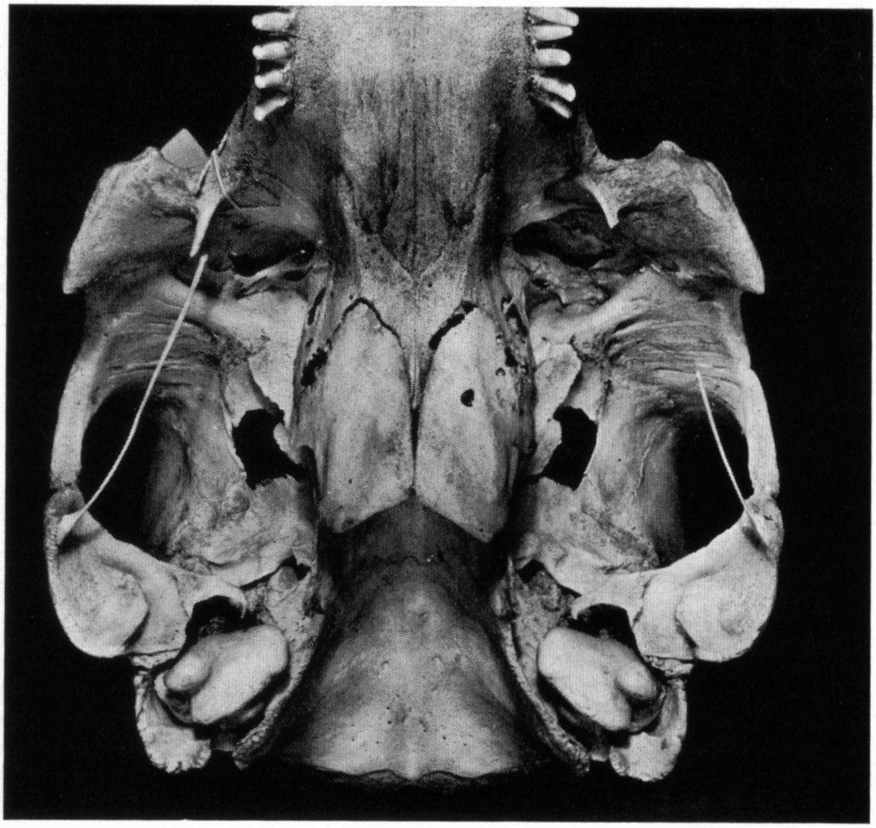
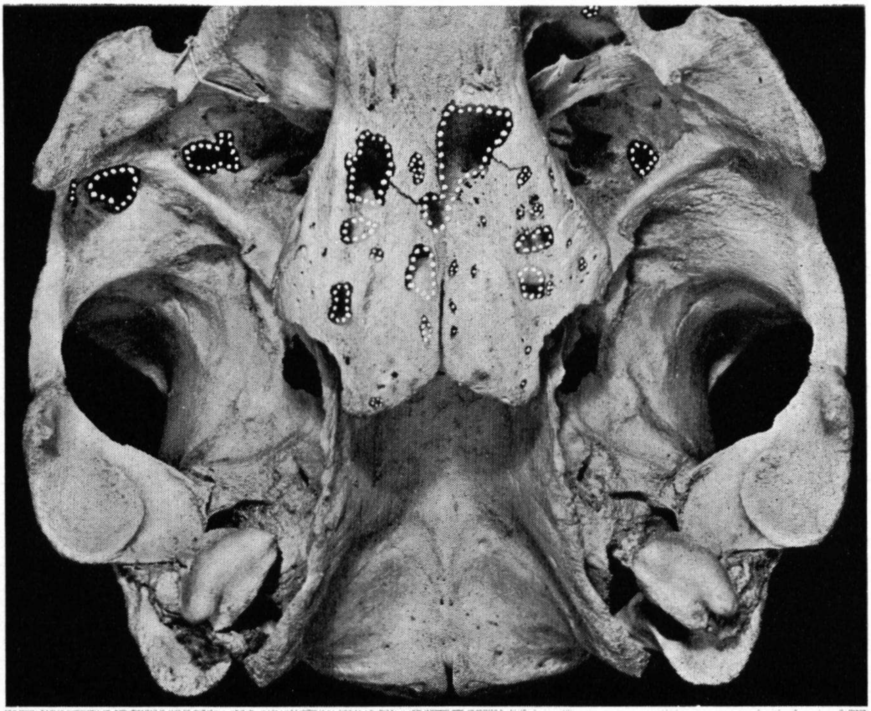


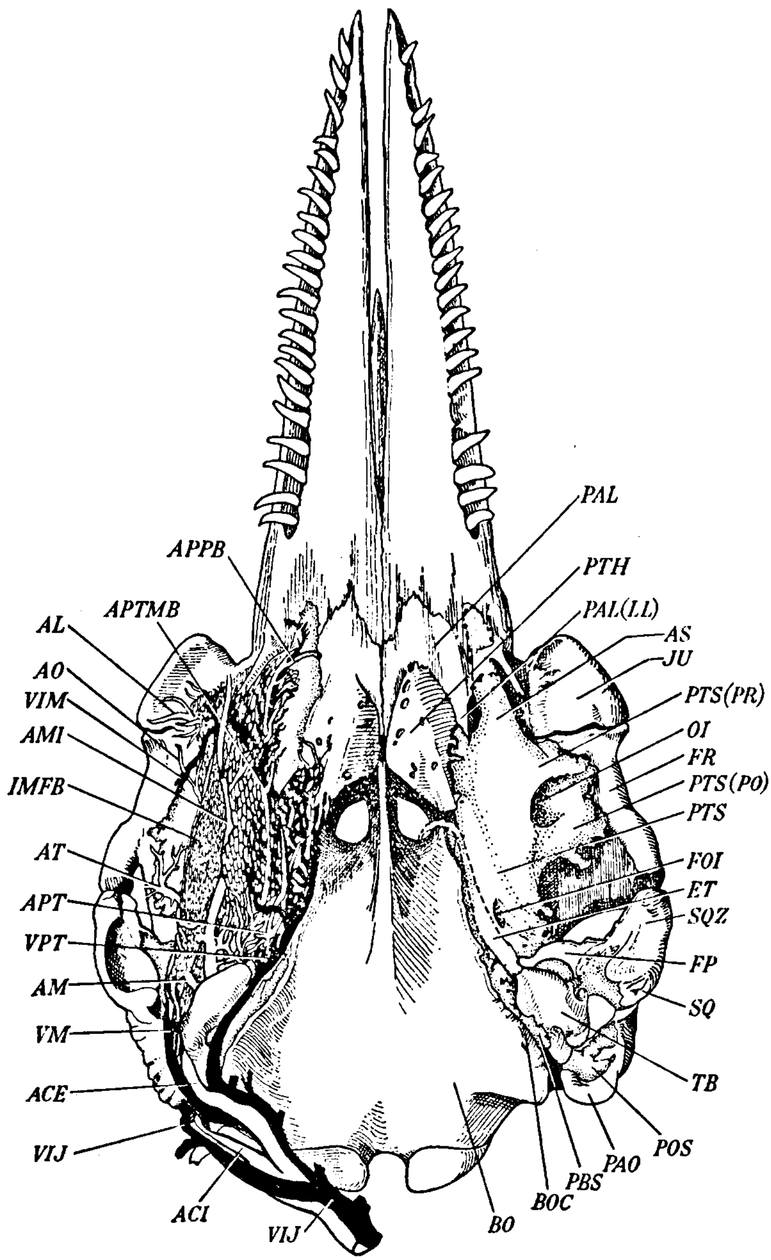
FIG. 1. Ventral view of the skull of a sub-adult specimen of the Bottle-nosed Dolphin, *Tursiops truncatus*, showing normal condition of bone.

gus and stomach of *Tursiops* harpooned off Vridi, Ivory Coast, and after a careful survey of the hydrological conditions and contents of midwater trawls at various seasons and times of day, produced clear evidence that these animals had dived to at least 500 metres and had probably reached the bottom at 800 metres. Kooyman (1968) has shown that the Weddell Seal *Leptonychotes weddelli* makes many dives to midwater depth (300—400 metres) but that dives in excess of 400 metres were rare. The maximum recorded depth for the Weddell Seal was 600 metres.

The abnormal condition of the skull in the specimens described above could be due to some congenital deformity but its restriction to the older animals seems to indicate a pathological condition brought about by exces-

FIG. 2. Ventral aspect of the skulls of adult specimens of the Bottle-nosed Dolphin, *Tursiops truncatus*, showing distension and fenestration of bones associated with accessory air sinuses of the middle ear. The tympo-periotic bones have been removed from the lower skull.

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sive positive pressure in the middle ear sinus system. The gaseous pressure in the middle ear of seals and cetaceans is normally adjusted to the hydrostatic pressure by the flow of blood into or from the cavernous lining in the middle ear or sinus systems respectively, and it is difficult to see how a pressure difference could arise in a healthy animal. If a gas secreting function could be assigned to the mucous lining of the air sinuses in cetaceans, it can be imagined that during rapid surfacing from a deep dive when the blowhole would be occluded, a positive pressure could develop in the middle ear. An alternative explanation could be that the excess was due to voluntary inflation of the air sinus system prior to deep diving. Ridgway et al. (1969) stated that a Bottle-nosed Dolphin trained to carry out deep dives on command, always hyperventilated the lungs by taking three to ten breaths rapid in succession prior to dives of more than 150 metres; "it appeared that he always achieved a certain minimum state of ventilation before he dived." Fraser & Purves (1960b) noted positive pressure in the middle ear of a stranded specimen of the Pilot Whale, *Globicephala melaena.* Owing to the extreme modification of the ear drum and external auditory meatus, habitual hyperinflation of the middle ear could bring about eventual destruction of the bone without any immediate discomfort.

Whatever the explanation, the condition is interesting from the evolutionary point of view. In their study of the evolution of the ear in cetaceans, Fraser & Purves (1960b) demonstrated that the accessory air sinuses of the middle

FIG. 3. Ventral aspect of the skull of a Bottle-nosed Dolphin, *Tursiops truncatus,* showing distribution of arteries, veins and air sacks (stippled); after Fraser & Purves (1960a).

ACE	external carotid artery
ACI	internal carotid artery
AL	lachrymal artery
AM	mandibular artery
AMI	internal maxillary artery
AO	orbital artery
APPB	palato-pharyngeal branch of AMI
APT	pterygoid artery
APTMB	arterial branches to internal pterygoid muscle
AS	anterior sinus
AT	temporal artery (deep)
BO	basioccipital
BOC	basioccipital crest
ET	Eustachian tube
FOI	infundibulum of foramen ovale
FP	falciform process
FR	frontal
FVP	fibro-venous plexus
IMFB	intra-mandibular fatty body
JU	jugal
MS	middle sac
MX	maxilla
OI	optic infundibulum
PAL	palatine
PAL(LL)	lateral lamina of palatine
PAO	paroccipital process
PBS	peribullary sac
POS	posterior sac
PTH	pterygoid hamulus
PTS	pterygoid sac
PTS(PO)	pterygoid sac (post-orbital lobe)
PTS(PR)	pterygoid sac (pre-orbital lobe)
SQ	squamosal
SQZ	zygomatic process of squamosal
TB	tympanic bulla
VIJ	internal jugular vein
VIM	internal maxillary vein
VM	mandibular vein
VPT	pterygoid vein
ZA	zygomatic arch

ear were developed from a diverticulum of the Eustachian tube and that during their evolution, had enveloped the periotics, severing their osseous connection with the skull and distending the exoccipital bones in that region. During further evolution from the primitive river dolphins to the more highly specialized marine forms, these sinuses had invaded and inflated the pterygoid bones and extended into the sphenoidal, orbital and rostral regions of the skull, removing the calcified element of the bones and leaving only periosteal membranes and elaborate vascular systems which were the hypertrophied Haversian systems of the ancestral bone (fig. 3).

The constitution of the air sac system, the dissociation of the tympano-periotic bones from the skull and the modification of the skull itself are present in the normal animal and in the unborn foetus and their genetic origin is obvious. Nevertheless, these modifications can be interpreted in terms of the mechanical effect of pressure and tension on bone. The natural condition of rarification of bones is so strikingly similar to the abnormal conditions found in bone subjected to excessive mechanical stresses, that some principle such as the so-called "Baldwin Effect" must be invoked to link the natural to the abnormal. It has long been recognized that of all the tissues comprising the body of an animal, with the single exception of blood, bone is the most plastic, in the sense that it is the most subject to modification under mechanical stresses.

According to Weinmann & Sicher (1947), who quote Wolff's Law of transformation of bone, the effect of increased pressure or tension on bone can be summarized as follows: "(1) Increase of pressure beyond the limits of tolerance leads to destruction of bone by resorption. (2) Within the limits of tolerance an increase of the normal forces of pressure or tension leads to formation of new bone". Increased pressure in such instances acts upon a bony surface which is normally subjected to pressure and able to withstand it. Such areas are often characterized by a covering of avascular tissue. Increased traction in an area adapted to traction will also lead to acquisition of bone. *Slight pressure will lead to resorption of bone if the forces are applied to an area which is normally neutral or under tension and consequently not able to withstand pressure.* One characteristic of this adaptation may be the covering of the bony surface by vascularized epithelium.

The most violent changes in pressure in the middle ear of terrestrial mammals are expressible in terms of small fractions of an atmosphere. In aquatic animals a diving depth of a few metres can bring about a rapid increase of pressure and a depth of 10 metres increases the pressure by one atmosphere. If cetaceans dive to the great depths recorded in this paper it is not surprising that during the acquisition of the aquatic habit, a chain of evolutionary adjustments has occurred to meet the effects of the stresses imposed. It would seem that the specimens under consideration here were subjected to pressures beyond the limits of tolerance.

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