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OBSERVATIONS ON THE ORBITAL REGION OF THE SKULL OF THE MYSTACOCETI

by

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It is well known that the main functional components of the skull in the Whalebone Whales (Mystacoceti) attain an ultimate size, which is out of normal proportion to the rest of the skeleton as compared to the proportions existing in land-mammals. As generally supposed the aquatic mode of life has greatly influenced the shape of the skull. Therefore, it is to be expected that the various species, which all have the same mode of life, show a certain amount of convergence. However, not all bones have become enlarged to the same degree; e.g., the alisphenoid and the orbitosphenoid have remained relatively small. Apparently these bones of the orbit have not been influenced by the aquatic mode of life to the same extent as is the case with other elements of the skull. In the present paper some features of the orbit of the Mystacoceti are described; the variability and the systematic importance of these peculiarities have been examined.

In order to indicate the degree of modification undergone by the Whale skull, it is necessary to have a clear idea of the typical arrangement of the elements bordering the orbit in the skull of a primitive mammal (fig. 1*a*). This figure shows that the orbit is lined by several elements; of these the alisphenoid and the orbitosphenoid lie in the lateral wall of the skull and they immediately surround the foramen opticum. It also shows that these two bones are contiguous with the frontal, the parietal, and the squamosal. In these respects the skull of juvenile Cetacea shows more resemblance to the primitive mammalian skull than do those of the adults.

Comparison of the skulls of juvenile *Tursiops tursio* (Fabr.) (fig. 1*b*) and *Balaenoptera borealis* Lesson (fig. 1*c*) with those of adult specimens shows that in the adult the shape of some of the orbital bones has under-

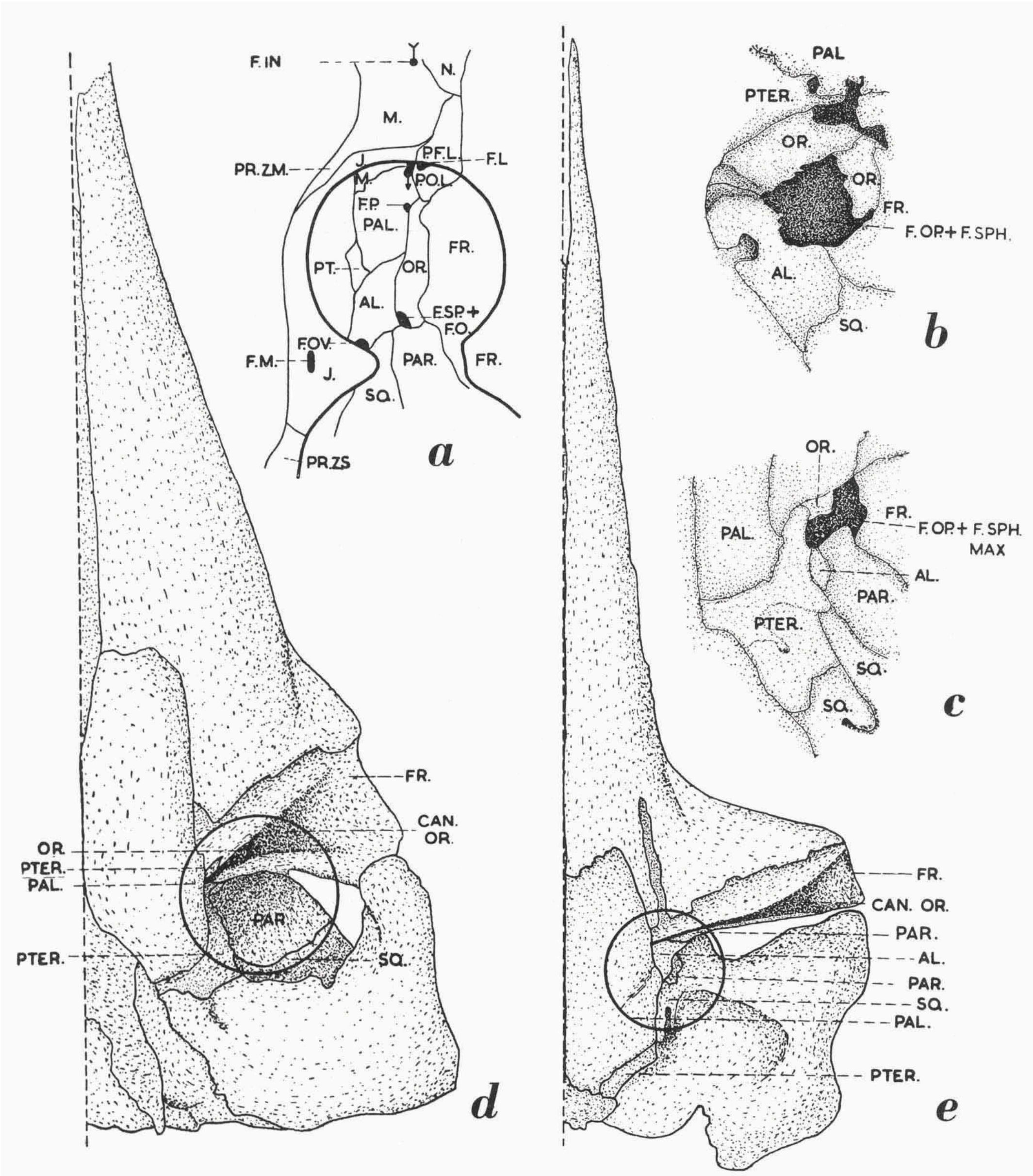

Fig. 1. *a*, lateral view of an ideal left orbit of a primitive mammal; *b*, orbital region of a juvenile *Tursiops tursio* (Fabr.), L. M., reg. no. 16093; *c*, orbital region of a foetal *Balaenoptera borealis* Lesson, B. M., reg. no. 1-5-7-12; *d*, *Balaenoptera acuto-rostrata* Lac., ventral view of skull showing Type A of the optic tube, L. M.; *e*, *Balaena glacialis* Bonn., ventral view of skull, showing Type B of the optic tube, L. M. b, c, × ½; d, × 1/10; e, × 1/14.

gone considerable secondary modification due to the growth of surrounding structures. The degree of modification varies from species to species.

In the adult skulls a distinct bony tube has been formed, which conducts

Table I. Orbitosphenoid

Species	Number of specimens	Number of elements	Shape and Situation of Orbitosphenoid	Contact of Orbitosphenoid
Balaenoptera acuto-rostrata Lacép.	9	2	The optic tube is open throughout its length. The orbitosphenoid elements lie within the tube.	The parietal does not form a part of the optic tube, there is no contact with the orbitosphenoid.
Balaenoptera huttonii Gray	1	2	ditto	ditto
Balaenoptera borealis Lesson	9	1	The proximal part of the optic tube is closed in adult skulls. The elements of the orbitosphenoid are lying within the tube.	The parietal forms the proximal part of the ventral wall of the optic tube and overlaps the orbitosphenoid.
Balaenoptera brydei Olsen	2	1	The optic tube is closed for the greater part of its length; only a smaller part of the orbitosphenoid is visible.	The parietal forms part of the ventral wall of the optic tube but does not touch the orbitosphenoid.
Balaenoptera musculus L.	3	—	The optic tube is not fully closed; however, no orbitosphenoid can be seen in adult skulls.	The parietal forms part of the optic tube, and there is no contact with the orbitosphenoid.
Balaenoptera physalus L.	9	—	The optic tube is partly closed; no orbitosphenoid can be seen.	The parietal does not form a part of the optic tube, and there is no contact with the orbitosphenoid.
Megaptera	5	—	The optic tube is partly closed; the orbitosphenoid is hardly if at all visible.	ditto
Eschrichtius gibbosus (Erxleben) (*Rhachianectes glaucus* (Cope)	3	2	The optic tube is distinctly open throughout its length; the orbitosphenoid elements lying within the tube.	The parietal does not form a part of the optic tube, and there is no contact with the orbitosphenoid.
Neobalaena marginata Gray	1	2	The optic tube is closed. The elements of the orbitosphenoid are lying within the tube.	The parietal forms the proximal part of the ventral wall of the optic tube, and overlaps the orbitosphenoid.

the optic nerve to the eye; in the present paper this tube will be referred to as the optic tube. The degree of development of the optic tube appears to be a function of the absolute size of the skull. In juvenile skulls the optic tube has less developed than in adults. In the adult *Balaenoptera acuto-rostrata* Lacép. the optic tube has less developed than in the adult *Balaenoptera physalus* L. It is, therefore, considered that as far as this orbital feature is concerned *Balaenoptera acuto-rostrata* is the more primitive. A comparison of the general form of the optic tube in the various species of Mystacoceti shows two distinct types:

Type A: The optic tube is shallow; dorsally it is wide as compared to the squamosal processus. The orbitosphenoid and alisphenoid form a relatively small part of its ventral wall (fig. 1*d*).

Type B: The optic tube dorsally is narrow as compared to the squamosal processus. It is more nearly tubular than in Type A. The parietal and the alisphenoid form an appreciable part of the ventral wall of the optic tube (fig. 1*e*).

Although the general shape of the optic tube of the Balaenopteridae conforms with Type A (above), the detailed arrangement and number of elements of the orbito- and alisphenoid which can be seen on the lateral aspect of the skull, varies from one species to another in adult skulls. Tables I and II show the situation and the contact of these two bones in various species and the number of specimens examined of each.

A. Balaenopteridae (Tables I, II).

Balaenoptera acuto-rostrata Lacép. (fig. 2*a*).

As previously stated the optic tube is rather primitive and remains a wide, conical groove throughout life. A portion of the orbitosphenoid can be seen lining the dorsal surface of the groove. Individual variations are to be found in the shape of the alisphenoid posterior to the tube; the number of visible portions varying from 1 to 3.

Balaenoptera huttonii Gray (fig. 2*b*).

Only a partly disarticulated skull of this species was available. The only difference between it and *Balaenoptera acuto-rostrata* is the absence of contact between the alisphenoid and squamosal.

Balaenoptera borealis Lesson (fig. 2*c*).

The shape of the orbitosphenoid is a means of distinguishing this species from *Balaenoptera acuto-rostrata*, as only one comparatively longish portion can be seen. The overlapping of the orbitosphenoid by the parietal at the proximal end of the optic tube is a valuable distinguishing character.

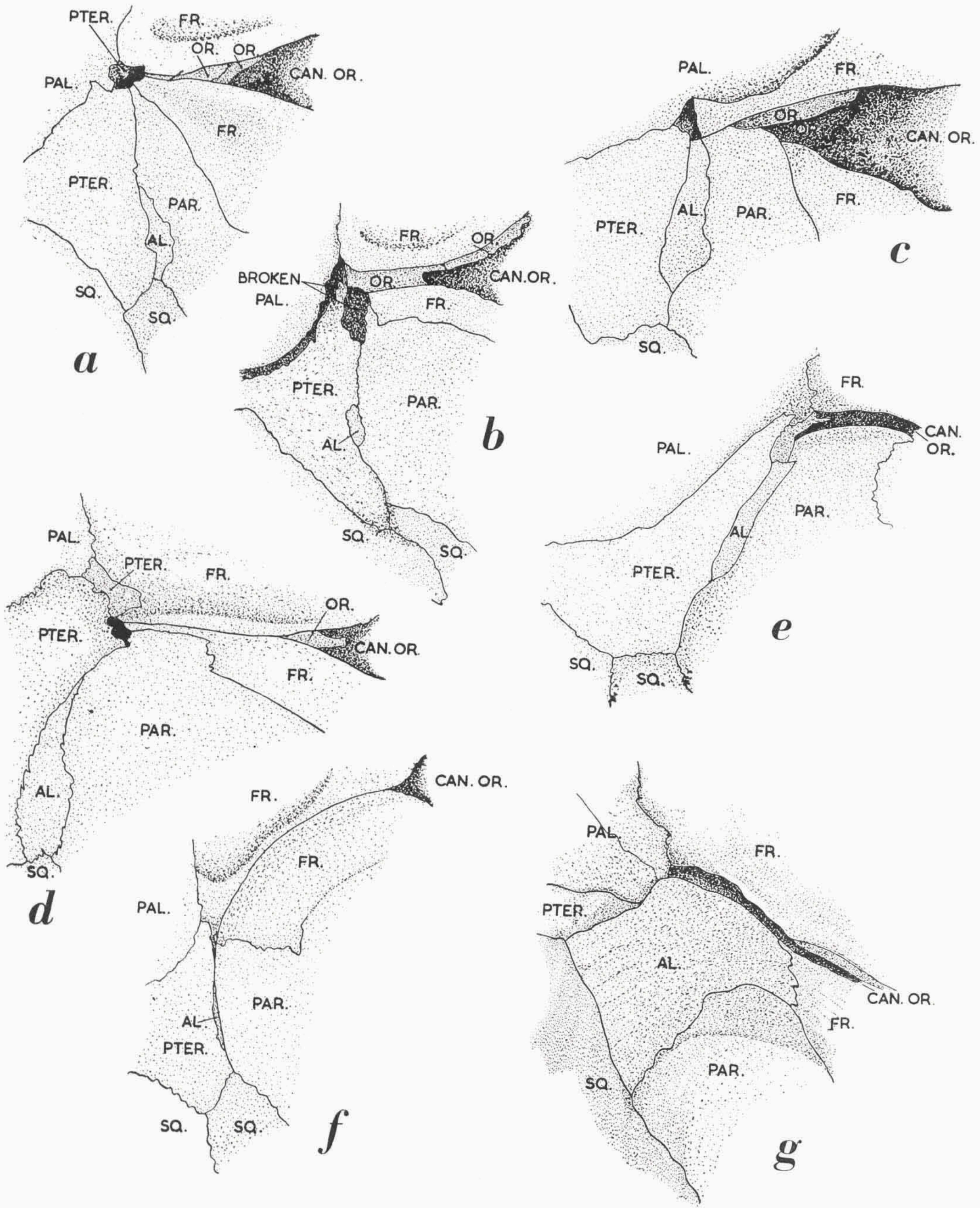

Fig. 2. Left orbito-temporal region of the skull, seen from beneath, more or less diagrammatic; *a, Balaenoptera acuto-rostrata* Lac., L. M., 17-9-1920; *b, Balaenoptera huttonii* Gray, B. M., reg. no. 74-4-13-2; *c, Balaenoptera borealis* Lesson, Monnikendam, 29.VIII.1811; *d, Balaenoptera brydei* Olsen, B. M. reg. no 1920-12-31-1; *e, Balaenoptera musculus* L., B. M., no number; *f, Balaenoptera physalus* L., L. M., Katwijk, XI.1914; *g, Megaptera "boops"*, B. M., 1829. a-d, × 1/4; e, × 1/10; f, × 1/8; g, × 1/6.

Balaenoptera brydei Olsen (fig. 2*d*).

The orbitosphenoid resembles that of *Balaenoptera borealis* in being attenuated and in being only visible at the lateral extremity of the optic

Table II. Alisphenoid

Species	Number of specimens	Number of elements	Shape and Situation of Alisphenoid	Contact of Alisphenoid
Balaenoptera acuto-rostrata Lacép.	9	1-2-3	The alisphenoid is visible in the lateral skull wall, as one or more small bones, posterio-mesially to the optic tube.	The alisphenoid has contact with the squamosal posteriorly.
Balaenoptera huttonii Gray	1	1	The alisphenoid is visible as one rather small bone posterio-mesially to the optic tube.	The alisphenoid has no contact posteriorly with the squamosal.
Balaenoptera borealis Lesson	9	1	The alisphenoid forms a small part of the proximal, ventral wall of the optic tube, and lies also mesial to this tube.	The alisphenoid has contact with the squamosal posteriorly.
Balaenoptera brydei Olsen	2	1	The alisphenoid is distinct in the lateral skull wall, but does not form part of the optic tube.	The alisphenoid has contact with the squamosal posteriorly.
Balaenoptera musculus L.	3	1-nil	Generally variable, rather small in some cases, lying close to the ventral part of the optic tube.	If there is an alisphenoid visible in the lateral skull wall, there is posteriorly no contact with the squamosal.
Balaenoptera physalus L.	9	1	Shape variable, generally rather small; when it is present, it does not form part of the ventral wall of the optic tube.	If there is an alisphenoid visible in the lateral skull wall, there is posteriorly no contact with the squamosal.
Megaptera	5	1-2	The alisphenoid is distinctly visible in the ventral wall of the optic tube.	The alisphenoid has contact posteriorly with the squamosal.
Eschrichtius gibbosus (Erxleben) (*Rhachianectes glaucus* (Cope))	3	2	The alisphenoid is a relatively large bone lying posterio-mesially to the optic tube.	The alisphenoid has contact posteriorly with the squamosal.
Neobalaena marginata Gray	1	1	The alisphenoid is visible as one rather small bone posterio-mesial to the optic tube.	The alisphenoid has no contact posteriorly with the squamosal.

tube. The alisphenoid differs from that in *Balaenoptera borealis* by its lack of contiguity with the optic tube. This feature is, however, not very obvious in the skull of *Balaenoptera brydei* in the Leiden Museum. Posteriorly the alisphenoid makes contact with the squamosal, a feature in which this species differs from *Balaenoptera borealis*. The systematic position of *Balaenoptera brydei* has been investigated by Lönnberg (1931), Andrews (1936), and Junge (1950), and all are agreed that it is closely related to *Balaenoptera borealis*.

Balaenoptera musculus L. (fig. 2*e*).

The orbitosphenoid is not visible, being completely overlapped by the parietal, which forms the ventral wall of the proximal end of the optic tube. The alisphenoid is small, variable in shape and may be invisible externally.

Balaenoptera physalus L. (fig. 2*f*).

The orbitosphenoid is concealed by the optic tube; no part of the former being visible. There are many individual variations in the shape of the alisphenoid, which sometimes is very small. The most distinguishing character is the position of the parietal, which has no contact with the orbitosphenoid. It does not form part of the optic tube and it is separated from the latter by a portion of the frontal.

Megaptera spec. (fig. 2*g*).

The comparatively large extension of the alisphenoid on the posterior wall of the mesial end of the optic tube is particularly characteristic. This feature is reminiscent of the alisphenoid of the Balaenidae and it appears to be a more primitive condition of the bone than that found in the other Balaenopteridae. The orbitosphenoid is hardly visible.

B. Rhachianectidae (Tables I, II).

Eschrichtius gibbosus (Erxleben) (figs. 3*a*, *b*).

The optic tube is rather wide and shallow as in *Balaenoptera acutorostrata*, and two portions of the orbitosphenoid can be seen occupying its dorsal wall and mesially its ventral wall. The alisphenoid is a relatively large bone, lying mesially and posteriorly of the optic tube. In this latter respect the orbital features of the Rhachianectidae have something in common with those of the Balaenidae. The specimens examined in this group are variously labelled *Rhachianectes glaucus* (Cope) or *Eschrichtius gibbosus* (Erxleben). Junge and van Deinse (1937) have shown that the last name is correct.

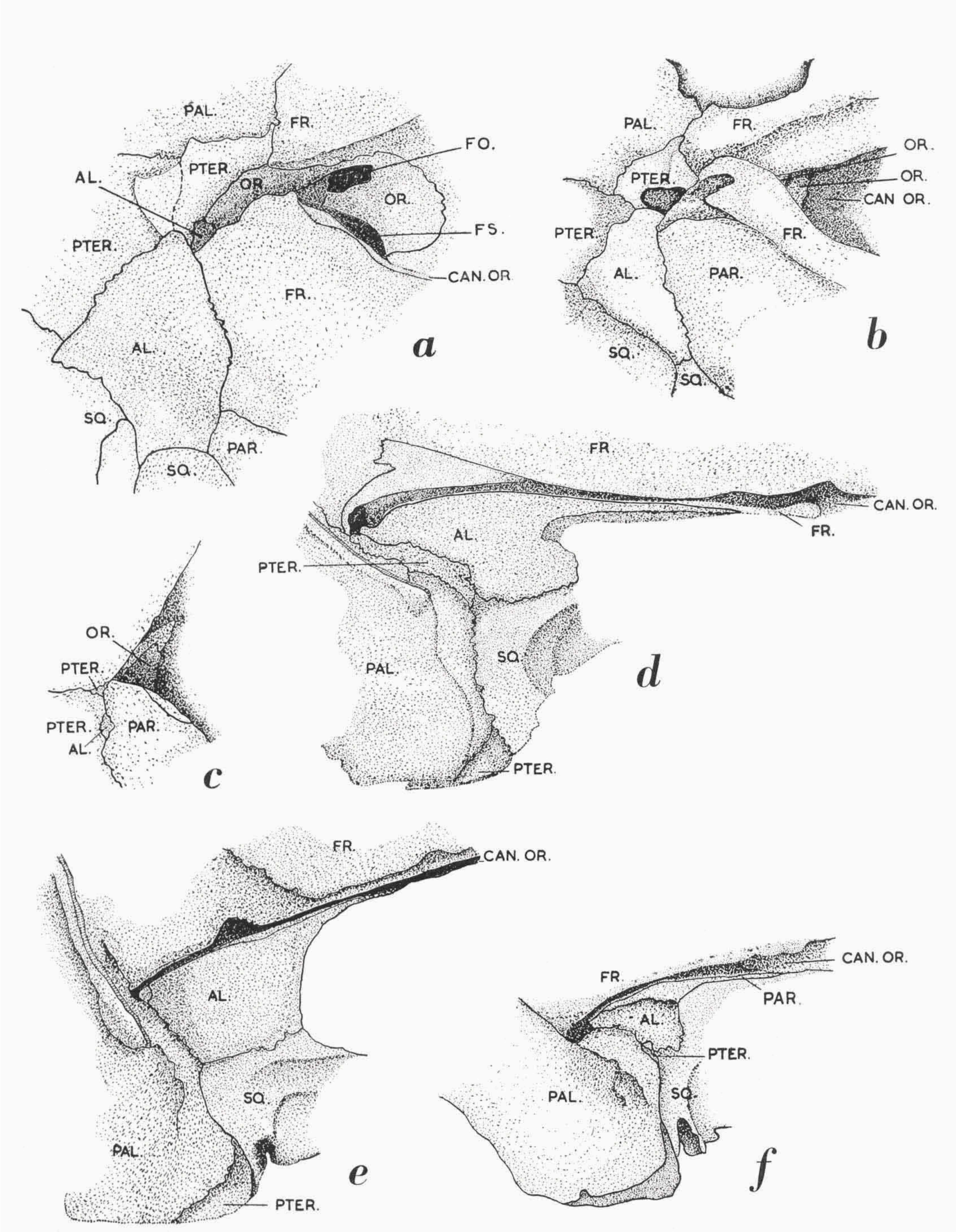

Fig. 3. Left orbito-temporal region of the skull, seen from beneath, more or less diagrammatic; *a, Eschrichtius gibbosus* (Erxl.), B. M., 91-3-3-1; *b,* ventral view of optic tube of *Eschrichtius gibbosus* (Erxl.), showing the components of the dorsal wall, G. M. L., no. St. 20350; *c, Neobalaena marginata* Gray, B. M., reg. no. 86-1-27-1; *d, Balaena mysticetus* L., B. M., reg. no. 338a; *e, Balaena glacialis* Bonn., B. M., reg. no. 1911-5-31-1; *f, Balaena australis* Desm., B. M., 73-3-3-1. a, b, × 1/4; c, × 1/6; d-f, × 1/10.

C. Balaenidae.

With the exception of *Neobalaena marginata* Gray (fig. 3*c*, Tables I, II) this group of the Mystacoceti conforms in its orbital characteristics with Type B of the optic tube (vide supra). In all the species examined the alisphenoid is relatively much more conspicuous than that in the Balaenopteridae. The orbitosphenoids appear to lie completely within the optic tube, and as no well defined portions could be identified, the description of the orbital features will be confined to alisphenoid and parietal. Of the specimens examined two were *Balaena mysticetus* L., four were *Balaena glacialis* Bonn., four were *Balaena australis* Desm. In the shape and extent of the alisphenoid all three species are strikingly different, and as the shape of this bone is more or less constant within one species, a separate description will be given for each species.

Balaena mysticetus L. (fig. 3*d*).

The external walls of the optic tube are formed anteriorly by the frontal, and mesially-posteriorly by a narrow rim of the frontal and by the alisphenoid. In shape the alisphenoid resembles an anvil; greatest diameter of the visible portion is about 36 cm, of which 20 cm constitute the length of the strong lateral processus, which extends laterally along the anterior border of the parietal.

Balaena glacialis Bonn. (fig. 3*e*).

The constituents of the wall of the optic tube are as in *Balaena mysticetus* L. The alisphenoid is relatively smaller and it is rectangular in shape. The lateral process is poorly developed and is never more than 9 cm in length. The anterior margin of the alisphenoid is coincident with the posterior edge of the suborbital fissure mesially, but is separated from the latter by a small interval laterally.

Balaena australis Desm. (fig. 3*f*).

The constituents of the optic tube are as in the above two species, but the alisphenoid is relatively smaller. It is roughly triangular in shape, and the lateral process is absent. Its anterior margin is coincident with the posterior edge of the suborbital fissure mesially, but diverges from it laterally so that a considerable part of the parietal is visible on the edge of the fissure.

Discussion

In taking into account the foregoing characteristics as being diagnostic of the various species of Mystacoceti, it is important to correlate all the features described. The use of any single character would give misleading results. For instance in the general shape and degree of development, the optic tube in *Balaenoptera acuto-rostrata* strongly resembles that of the immature skulls of *Balaenoptera borealis*. Moreover, the shape of the orbitosphenoid is somewhat similar in immature skulls of these two species. Nevertheless, when the position and shape of the parietals are considered, the distinction between the two at once becomes apparent. This change of skull characteristics with growth is a special feature of the Mystacoceti and has been investigated by True (1904), Andrews (1908), Matthews (1937), etc.

Within all species there are a certain number of individual variations, this phenomenon being more common in some species than in others, viz., *Balaenoptera musculus* and *Balaenoptera physalus*. In three of the specimens of *Balaenoptera physalus* examined, there is an abnormal condition of the parietal. It is significant that this abnormality is the same in the three specimens, and represents a form, which is intermediate between the shape and position of the parietal in *Balaenoptera physalus* and those in *Balaenoptera musculus*.

Within the range of specimens examined of *Megaptera*, two distinct conditions of the parietal were noted, similar to those found in *Balaenoptera physalus* and *Balaenoptera musculus*. Matthews (1937) noted four different colour groups among the specimens of *Megaptera*, the Southern Humpbacks being predominantly darker in colour than those of the Northern hemisphere. The same author has found a difference in the range of variation between males and females, but no marked difference in measurements when the northern and southern specimens are taken together. Whether the above differences in the parietal are sex-linked or related to locality is a matter requiring further investigation.

The identification of different species of Balaenidae has been studied by a number of Zoologists in the past; Eschricht (1866) distinguishes two species, *Balaena mysticetus*, Greenland Right Whale, and the Sarde or Nordcaper, *Balaena glacialis*, which frequented the Bay of Biscay. Racovitza (1903) distinguished *Balaena mysticetus*, but states that all the other species, viz., *Balaena glacialis*, *Balaena japonica*, and *Balaena australis*, must be united into one, which he named *Balaena glacialis* Bonn. Oliver (1922) describing the Cetacea of the New Zealand seas states: "The Southern Right Whale, which is confined to the Southern Temperate and Subantarctic Oceans appears to differ from the Nordcaper (*B. glacialis*) in the number of ribs and other osteological features". Lönnberg (1923) distinguishes *Balaena australis* from *Balaena glacialis* using the length and breadth of the skulls. On the basis of the shape and arrangement of the bones of the orbit, particularly that of the alisphenoid, it is possible to distinguish three definite species, namely *Balaena mysticetus*, *Balaena glacialis*, and *Balaena australis*.

Uniformity in the shape of the alisphenoid, within any one species, is so obvious that any specimen can be identified from this feature alone.

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Explanation of Lettering

AL., alisphenoid; CAN. OR., canalis orbitalis; F. IN., foramen infraorbitale; F. L., foramen lacrymale; F. M., foramen malare; F. O., F. OP., foramen opticum; F. OV., foramen ovale; F. P., foramen palatinum; FR., frontal; F. S., foramen supraorbitale; F. SP., foramen sphenorbitale; J., jugal; M., maxilla; N., nasal; OR., orbitosphenoid; PAL., palatine; PAR., parietal; P. F. L., pars facialis of the lacrymal; P. O. L., pars orbitalis of the lacrymal; PR. OR., processus orbitalis; PR. Z. M., processus zygomaticus of the maxilla; PR. Z. S., processus zygomaticus of the squamosal; PT., PTER., pterygoid; SQ., squamosal.

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