V.—*Observations on the Skull in Fœtal Specimens of Whales of the Genera* Megaptera *and* Balænoptera.

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INTRODUCTION.

This paper furnishes descriptions of five skulls of fœtal Whales—three of *Megaptera* and two of *Balænoptera*. The investigation was begun in July, 1912, at the British Museum (Natural History), but was discontinued, partly in consequence of the pressure of other work, and partly owing to the superior attraction of *Cephalodiscus* as a subject of research; it was resumed in November, 1920, in the Huxley Research Laboratory at the Royal College of Science.

My thanks are due to Sir SIDNEY F. HARMER, Director of the Natural History Departments of the British Museum, for permission to prepare and describe the skulls; also to Prof. E. W. MACBRIDE, and the administrative officers of the Royal College of Science, for the facilities offered by the Huxley Research Laboratory for the prosecution of the Research. For frequent hints and suggestions during the progress of the work, and for much valuable advice, I am indebted to Sir SIDNEY HARMER, Prof. E. W. MACBRIDE, Dr. D. M. S. WATSON, Dr. C. W. ANDREWS, and others.

In planning out the paper it was found convenient first to describe the smallest skull of *Megaptera*, then to consider the other two skulls of *Megaptera*, and finally the two skulls of *Balænoptera*.

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SPECIFIC NAMES OF *Megaptera* AND *Balænoptera.*

In his review of the literature regarding the Humpback Whales, TRUE (**32**, 1904, p. 211) gives the reasons why, assuming, as is now customary, that the Humpbacks belong all to a single species, the specific name *nodosa*, applied by BONNATERRE[*] in 1789, should be retained for them. The earlier name of *Balæna boöps*, given by FABRICIUS[†] in 1780, is pre-occupied by *Balæna boöps* LINN. 1758, a name applied to a Whale that is not the Humpback, but a species of what is now the genus *Balænoptera*, namely, *B. physalus*. RUDOLPHI (**27**), in a paper published in 1832, describing a Humpback caught at the mouth of the Elbe in 1824—the earlier specimens were from New England waters and Greenland—gave to it the name *Balæna longimana*. In 1845 BRANDT[‡] established for the Humpbacks the subgeneric name of *Boöps*; but this name being pre-occupied by *Boöps* CUVIER, 1817, for a genus of Fishes, GRAY,[§] in 1846, substituted the name *Megaptera*, a term of generic, and not subgeneric, rank. So that, on these arguments, the name for the Humpback Whales stands as *Megaptera nodosa* BONNATERRE.

ALLEN (1916,[||] p. 289) discusses the question of nomenclature on much the same lines as TRUE. Arriving at the same conclusion, he adopts the name *nodosa*, as also do KÜKENTHAL (1914,[¶] pp. 6–7), and COLLETT (1912,[**] p. 606).

The great majority of the specific names that have at various times been introduced are now absorbed as synonyms; these names include: *poeskop*, *antarctica*, *americana*, *longipinna*, *novæ-zelandiæ*, *burmeisteri*, *indica*, *osphyia*, *bellicosa*, *versabilis*, *kuziza* (*kuzira*), *brasiliensis*, and possibly others.

The names about which discussion still centres are *lalandii* and *longimana*. The species *Balæna lalandii*, FISCHER, 1829, was retained by GRAY[††] as *Megaptera lalandii*, although in 1846 he had termed it *Megaptera poeskop*. This is the southern Humpback Whale. LÖNNBERG (1906,[‡‡] pp. 33–34) regards it as specifically distinct

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[*] *Balena nodosa*, p. 5—BONNATERRE (Abbé), 'Tableau encyclopédique et méthodique des Trois Règnes de la Nature,' Paris, 4to, Cétologie, 1789, pp. 42 + 28, 12 plates.

[†] FABRICIUS, O., 'Fauna Grœnlandica,' Copenhagen and Leipzig, 1780, 8vo, pp. 452, 1 plate.

[‡] BRANDT, F., 'Animaux Vertébrés,' pp. 419–466, in P. DE TCHIHATCHEFF, 'Voyage Scientifique dans l'Altaï Oriental,' Paris, 1845, 4to.

[§] *Megaptera longipinna*, p. 83—GRAY, J. E., "On the British Cetacea," 'Annals and Mag. Nat. Hist.,' 17, 110, Feb., 1846, pp. 82–85. See also 'Zoology of the Voyage of H.M.S. *Erebus* and *Terror*,' 1, Cetacea, London, 1846, 4to, pp. 13–53, 38 plates; *Megaptera longimana*, p. 17.

[||] ALLEN, G. M., "The Whalebone Whales of New England," 'Mem. Boston Soc. Nat. Hist.,' 8, 2, September, 1916, pp. 105–322, 9 plates.

[¶] KÜKENTHAL, W., "Untersuchungen an Walen, II," 'Jena. Zeitschr. Naturwiss.,' 51, 1, Jan., 1914, pp. 1-122, 6 plates, 24 text-figs.

[**] COLLETT, R., 'Norges Pattedyr,' Kristiania, 1911–12.

[††] 'Proc. Zool. Soc.,' May, 1864, p. 207.

[‡‡] LÖNNBERG, E., "The Fauna of South Georgia: I, Vertebrates," 'Kungl. Svenska Vetensk. Handl.,' 40, 5, 1906, pp. 1–104, 12 plates, 7 text-figs.

from the northern Humpback, on account of its smaller size, and accepts the name *M. lalandii*, but it is to be noted that LILLIE (**25**, 1915, pp. 106, 108) expresses his inability to distinguish its tympanic bone and scapula, upon which the specific independence is largely based, from those of the northern form, *M. nodosa.* There still remains the difference in the outline of the face of the centrum of the cervical vertebræ, oval or sub-circular in the northern form, and oblong, with four rounded corners, in the southern, but the differences seem scarcely of more than varietal value.

RACOVITZA (1903,* pp. 32–33, 53) is of opinion that the southern Humpback is the same as that of the eastern Atlantic, but is doubtful whether the latter is the same as that of the western Atlantic, to which the name *M. nodosa* would apply; he therefore adopts for the southern form the name *M. longimana.* LIOUVILLE (1913,† pp. 118–124), also, being unable to satisfy himself as to the identity of the American Humpback with that of Antarctic waters, admits the priority of *nodosa* for the former, and adopts the name *longimana* for the southern Whales that he is describing in his report. SALVESEN (1914,‡ p. 482) and BRUCE (1915,§ p. 493) refer to the southern Humpback as *M. boöps.*

As regards the species of *Balænoptera*, the names employed in the present paper are those that are in use at the British Museum (Natural History). I take the opportunity of thanking Mr. W. P. PYCRAFT for his kindness in checking the list given below.

Common Rorqual, Common Finner, Herring Whale, Finhval, Sildehval:—*Balænoptera physalus* LINN. (= *B. musculus* auctt.).

Blue Whale, Sibbald's Whale, Sulphurbottom, Blaahval:—*Balænoptera musculus* LINN. (= *B. sibbaldii* GRAY).

Sei Whale, Pollack Whale, Rudolphi's Rorqual:—*Balænoptera borealis* LESSON (= *B. laticeps* GRAY).

Lesser Rorqual, Lesser Finner, Little Piked Whale, Minkehval, Vaagehval, Zwergwal:—*Balænoptera acuto-rostrata,* LACÉPÈDE (= *B. rostrata* auctt.).

Little is as yet known concerning the skeleton and general anatomy of the South African form *Balænoptera brydei*, but the Whale seems to be distinct from the four species enumerated above.‖

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* RACOVITZA, E. G., "Résultats du Voyage du S.Y. *Belgica*," 'Zoologie,' Cétacés, 4to, Anvers, 1903, pp. 1–142, 4 plates, 15 text-figs.

† LIOUVILLE, J., "Cétacés de l'Antarctique," 'Deux. Expéd. Antarctique Française' (1908–10), Paris, 1913, pp. vi+276, 15 plates, 21 text-figs.

‡ SALVESEN, T. E., "The Whale Fisheries of the Falkland Islands and Dependencies," 'Rep. Scot. Nat. Antarctic Exped.,' 4, 19, Edinburgh, May, 1914, pp. 479–486, 10 plates, 1 text-fig.

§ BRUCE, W. S., "Some Observations on Antarctic Cetacea," 'Rep. Scot. Nat. Antarctic Exped.,' 4, 20, Edinburgh, March, 1915, pp. 491–505, 2 plates, 1 text-fig.

‖ See OLSEN, OE., 'Proc. Zool. Soc.,' 1913, pp. 1073–1090, 5 plates.

LITERATURE.

In this review of the literature it will be sufficient to mention the published accounts and figures of the skull in fœtal Mystacocetes; a good deal has been written upon the early skull in the Odontocetes, but sufficient is already known of the fœtal stages in the baleen whales to make it unnecessary to extend the limits of the review to include the toothed whales.

The earliest account of the skull in fœtal Mystacocetes is that given by ESCHRICHT (**9**, **10**). His smallest skull was taken from a 9-inch fœtus (229 mm.) of the Vaagehval (*Balænoptera acuto-rostrata* LACÉPÈDE), and measures $2\frac{2}{3}$ inches (68 mm.) in length (**10**, 1849, pp. 113, *et seq.*; Plates 11 and 14, fig. 1). ESCHRICHT also gives a description and some figures of the skull of a large fœtus of the Vaagehval measuring $6\frac{1}{2}$ feet, or 1·980 metre (**10**, Plates 10, 13), and a figure of a longitudinal section of the skull of another fœtus (Tikagulik, or Greenland variety) of about the same size (Plate 12). He examined also the skulls of fœtal, young and adult *Megaptera*, but neither describes nor figures them; he merely mentions a few points in which these skulls differ from those of *Balænoptera*, with which genus he was at the time more directly concerned (**10**, pp. 118–119). He had three fœtal *Megaptera* for study, measuring respectively 35, 45 and $74\frac{1}{4}$ inches, and the skeleton was prepared from the 45-inch fœtus.

In 1885 SMETS (**29**) gave a short account of the skull of a fœtal specimen of *Balænoptera musculus* (*sibbaldii* GRAY) in the museum of Louvain University. The specimen was obtained in 1876 at Vadsö, in the Gulf of Varanger, Lapland. SMETS does not state the length of the fœtus—apparently only the head was kept—but he gives the length and breadth of the skull as 400 mm. and 300 mm. respectively (= $15\frac{3}{4}$ inches and $11\frac{4}{5}$ inches).

KÜKENTHAL (**23**, II, 1893, Plate 21, fig. 6) has given a figure of a median section of the head of a fœtus of *Balænoptera physalus* (*musculus* auctt.) measuring 1180 mm.; and some transverse and longitudinal diagrammatic sections of the head (text-figs. 42–47, pp. 318–319). And WEBER (1904,* fig. 418, p. 563) gives an internal view of the right half of the skull of a young (not fœtal) *Balænoptera acuto-rostrata*, measuring 5·8 metres (19 feet) in length.

In recent years DE BURLET has been devoting much attention to the primordial cranium of the Cetacea, and has described and figured reconstructed models based upon serial sections of the chondrocranium of *Phocæna* (**6**, I, II), *Balænoptera* (**6**, III), and *Lagenorhynchus* (**6**, IV), together with a general review of the subject (**6**, V). The paper on *Balænoptera acuto-rostrata* (**6**, III, 1914) is of particular interest in connection with the small skull of *Megaptera* (Skull X) described in the following pages; his embryo measured 105 mm. ($4\frac{1}{8}$ inches).

The latest paper on the skull of a fœtal *Balænoptera* is one by SCHULTE (**28**, 1916).

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* WEBER, M., 'Die Säugetiere,' 8vo, 1904, Jena, pp. 866, 567 text-figs.

giving a very detailed account of the cartilages and bones of the head of a fœtus of *B. borealis* from Japan, measuring 14¾ inches (375 mm.). The length of the skull is 100 mm., or just upon 4 inches, and the maximum breadth is 61 mm.

In 1915 there appeared a short paper by HONIGMANN (**19**) on the primordial cranium of *Megaptera*, based upon reconstruction-models of the skull of two embryos, measuring 49 (? 42) mm. and 69 mm. respectively (Stages V and IX of KÜKENTHAL, 1914).* Three illustrations are given of the smaller model, but the several cartilages and bones are not named. In a later and larger work, published in 1917 (**20**), HONIGMANN gives four carefully executed and labelled figures of this same model (Stage V), together with a detailed description of it, and additional observations on the skulls of three other embryos of *Megaptera* (Stage III of KÜKENTHAL, 30 mm. in direct length, and 62 mm. along the curve of the back; Stage IX, 69 mm. direct, and 114 mm. along back; Stage XII, 145 mm. direct, and 210 mm. along back).

The account of the three fœtal skulls of *Megaptera* given in the present paper thus fills a gap in our knowledge by tracing the later development of the cartilages and bones, and connecting up the published accounts of the primordial cranium with those of the adult skull of the Humpback.

The fœtal skull of *Rhachianectes* appears not to have been studied. As regards *Balæna*, ESCHRICHT has given figures of the skull of a late fœtus (5¼ feet or 1·6 metre) of *B. japonica* (**13**, 1869, Plates 1 and 2); and VAN BENEDEN and GERVAIS give a longitudinal section and a side view of the skull of a large fœtus of *Balæna mysticetus* (**4**, Plate 4, fig. 3: Plate 6, fig. 1). GERVAIS has also figured the isolated sphenoidal region of a fœtus of *Balæna antipodum* measuring a little over a metre in length (**17**, 1871, Plate 4, figs. 3 and 3A).

There is a rather indistinct figure of a median section of the skull of a fœtal Southern Right Whale (*Balæna australis*) in FLOWER's 'Osteology of the Mammalia' (London, Ed. 1, 1870, p. 195; Ed. 3, 1885, p. 221); and dorsal and lateral views of the skull of a fœtus of the same species appear in HUXLEY's 'Anatomy of Vertebrated Animals' (London, 1871, p. 337). The skull of *Balæna mysticetus* figured by ESCHRICHT and REINHARDT (**11**, Plate 3, fig. 1, and p. 103; **12**, Plate 3, fig. 1, and p. 92) is from a new-born specimen, 13 feet long.

MATERIAL STUDIED.

Five skulls were prepared and examined, three of the Humpback Whale, *Megaptera nodosa* BONN., one of the Sei Whale or RUDOLPHI'S Rorqual, *Balænoptera borealis* LESSON, and one of the Blue Whale or SIBBALD'S Whale, *Balænoptera musculus* LINN. To facilitate reference they may be distinguished by the letters X, Y, Z, R, S.

The smallest *Megaptera* skull (Skull X) is that of a fœtus measuring 6 inches from

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* KÜKENTHAL, W., "Untersuchungen an Walen, II," 'Jena. Zeitschr. Naturwiss.,' 51, 1, Jan., 1914, pp. 1–122, 6 plates, 24 text-figs.

the vertex of the head* to the cleft of the tail-fin, collected by Dr. G. Cruickshank, October 1, 1910, off South Georgia. Skull Y is that of a fœtus of *Megaptera* measuring 16 inches from the tip of the snout to the cleft of the tail-fin, collected by Dr. G. Cruickshank off South Georgia. Skull Z is that of a fœtus of *Megaptera*, measuring 27 inches from the tip of the snout to the cleft of the tail-fin, collected off South Georgia on the Major G. E. H. Barrett-Hamilton Whaling Mission, 1913.

Skull R is that of a fœtus of *Balænoptera borealis*, measuring 3 feet 11 inches, collected off the Shetland Isles on behalf of the British Museum (Natural History) in June, 1912. Skull S is that of a fœtus of *Balænoptera musculus*, computed to be 6 feet 4 inches in length, collected off South Georgia on the Major G. E. H. Barrett-Hamilton Whaling Mission. Expressed in tabular form, the particulars of the five skulls are as set out below :—

Species.	Reference letter.	Register number at Brit. Mus. (N.H.).	Locality.	Length of fœtus.	Length of skull.	Maximum breadth of skull.
M. nodosa, Bonn.	Skull X	9.31.10.11	South Georgia	6 in. = 152 mm.	$2\frac{7}{16}$ in. = 62 mm.	$1\frac{3}{8}$ in. = 35 mm.
M. nodosa, Bonn.	Skull Y	1.1.5.12	South Georgia	16 in. = 406 mm.	$4\frac{3}{4}$ in. = 121 mm.	$3\frac{1}{4}$ in. = 83 mm.
M. nodosa, Bonn.	Skull Z	2.19.3.14	South Georgia	27 in. = 686 mm.	$8\frac{11}{16}$ in. = 205 mm.	$4\frac{15}{16}$ in. = 125 mm.
B. borealis, Lesson.	Skull R	1.5.7.12	Shetland Isles	3 ft. 11 in. = 1·194 m.	$11\frac{1}{2}$ in. = 292 mm.	$6\frac{1}{4}$ in. = 159 mm.
B. musculus, Linn.	Skull S	1.7.7.14	South Georgia	6 ft. 4 in. = 1·930 m.	19 in. = 483 mm.	12 in. = 305 mm.

SKULL OF A 6-INCH FŒTUS OF *Megaptera nodosa* BONN.

This skull (Skull X) is that of a fœtus, measuring 6 inches (152 mm.) from the vertex of the head to the cleft of the tail-fin, collected by Dr. G. Cruickshank, in October, 1910, off South Georgia, and sent to the British Museum (Nat. Hist.). The length of the skull, from condyles to the tip of the rostrum, is $2\frac{7}{16}$ inches, or 62 mm.; the maximum width, across the zygomatic process of the squamosal, is $1\frac{3}{8}$ inches, or 35 mm. Figs. 1–4 represent the skull somewhat enlarged (× 1·8).

The skull has reached that stage of development at which the chondrocranium is composed of firm hyaline cartilage, as distinct from the earlier soft and delicate procartilage; and the reduction of those parts that disappear later, *e.g.*, the upper parts of the lamina parietalis, has scarcely begun; the general ossification of the chondrocranium, moreover, has hardly commenced, for while the supraoccipital is

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* In young fœtuses, such as that from which Skull X was prepared, the head is bent down to such an extent that it cannot be straightened out for a snout-measurement, and the vertex-measurement is taken instead. The measurements in this and other cases are direct or caliper measurements, not measurements taken along the curve of the back.

already well formed, the only other indications are small centres of ossification in the basioccipital and basisphenoidal regions. The membrane-bones are already assuming their definitive relations to one another, but they do not yet show any signs of those grotesque proportions that characterise the membrane-bones of the skull of adult Whales.

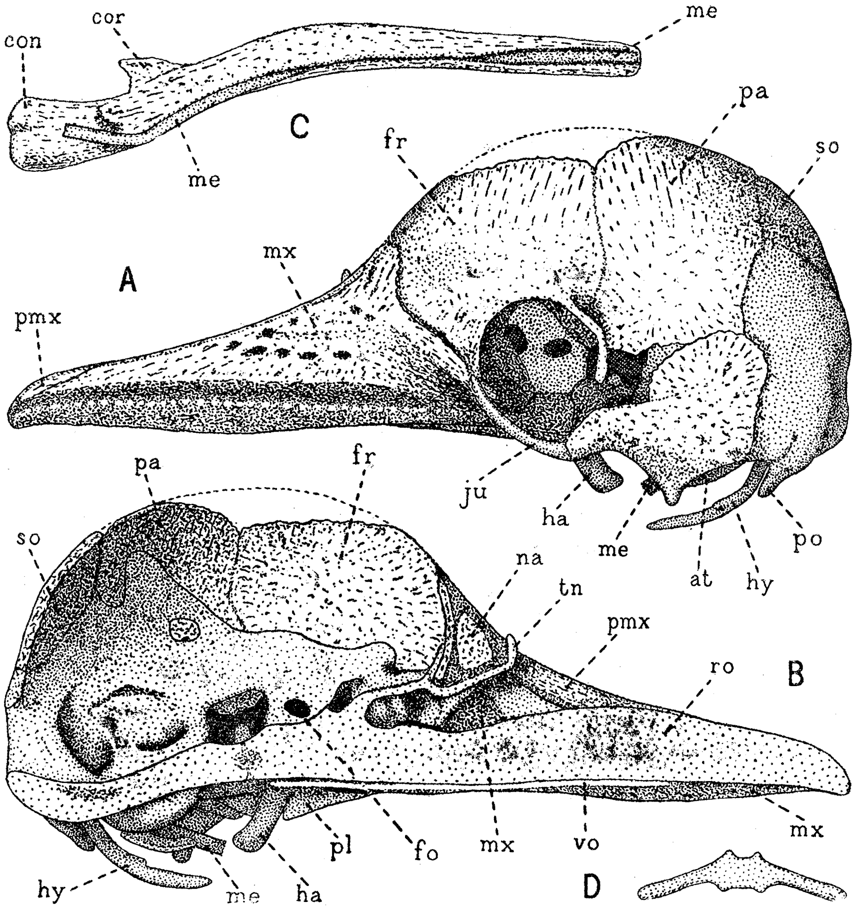

Fig. 1.—Skull of a fœtus of *Megaptera nodosa* measuring 6 inches: × 1·8. A, view of left side. B, left half of bisected skull seen from within. C, left ramus of mandible seen from the mesial side; the Meckelian cartilage is cut across, and would fit upon the part marked *me* in B. D, hyoid bar.

at, annulus tympanicus, the first-formed part of the tympanic bone; *con*, articular condyle of mandible; *cor*, coronoid process; *fo*, foramen opticum; *fr*, frontal; *ha*, hamular process of pterygoid; *hy*, hyoid cornu, stylohyal or Reichert's cartilage; *ju*, jugal; *me*, Meckel's cartilage; *mx*, maxilla; *na*, nasal; *pa*, parietal; *pl*, palatine; *pmx*, premaxilla; *po*, paroccipital process of exoccipital cartilage; *ro*, rostral cartilage; *so*, supraoccipital; *tn*, tectum nasi; *vo*, vomer.

It is remarkable how closely, except in the exaggerated length of the prenasal maxillary region of the beak, the skull resembles that of an ordinary mammal, for the membrane-bones are all sufficiently well formed to show that their relations are just those that would be found in a late fœtus of any typical Eutherian. The enormously disproportionate growth of the facial over the cranial parts, which renders an adult Whale's skull so remarkable, is not very advanced, even in Skull Z, from a 27-inch fœtus.

Primordial Cranium.—The chondrocranium of *Megaptera nodosa* has been so minutely described by HONIGMANN (**19**, **20**), and that of *Balænoptera acuto-rostrata* by DE BURLET (**6**, III), that only the salient features of Skull X need here be referred to. HONIGMANN studied four skulls, including one of a fœtus as long as 145 mm., *i.e.*, almost as large as that (152 mm.) from which Skull X was prepared, but his observations apply mainly to the skull of a fœtus of a direct length of 49 mm. The fœtus of *Balænoptera* of which the skull was studied by DE BURLET measured 105 mm.

The foramen magnum of Skull X is relatively large, and is not as strictly circular as it becomes later (*cf.* figs. 2 and 6); the margin is entirely cartilaginous, and even in Skull Z the supraoccipital ossification is separated from the foramen by a considerable tract of cartilage. The occipital condyles are feebly differentiated, and are relatively wider apart than in later stages of development. There are no signs of ossification of the exoccipitals, but the supraoccipital is well developed (figs. 1, A and B, 2, 3, *so*), and has the form of a half-dome behind the parietal bones. It is a cartilage-bone, an ossification of the tectum posterius, without any interparietal element; the front edge is nearly transverse (fig. 3), and scarcely overlaps the parietal bones; and there is as yet very little suggestion of the forwardly directed angle of bone that is coming into prominence in Skull Z (fig. 8) and is still more pronounced in the adult (**12**, Plate 3, fig. 2).

There is no indication of the supraoccipital having arisen as a paired bone; the skull is clearly too old to show whether the centre of ossification was double or single. Neither is there any suggestion of a partial division of the bone into right and left parts, as one might expect from a statement of WEBER (1904,* p. 49), who, after noting that in Mammals the supraoccipital is usually unpaired, continues: "Zuweilen entsteht es aber aus zwei Knochenkernen, wie bei *Tatusia*, *Erinaceus* und den Cetaceen. Bei letzteren kann es dies noch lange verraten durch unvollständige Teilung in der Medianlinie." HONIGMANN (**20**, p. 24) finds that in his 49-mm. fœtus of *Megaptera* the tectum posterius shows no signs of ossification, and DE BURLET, in his description of the skull of a 105-mm. fœtus of *Balænoptera acuto-rostrata*, does not go into the question; he merely says that the tectum posterius is partially ossified (**6**, III, p. 128). From his text-fig. 1 (p. 122) one would conclude that the ossification is single, not paired.

The paroccipital or paracondylar processes (figs. 1, A, and 2, *po*) are already well marked at the lower ends of the laminæ alares, and are wider apart, relatively to the total width of the skull, than in later stages (*cf.* figs. 2 and 6, *po*); the subsequent increase in the width of the skull, it may here be remarked, is due to a lateral

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* WEBER, M., 'Die Säugetiere,' 1904, 8vo, Jena, pp. 866, 567 text-figs.

expansion of the squamosal and frontal bones rather than to a uniform growth of all parts. In the skull of an earlier fœtus of *Megaptera* figured by HONIGMANN (**20**, Plate 1) the paroccipital processes are remarkably long and forwardly bent.

The centres of ossification of the basioccipital and basisphenoid can be seen in a longitudinal section of the skull (fig. 1, B), but are not visible otherwise, since the ossification is not yet sufficiently far advanced to reach the upper and lower surfaces of the cartilage. The craniopharyngeal canal traverses the middle of the ossification-centre of the basisphenoid (fig. 1, B); in fig. 4 the lower orifice of the canal is seen just behind the posterior edge of the vomer. The presphenoid cartilage shows no signs of ossification and passes imperceptibly in front into the rostral cartilage, a cartilage of nasal (mesethmoidal) origin (fig. 1, B, *ro*).

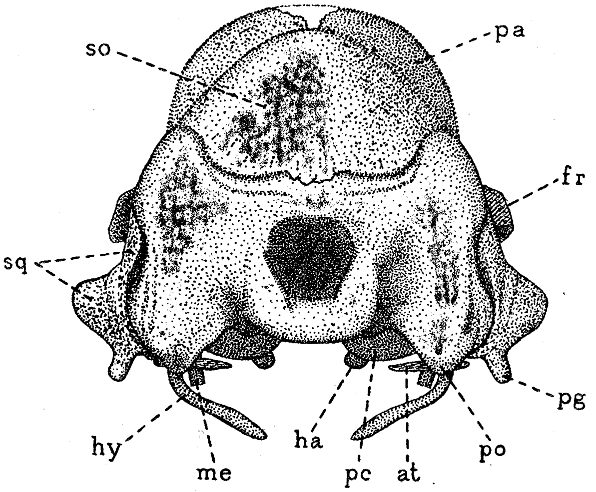

FIG. 2.—Back view of the skull of a fœtus of *Megaptera nodosa* measuring 6 inches, × 1·8.

at, annulus tympanicus; *fr*, frontal; *ha*, hamular process of the pterygoid; *hy*, hyoid cornu, stylohyal or REICHERT'S cartilage; *me*, MECKEL'S cartilage, cut short; *pa*, parietal; *pc*, pars cochlearis of the auditory capsule; *pg*, postglenoid process of the squamosal; *po*, paroccipital process of the exoccipital cartilage; *so*, supraoccipital; *sq*, squamosal.

The auditory capsule is relatively large, and the pars cochlearis prominent in a ventral view (fig. 4, *pc*). Behind it is the foramen lacerum posterius or jugular foramen, and in front of it is the foramen lacerum medium, at present in the form of a large, crescentic fissure bounded anteriorly by the back of the pterygoid bone. There is no separate foramen for the hypoglossal nerve, which issues through the hinder part of the foramen lacerum posterius; there is no special notch for it, as was found by DE BURLET in the fœtal skull of *Balænoptera acuto-rostrata* (**6**, III, Plates 5, 6).

In the median section of the skull (fig. 1, B) the pars cochlearis presents itself as a smooth, rounded prominence beneath the basicranial axis, and the pars canalicularis is seen above it. The back of the pars canalicularis is separated from the exoccipital cartilage (lamina alaris) by the foramen lacerum posterius, which in this view shows as a large crescentic fissure; and at the lower part of the fissure, seen edgewise in the figure, is the foramen perilymphaticum, opening backwards. In advance of this, seen so obliquely that they appear as one, are the fossa acustica and the canalis facialis, for the eighth and seventh nerves repectively.

The crista parotica, concealed in the figures by the squamosal bone, is a longitudinal ridge projecting outward from the lower edge of the pars canalicularis. The seventh nerve emerges immediately behind the upper end of the hyoid (REICHERT'S) cartilage, which is confluent with the hind end of the crista parotica (fig. 4, *hy*).

The five commissures between the pars cochlearis of the auditory capsule and the basicranial cartilage, described by DE BURLET in *Balænoptera* (**6**, III), are not here distinguishable; the cartilage in the present skull is continuous behind at one point only, namely, at the inner or mesial extremity of the jugular foramen. This connection corresponds with the hindermost—or No. 1—of the basicochlear commissures of DE BURLET, but it is much wider. The cartilage of the auditory capsule is also directly continuous with the side wall of the chondrocranium, and with the basisphenoid cartilage, by the upper and lower parts of the commissura prefacialis; and the pars canalicularis of the capsule is extensively continuous with the lamina parietalis and lamina supracapsularis above and with the lamina alaris behind.

In front of the pars canalicularis, and separated from it by the commissura prefacialis, is the large fenestra spheno-parietalis, which in fig. 1, A and B, is seen to be slightly overlapped by a thin descending lamina of the parietal bone. The small cartilage seen in the distance in fig. 1, B, above the centre of ossification of the basisphenoid, is the lateral extremity of the ala temporalis. In fig. 1, A, it just rises above the level of the pterygoid bone.

In front of the fenestra spheno-parietalis is the oval foramen opticum (fig. 1, B, *fo*), and in front of this again is the fissura orbito-nasalis. The ala orbitalis, an extensive plate of cartilage, lying dorsolaterally to the optic foramen, is flanked externally by the lower part of the frontal bone; it is continued backward, by means of the commissura orbito-parietalis, lying dorsolaterally to the fenestra spheno-parietalis (fig. 1, B), into the lamina parietalis, situated internally to the lower part of the parietal bone. The lamina parietalis has a small oval fenestra, through which the bone is visible in fig. 1, B. The lamina parietalis continues back into the lamina supracapsularis, and thus into the lamina alaris and tectum posterius of the occipital region.

The ala temporalis shows no signs of ossification, and thus agrees with that of the 145-mm. embryo of *Megaptera* examined by HONIGMANN (**20**, p. 63). When viewed from above it is seen to lie in a shallow groove in the upper surface of the pterygoid bone. A considerable portion of the pterygoid is visible in a dorsal view of the cranial floor, in front of the ala temporalis—as is also the case in Skull Z (fig. 5, *pt*)—and a narrow edge of the pterygoid shows behind the ala temporalis, and also on the mesial side of the foramen ovale; but one cannot say that the pterygoid forms any part of the floor for the brain to rest upon—it is situated too much below the level of the spheno-parietal fenestra, which is partially closed by membrane. The foramen caroticum occurs in the lateral part of the basisphenoid cartilage, behind the transverse level of the processus alaris, and in front of the mesial end of the commissura prefacialis, exactly as is shown by DE BURLET in his figure of *Balænoptera* (**6**, III, Plate 5). The mandibular division of the trigeminal nerve does not perforate the ala temporalis, as it does in some Mammals, but issues immediately behind it.

In a dorsal view of the cranial floor the processus alaris is slightly above the level of the ala temporalis, and is marked off from it by a projecting edge of cartilage; the cartilage of the processus and the ala is nevertheless continuous. HONIGMANN, in his study of a much earlier embryo of *Megaptera* (Stage III, direct length 30 mm., length along the curve of the back 62 mm.; **20**, pp. 62 and 81), finds that the ala temporalis chondrifies separately, and fuses with the basicranial axis later (Stage V, direct length 42 mm.). The ala temporalis is also reported as of independent origin in a number of other Mammals, lists of which are given by WIŃCZA (**35**, 1896), WATSON (**34**, 1916, p. 350), TERRY (1917,[*] pp. 374–375), and FAWCETT (1917,[†] p. 327; see also 1918).[‡]

The view of BROOM that the ala temporalis of the mammalian skull—becoming later the cartilage-bone portion of the alisphenoid—is the equivalent of the epipterygoid or columella cranii of Lizards, and is a derivative of the visceral skeleton (palato-pterygo-quadrate bar), and not of the primary or trabecular cranial wall, is based largely upon this independence of origin. The suggestion was first put forward in 1907,[§] in a two-page note in which he recorded the independent chondrification of the ala temporalis in *Trichosurus*, and it was re-stated a couple of years later (1909),[||] in a more extended form.

BROOM'S contention is supported by the mode of development of the epipterygoid in Reptiles, and the relation of this bone to the Gasserian ganglion. GAUPP, for instance, finds in *Lacerta* (1900,[¶] pp. 489, 542), and HOWES and SWINNERTON find

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[*] TERRY, R. J., "The Primordial Cranium of the Cat," 'Journ. Morph.,' 29, 2, Philad., Sept., 1917, pp. 281–433, 13 plates.

[†] FAWCETT, E., "The Primordial Cranium of *Microtus amphibius* (Water-Rat)," 'Journ. Anat.,' 51, 4, July, 1917, pp. 309–359, 10 plates, 4 text-figs.

[‡] FAWCETT, E., "The Primordial Cranium of *Erinaceus europæus*," 'Journ. Anat.,' 52, 2, Jan., 1918, pp. 211–250, 23 plates, 15 text-figs.; see Plate 13, *Bos taurus*. Also FAWCETT, E., "The Primordial Cranium of *Pœcilophoca weddelli* (Weddell's Seal)," 'Journ. Anat.,' 52, 4, July, 1918, pp. 412–441, 12 plates; see Plate 2, Seal, and Plate 11, Cat.

[§] BROOM, R., "On the Homology of the Mammalian Alisphenoid Bone," 'Rept. S. African Ass. Adv. Sci.,' 1907 (1908), pp. 114–115.

[||] BROOM, R., "Observations on the Development of the Marsupial Skull," 'Proc. Linn. Soc. N.S. Wales,' 34, 2, Sept., 1909, pp. 195–214, 8 plates.

[¶] GAUPP, E., "Das Chondrocranium von *Lacerta agilis*. Ein Beitrag zum Verständnis des Amniotenschädels," 'Anat. Hefte,' 1, 49 (15, 3), Wiesbaden, 1900, pp. 433–595, 3 double plates. GAUPP regards in *Sphenodon* (1901,* p. 45, and Plate 4, fig. 3), that the columella cranii (antipterygoid, epipterygoid) arises from the pterygo-quadrate cartilage as a vertical process situated externally to the root of the first division of the trigeminal nerve; and GAUPP (1902,† and BROOM (1909, *loc. cit.*, p. 212) have shown that the ala temporalis of the mammalian chondrocranium arises as a tract of cartilage external to and below the Gasserian ganglion. Seeing that the "alisphenoid" bone of the Crocodile is situated on the mesial side of the cavum epiptericum, it is claimed by some authors that this bone cannot be the equivalent of the mammalian alisphenoid, and that therefore in the reptilian skull some other structure must be sought as the homologue of the mammalian alisphenoid. The epipterygoid, they maintain, satisfies the requirements.

KESTEVEN (1918,‡ pp. 452–458), on the other hand, is of opinion that too much stress has been laid on the relations of the skeletal parts to the Gasserian ganglion, and contends that the alisphenoid of the Crocodilia and Ophidia really does represent the alisphenoid of Mammalia. And TERRY, while not discussing BROOM'S thesis that the ala temporalis of the Mammal represents a part of the palato-quadrate system, and is consequently not a primary "cranial" constituent, maintains the view that the ala is "not an independent element genetically" (1917, *loc. cit.*, p. 380).

WATSON, approaching the subject from a palæontological standpoint (**34**, 1916), supports BROOM'S thesis, but with certain modifications. In some Therapsids he finds that the epipterygoid has the form of a typical reptilian columella cranii, with a tendency for the lower end to spread backward, and even to reach the quadrate. The latter extension he regards as the equivalent of the Echidna-pterygoid, the ascending part as the homologue of the mammalian alisphenoid bone. This view, it is to be noted, is not in accord with GAUPP'S contention that the Echidna-pterygoid represents the reptilian pterygoid, a matter discussed on p. 265 of the present paper.

Whatever be the origin and morphological value of the ala temporalis, there can be little doubt that the processus alaris is a derivative of the trabecular skeleton, and is, in fact, a lateral outgrowth of the basisphenoid cartilage. In Mystacocetes the boundary line between the ala temporalis and the processus alaris persists for a long time after ossification is well advanced; it is clearly marked in the 3-feet 11-inch fœtus of *Balænoptera borealis* (Skull R), but has practically disappeared in the 6-feet 4-inch fœtus of *Balænoptera musculus* (Skull S).

The tract of cartilage seen in fig. 4 to the external side of the hinder part of the

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the ala temporalis of the Mammal as the homologue of the processus basipterygoideus of the Reptile (pp. 542, 585), the epipterygoid (antipterygoid) being wanting in Mammals (p. 546).

* HOWES, G. B., and SWINNERTON, H. H., "On the Development of the Skeleton of the Tuatara, *Sphenodon punctatus*," 'Trans. Zool. Soc.,' 16, 1, Feb., 1901, pp. 1–86, 6 plates, 18 text-figs.

† GAUPP, E., "Ueber die Ala temporalis des Säugerschädels," 'Anat. Hefte,' 19, 1, Wiesbaden, 1902, pp. 155–230, 15 text-figs.

‡ KESTEVEN, H. L., "The Homology of the Mammalian Alisphenoid and of the Echidna-Pterygoid," 'Journ. Anat.,' 52, 4, London, July, 1918, pp. 449–466, 10 text-figs.

palatine bone, and to the internal side of the supraorbital process of the frontal, is part of the ala orbitalis, the lamina of cartilage situated dorsolaterally to the optic foramen (*cf.* fig. 1, B).

The nasal capsule commences at the fissura orbito-nasalis, and its pars subcerebralis extends forward as an almost horizontal tract of cartilage, with a slight median ridge* that is continued in front into the upstanding spina mesethmoidea. The spine is lodged in a shallow groove behind the lower half of the vertical suture between the two frontal bones (fig. 1, B), and to its posterior surface is attached the front edge of the falx cerebri.

The cribriform areas are subcircular depressions, as yet unchondrified, lying on the right and left sides of the shallow mesethmoid ridge; they are relatively smaller than in DE BURLET'S *Balænoptera* (**6**, III, Plate 5), and do not extend so far forward. The section of Skull X is taken a little to the left of the true median plane, and consequently it happens that the interior of the left nasal chamber is visible in fig. 1, B; the lower part of the septum nasi, however, is thicker than the upper part, and the left postnasal passage is not exposed. The passage extends obliquely backward from the black line drawn in the floor of the nasal chamber in fig. 1, B, to the black line beneath the vomer; the palatine bone (*pl*) is presenting its oblique upper surface, and continues the oro-nasal passage still farther back.

The two mounds seen at the back of the left nasal chamber in fig. 1, B, are the future ethmoturbinals; they are situated just below the cribriform area, and receive olfactory nerves passing vertically downward. The tectum nasi continues forward in front of the mesethmoid spine, beneath the nasal bones, and terminates in an upstanding part (fig. 1, B, and fig. 3, *tn*) that forms the posterior support of the blow-holes.

The lateral wall of the front part of the nasal chamber is mainly supported by the premaxillæ and maxillæ (*pmx* and *mx* in fig. 1, B), but there is a flat plate of alinasal cartilage (lamina transversalis anterior of DE BURLET, **6**, III, p. 162), lining the maxilla, and extending obliquely downward and forward to the paraseptal and rostral cartilage. The internasal septum (partly missing in fig. 1, B, as explained above), does not extend farther forward than a vertical line drawn through the front of the nasal bone; the tough connective tissue between the two blow-holes, situated just anterior to the part marked *tn*, is not supported by cartilage.

The nasal rostrum (fig. 1, B, *ro*) is massive and in a direct line with the basicranial axis; it extends to the anterior extremity of the snout, and its front portion separates the two premaxillæ above and the two maxillæ below (figs. 3 and 4).

The triangular tract of cartilage that lies in the shadow in fig. 4 to the outer side of the front part of the palatine, in front of the antorbital part of the frontal, and behind the back of the maxilla, is the subcerebral part of the nasal capsule, the part that lies laterally to the cribriform depression.

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* *Cf.* ESCHRICHT, **10**, Plate 14, fig. 1, in a 9-inch fœtus of *Balænoptera acuto-rostrata*.

Auditory Ossicles.—The incus and stapes are unossified, and the former has a definite attachment to the crista parotica. The malleus is relatively large, and the processus anterior (longus, gracilis, folianus) passes forward and downward and, without any change in thickness, is continued into the Meckelian cartilage of the lower jaw (figs. 1, B, and 4, *me*). There is no fusion of the malleus with the tympanic bone, nor, indeed, any close attachment to it. The caput of the malleus is perforated longitudinally; the manubrium is bluntly pointed, and is directed mesially and slightly backward; it is attached by fibrous tissue to the middle, or near the middle, of the dorsal surface of the membrana tympanica. The cartridge of the malleus is unossified, but a membrane-bone, the goniale, has already begun to develop upon the surface of the processus anterior (fig. 11, A, *go*).

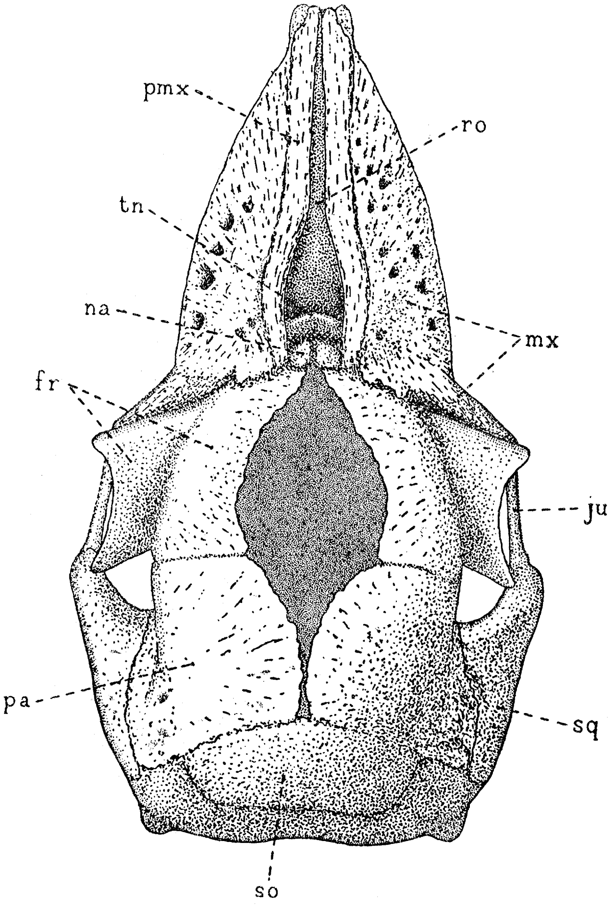

FIG. 3.—Upper view of the skull of a fœtus of *Megaptera nodosa* measuring 6 inches, × 1·8. *fr*, frontal; *ju*, jugal; *mx*, maxilla; *na*, nasal; *pa*, parietal; *pmx*, premaxilla; *ro*, rostral cartilage; *so*, supraoccipital; *sq*, squamosal; *tn*, tectum nasi.

Membrane-Bones.—The maxillary bones do not meet one another (fig. 4), but are separated by the rostral cartilage in front and by the vomer behind. The posterior edge of each joins the front of the palatine bone, and the posterolateral corner of the antorbital process is connected with the jugal. There is an extensive junction between the back of the maxilla and the frontal bone, but the maxilla has not yet grown over the roof of the frontal as it does later (*cf.* figs. 3 and 8).

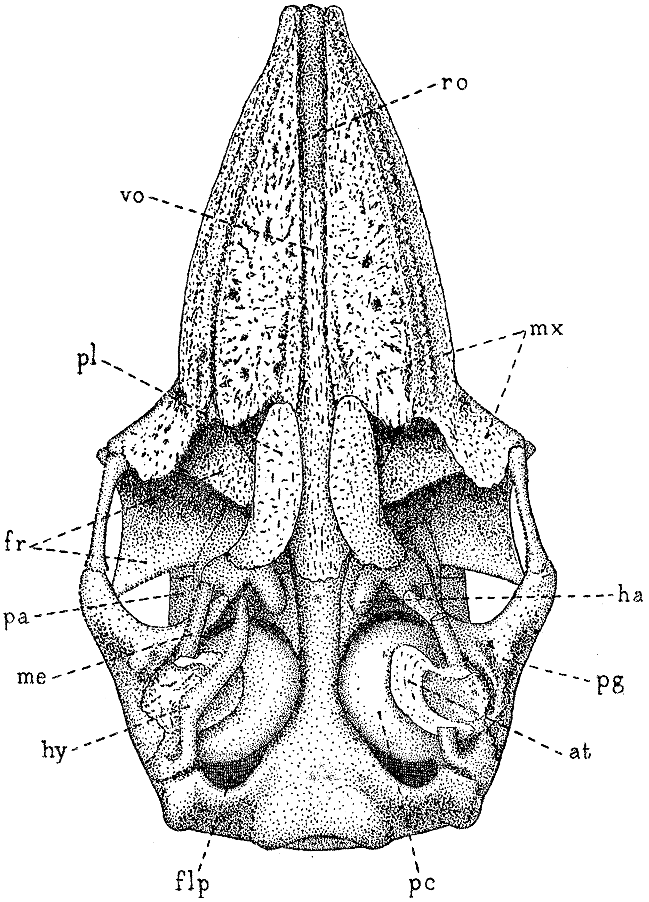

FIG. 4.—Palatal view of the skull of a fœtus of *Megaptera nodosa* measuring 6 inches, × 1·8.

at, annulus tympanicus, the first-formed part of the tympanic bone; *flp*, foramen lacerum posterius or foramen jugulare; *fr*, frontal; *ha*, hamular process of the pterygoid; *hy*, hyoid cornu, stylohyal or REICHERT'S cartilage; *me*, MECKEL'S cartilage, cut across in front; *mx*, maxilla; *pa*, parietal; *pc*, pars cochlearis of the auditory capsule; *pg*, postglenoid process of the squamosal; *pl*, palatine; *ro*, rostral cartilage; *vo*, vomer.

The gums are smooth, soft and white; the teeth, exposed by dissection, are roughly indicated in the left maxilla in fig. 4, and in fig. 1, A. The teeth are mostly simple, of the form of small hemispheres, but a few are double, one tooth immediately behind the other. Each maxilla and each dentary carries from 35 to 37 teeth. The maxillary teeth are all directed outward and downward, and they are rather uniformly spaced; but in the mandible the anterior teeth are more widely spaced than those of the posterior half of the series, and they point upward, whereas the hinder teeth point upward and inward.

The premaxillæ terminate anteriorly above the rostral cartilage, and bear no teeth; they nearly meet in front, but are widely divaricated behind in the region of the blow-holes (fig. 3, *pmx*). The posterior extremities just reach the frontal bones, and are separated by the nasals, which are small nodular bones, situated immediately in advance of the frontals, and above the tectum nasi (fig. 1, B, *na*, also fig. 3).

The jugal is a curved rod of bone, enlarged at its two extremities; its hind end is loosely connected with the front of the zygomatic process of the squamosal, and the anterior end is loosely wedged in between the antorbital process of the frontal and the back of the antorbital process of the maxilla (fig. 1, A, and fig. 3, *ju*). There is as yet no trace of a lachrymal bone, although it is recognisable in the later stage (Skull Z, fig. 7, *la*).

The frontal bones are relatively large, and meet in a vertical suture behind the nasal bones (fig. 1, B); they are widely separated above, the middle part of the roof of the skull being still largely membranous (fig. 3). The supraorbital crest is already strongly developed (fig. 3), and its free edge is semicircular (fig. 1, A); the hinder part is pointed, and is connected by tough fibrous tissue with the upper edge of the zygomatic process of the squamosal bone; the front part is connected with the anterior end of the jugal, and is continued inward and slightly downward, as the antorbital or palatine process, to meet the upper edge of the palatine bone. In fig. 1, A, the bone seen immediately above the jugal is the palatine, and the dark part of the figure that lies anterior to the pale cartilaginous tract is the palatine process of the frontal. In fig. 4 the palatine process is indicated by the longer of the two dotted lines leading from the letters *fr*.

The parietals are large, thin, curved bones, nearly joining one another posteriorly, but diverging in front (fig. 3); they are connected with the frontal, supraoccipital and squamosal bones, as shown in figs. 3 and 1, A. There is no sign of an interparietal bone.

The squamosal bone, which bulks so largely in the skull of the adult, is as yet relatively small; its squamous portion meets the hinder part of the ventral edge of the parietal, and overlaps it to a very slight extent (fig. 1, A). The front of the squamous portion is prolonged forward, inward and slightly downward as the bifid pterygoid process, the upper part of which overlaps the upper part of the pterygoid bone near, but behind and below the ala temporalis; the lower part of the fork, the processus falciformis, overlaps, *i.e.*, lies external to, the part of the pterygoid that forms the external boundary of the pterygoid fossa. Between the two parts of the pterygoid just mentioned is a broad notch opening backward, which, in conjunction with the notch in the squamosal bone immediately above the processus falciformis, constitutes the foramen ovale. In fig. 4 the dotted line from the letters *ha* passes just behind the foramen ovale.

Above the base of the forwardly projecting pterygoid limb of the squamosal, in a position just concealed in fig. 1, A, by the upper edge of the zygomatic process, the margin of the bone shows a horizontal notch, about four times as deep as wide. What passes through the base of the notch is probably a vein, but the point cannot now be determined in the skull under consideration, which was prepared before the interest of the notch was appreciated; it is curious, however, to observe that, as the squamosal bone grows forward with increasing age, the notch becomes longer and longer, and takes the form of a deep cleft in the bone. It occurs in *Balænoptera* as well as in *Megaptera*, and in fig. 15 the front part of it is seen between the two dotted lines that lead from the letters *sq*.

The zygomatic process ends bluntly in front, and is connected with the back of the jugal (fig. 1, A). The postglenoid process is small and delicate (figs. 2 and 4, *pg*), in marked contrast with that in later stages of development, when it becomes massive, and constitutes one of the most conspicuous features of the hinder part of the skull (*cf.* figs. 1, A, and 7, and adult skull, **4**, Plate 10, fig. 1); the articular surface for the condyle of the mandible is not differentiated. In fig. 1, B, the postglenoid process is seen as a small knob above the front part of REICHERT'S cartilage (*hy*); the zygomatic process of the squamosal again comes into view as a rhombic area above the Meckelian cartilage (*me*) and, lying anterodorsally to the rhomb, is seen the lower part of the pterygoid process of the squamosal.

The tympanic bone or annulus tympanicus is a thin, flat bone lying ventral to the pars cochlearis of the auditory capsule (fig. 4, *at*). The tympanic membrane is at this stage of development still flat, and has not yet acquired the shape of a glove-finger which is so characteristic of the ear-drum of adult Mystacocetes.* The membrane is horizontal in position, and instead of forming a transverse or oblique termination to the external auditory meatus, as in most adult Mammals, here forms part of its roof; the membrane is supported on three sides, anterior, mesial and posterior, by the tympanic annulus, and its outer edge passes into a mass of fibrous tissue attached to the lower edge of the squamosal bone.

The pale streak seen in the tympanic membrane just behind the dotted line *at* in fig. 4 marks a tract of fibrous tissue, to the mesial end of which the extremity of the manubrium mallei is attached; it is this fibrous tissue that develops later into the long conical "ligament" of the adult tympanic membrane (**24**, Plate 74, fig. 1, *e*). The tympanic annulus occupies a horizontal position beneath the pars cochlearis, as is shown at *at* in fig. 2: but in fig. 1, B, the antero-internal part is slightly dropped in order to expose the anterior process of the malleus, continuous with the Meckelian cartilage (*me*).

The tympanic bulla at this period of development does not exist. The cavum tympanicum, immediately ventral to the auditory capsule, is a cleft-like space, with the roof constituted by the bulging pars cochlearis; the floor, concave above and convex below, consists of a tough mucous membrane, in the lateral part of which the annulus tympanicus has already ossified. The more mesial part will later develop into a thick bullate bone by a spreading of the ossification from the mesial and front edges

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* See BEAUREGARD, **3**, III, p. 395; LILLIE, **24**, p. 776; HANKE, **18**, p. 510.

of the tympanic annulus as shown in fig. 10; but, having at present no skeletal structure, it does not appear in figs. 2 and 4, and the pars cochlearis is freely visible.

ESCHRICHT is clearly in error in his identification of the "bulla tympani" in his figure of the skull of a 9-inch fœtus of *Balænoptera acuto-rostrata* (**10**, Plate 11, fig. 2, *g*); there can be no doubt that the structure indicated is the pars cochlearis of the auditory capsule shown as *pc* in figs. 2 and 4 of the present paper. ESCHRICHT remarks (p. 120, *e*) that the part marked *g* is cartilaginous, and that it contains the cochlea; the error lies in his conclusion that it develops later into the bony tympanic bulla (*g* of Plate 10, fig. 2 and Plate 9, fig. 2). KERNAN (**22**, 1916, p. 493), in describing the cavum typanicum of a 14$\frac{3}{4}$-inch fœtus of *Balænoptera borealis*, writes that the bulla is still "fibrous." "The ventral wall [of the cavum tympanicum] contains in the lateral area the membrana tympani, surrounded by the crescentic os tympanicum. The rest of the ventral wall is made up of the fibrous bulla which fills in the space between os tympanicum and the marginal attachment of the bulla." The dorsal wall has "a layer of thick tissue which completely conceals the underlying cartilage and almost fills the cavity." "The tissue is cavernous."

The vomer of Skull X is as yet but a thin, delicate bone; the part that lies below the rostral cartilage and septum nasi is trough-shaped, the hinder part is flat and reaches to the transverse level of the bases of the hamular processes (figs. 4 and 1, B). In later stages of development it extends much further back than this, and in the adult underlies the front part of the basioccipital.

The palatine bones do not meet in the middle line (fig. 4); their front portions are nearly horizontally disposed, their hinder parts slope upward and outward. The outer surface of the hinder part is seen in the orbit in fig. 1, A, immediately above the jugal; the inner (and upper) surface of it shows in fig. 1, B, just in front of the hamular process of the pterygoid.

The pterygoid is distinguished by a strong hamular process projecting downward, backward and inward from the thick middle part of the bone. The front portion of the pterygoid is concave towards the median plane of the skull, and forms part of the lateral wall of the postnasal passage; its outer surface is flanked by the hinder part of the palatine bone; its upper surface has already been referred to as being visible in a view of the cranial floor from above. The posterior edge of the upper part of the pterygoid is concave, and forms the front boundary of the foramen lacerum medium, the crescentic slit which is seen in fig. 4 in front of the pars cochlearis of the auditory capsule. The postero-internal horn terminates in a blunt point; the postero-external limb is bifid, and the two parts are loosely connected by fibrous tissue with the two parts of the bifid pterygoid process of the squamosal. The foramen thus enclosed is the foramen ovale; in fig. 4 it lies just in front of the dotted line drawn to indicate the hamular process (*ha*).

The ala temporalis rests in a shallow groove in the upper surface of the pterygoid bone; it slopes outward and slightly upward, and its lateral extremity extends beyond the groove. This extremity is seen immediately behind the lower end of the postorbital process of the frontal in fig. 1, A, and above the basisphenoid centre of ossification in fig. 1, B. The part of the pterygoid seen below the extremity of the postorbital process of the frontal in fig. 1, A, is the upper part of the postero-external limb.

The postero-internal horn of the pterygoid lies beneath the basisphenoid cartilage (fig. 1, B), and extends backward from the base of the hamular process (*ha*) to the pars cochlearis of the auditory capsule ; and between the hamular process and the postero-internal horn is seen, in the distance, a small triangular part of the lower of the two divisions of the postero-external limb of the pterygoid. The edge of bone that shows below and behind this last is the processus falciformis, the lower of the two divisions of the pterygoid process of the squamosal bone.

Mandible and *Hyoid.*—The mandible consists of two readily separable rami, with no distinct anterior symphysis. The Meckelian cartilage in each is a rod of uniform thickness throughout, and extends from the processus anterior of the malleus to the front end of the mandibular ramus. In fig. 1, C, which represents a view of the left ramus from the mesial side, the cartilage is not visible in the middle part, but it continues without interruption in the interior of the dentary bone. The left-hand end of the Meckelian cartilage in fig. 1, C, is a cut end that fits on to the right-hand end of *me* in fig. 1, B. The articular head of the mandible (*con*) is but feebly differentiated ; the coronoid process (*cor*) is a thin lamina of bone lying in a vertical plane. Each dentary bone carries about 36 teeth ; those of the front half of the series point upward, those of the hinder half upward and inward ; the former are more widely spaced than the latter.

The hyoid bar (fig. 1, D) is a continuous rod of cartilage set horizontally and transversely in front of the thyroid cartilage of the larynx. The middle portion is flattened, and has two small projections in front and two behind, the former being closer together than the latter.

The upper part of the hyoid arch, the stylohyal or REICHERT's cartilage (figs. 1, A and B, 2, 4, *hy*), is a curved rod of unossified cartilage, which tapers off in front to a blunt point ; in fig. 4 the left stylohyal is represented as cut short, so that the annulus tympanicus may be more fully brought into view. The postero-dorsal extremity of the cartilage is fused with the hind end of the external ridge (crista parotica) of the pars canalicularis of the auditory capsule, near the back of the posterior vertical semicircular canal. The anterior end of the cartilage is free, and lies dorsally to the lateral part of the hyoid bar that will develop into the thyrohyal bone.

SKULLS OF A 16-INCH FŒTUS AND A 27-INCH FŒTUS OF *Megaptera nodosa* BONN.

These may be denoted Skulls Y and Z respectively. Skull Y is that of a fœtus, measuring 16 inches from the tip of the snout to the cleft of the tail-fin, collected by

Dr. G. Cruickshank off South Georgia, and sent to the British Museum (Natural History). Skull Z is that of a fœtus, measuring 27 inches from the tip of the snout to the cleft of the tail-fin, collected off South Georgia on the Major G. E. H. Barrett-Hamilton Whaling Mission, 1913. The length of Skull Y, from condyles to the tip of the rostrum, is $4\frac{3}{4}$ inches, or 121 mm.; that of Skull Z is $8\frac{1}{16}$ inches, or 205 mm. The maximum breadth of the skull, taken across the zygomatic process of the squamosal, is in Skull Y $3\frac{1}{4}$ inches, or 83 mm., and in Skull Z $4\frac{15}{16}$ inches, or 125 mm.

The median longitudinal section of Skull Y, as compared with that of Skull X, described in the preceding section of the paper, shows a reduction in the upper parts of the side-wall of the chondrocranium, particularly in the part above the fenestra spheno-parietalis, the commissura orbito-parietalis being here reduced to a narrow longitudinal tract, rather wider, however, than that shown in Schulte's figure of *Balænoptera* (**28**, Plate 56, fig. 2). The lamina parietalis has been absorbed below the level of the circular fenestra seen in fig. 1, B, of Skull X, and a much greater extent of the parietal bone is consequently visible from within than in the earlier stage.

The centres of ossification of the basioccipital and basisphenoid of Skull Y, as seen in a longitudinal section, are more clearly marked than in Skull X (fig. 1, B), and a presphenoid centre is now present. The basioccipital ossification is long, with a tendency to incompleteness in the middle of its length, where there is a groove in the cranial floor passing transversely across from one jugular foramen to the other. The front part of the basioccipital ossification shows prominently on the ventral surface, in the form of a pair of eminences situated immediately behind the pterygoid bones, and on the mesial side of the pars cochlearis of the auditory capsule of each side. Seen from below, the pair of bony eminences are separated by a tract of cartilage, but the two are continuous with the endochondral ossification-centre, and thereby with one another; in Skull Z the eminences have enlarged in a backward direction, so that they now have the form of two ridges, and the basioccipital cartilage between them is completely ossified (fig. 9, *bo*).

Owing to the fusion of the basioccipital with the basisphenoid bone in the adult whale, and the disappearance of the suture between them, the ventral ridges have proved a source of uncertainty in the past; it is only by the study of young skulls, like those now under consideration, that the ridges can be definitely allocated to the basioccipital bone. Liouville, in figuring the condylar region of an adult *Megaptera* (1913,* p. 186, text-fig. 19), marks them "exoccipital." Abel, again, in *Prosqualodon* (1912,† Plate 3), marks them "basisphenoid"; the skull he figures is one in the

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* Liouville, J., "Cétacés de l'Antarctique," 'Deux. Expéd. Antarctique Française (1908–1910),' Paris, 1913, pp. vi + 276, 15 plates, 21 text-figs.

† Abel, O., "Cetaceenstudien, III, Rekonstruktion des Schädels von *Prosqualodon australe* Lyd. aus dem Miozän Patagoniens," 'Sitzber. k. Akad. Wiss. Wien. Math.-naturw. Kl.,' vol. 121, 1, 1–3, 1912, pp. 57–75, 3 plates, 1 text-fig.

British Museum (Natural History), and an examination of it shows that the processes belong to the basioccipital, as in other whales.

The ossification-centre of the basisphenoid, which in the longitudinal section of Skull X is circular in outline (fig. 1, B), is in Skull Y elliptical, the long axis of the ellipse being horizontal. The progress of the ossification is evidently greater behind than in front, for the craniopharyngeal canal is now no longer central, but nearer the front limit of the bony centre. The ossification has not yet extended to the lower surface of the cartilage, but it has just reached the upper surface, and a small tract of bone is seen, in a dorsal view of the cranial floor, at the bottom of the slight depression that represents the sella turcica. The ala temporalis is relatively longer, and more slender at its mesial end, than in Skull X; it is firmer and more opaque, but is not yet ossified.

The basisphenoid bone in Skull Z is separated from the presphenoid and basioccipital ossifications by great masses of cartilage (fig. 5). The foramen caroticum is relatively much smaller than in Skull Y; it does not penetrate the ossified part of the basisphenoid, but lies in the front portion of the cartilaginous tract behind it. Near it, in a postero-external position, is a nodule of cartilage (Restknorpel) of unknown significance.

The ala temporalis is ossified, except at its outer (lateral) extremity, the right one being more extensively ossified than the left (fig. 5, *al*). It is rather rod-like, and narrower at its mesial than at its lateral end. It is disposed nearly horizontally, with a slight slope antero-dorsally. It lies in a groove in the postero-dorsal part of the pterygoid bone, a large portion of which is visible in a view of the cranial floor (fig. 5, *pt*), but situated at too low a level to form a direct support for the brain. There is a sharp line of demarcation between the mesial end of the alisphenoid and the processus alaris of the basisphenoid, but the two are co-ossified. A small spur of the basisphenoid bone bends outward and downward behind the mesial end of the alisphenoid, and ends against the pterygoid bone in the roof of the pterygoid fossa.

The presphenoidal centre of ossification of Skull Y, as seen in a median longitudinal section, is slightly smaller than the basisphenoidal centre, and is of circular outline; it reaches the upper surface of the cartilage, but is still remote from the lower surface; it extends the full width between the two optic foramina, and forms the inferior border of each. The orbitosphenoid develops independently of the presphenoid, as an ossification of that part of the ala orbitalis which lies immediately dorso-laterally to the optic foramen; in Skull Y it is separated from the presphenoidal ossification by still cartilaginous parts of the tænia pro-optica and tænia metoptica, although in the later skull, Skull Z, the tænia pro-optica is fully ossified, and the orbitosphenoid and presphenoid bones are continuous (fig. 5, *os*, *ps*).

The bony part that, in *Balænoptera*, SCHULTE describes as situated externally to the cribriform plate, and identifies as "ectethmoid" (**28**, Plate 56, fig. 2), I find, in the Skull Y of *Megaptera*, to be but a part of the inner, antorbital or palatine, process of the frontal that has intruded below the commissura sphenethmoidea, and now forms the anterior-ventro-external boundary of the orbito-nasal fissure.

The cribriform plates in Skulls Y and Z are not sharply marked off from the surrounding cartilage; between the two plates there is a slight eminence or ridge (fig. 5, *ms*) which is continuous in front with the upright spina mesethmoidea (*sm*) lodged in a groove at the back of the lower part of the suture between the two frontal bones. Each cribriform plate has one large perforation (crossed by the dotted line *ps* in fig. 5) and four small ones. In a fœtus of *Balænoptera borealis* SCHULTE finds three perforations (**28**, pp. 481, 483).

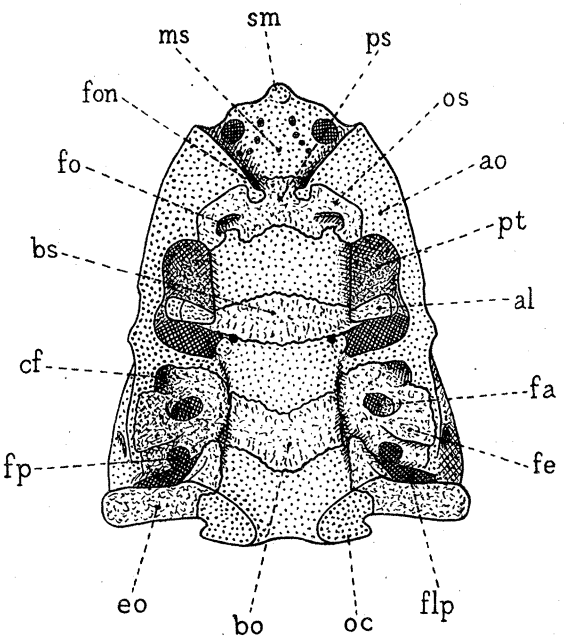

FIG. 5.—Cranial floor of a fœtus of *Megaptera nodosa* measuring 27 inches; view as seen after removal of the upper part of the cranium. The exoccipital bones and the condyles are cut horizontally, the other parts exhibit their upper or their dorsomesial surfaces. × 0·7.

al, alisphenoid; *ao*, ala orbitalis; *bo*, basioccipital; *bs*, basisphenoid; *cf*, canalis facialis; *eo*, exoccipital; *fa*, fossa acustica; *fe*, foramen endolymphaticum; *flp*, foramen lacerum posterius; *fo*, foramen opticum; *fon*, fissura orbitonasalis; *fp*, foramen perilymphaticum; *ms*, mesethmoid cartilage; *oc*, occipital condyle; *os*, orbitosphenoid; *ps*, presphenoid; *pt*, pterygoid; *sm*, spina mesethmoidea.

In both Skull Y and Skull Z the internasal septum terminates in front in a curved edge, concave anteriorly; the tectum nasi extends beyond the upper edge of this, and ends behind the blow-holes. The blow-holes are separate, but the tough connective tissue between them is not supported by cartilage. The rostral cartilage is to be regarded as a massive forward extension of the lower part of the septum nasi; the relations of the parts are much the same as those shown in the longitudinal section of the skull of *Balænoptera* (fig. 12).

The auditory capsule shows no signs of ossification in Skulls X and Y, but in Skull Z a uniform, diffuse, endochondral ossification has commenced, although it has not proceeded to the extent of a union of the calcified granulations to form a rigid structure; a fine needle can be pushed through the periotic bone in any direction. There is no suggestion that the periotic begins to ossify from two, three or more "centres," nor that the pars cochlearis ossifies separately from the pars canalicularis. The ossification of the dorsolateral portion of the periotic is incomplete, and the part lying externally to the fenestra ovalis is still cartilaginous.

The ossification of the periotic of Skull Z has not extended into the commissura prefacialis (fig. 5), so that the facial canal (*cf*) is bounded in front by cartilage, behind by bone. The cartilage lying dorso-laterally to the periotic bone—the lamina supracapsularis—is almost completely absorbed, and the squamosal bone, and in front of it the postero-ventral region of the parietal, can be seen in an inner view of the bisected skull; but a tract of cartilage, about 7 mm. wide, still extends obliquely forward and upward from the remnants of the commissura prefacialis and lamina supracapsularis, and continues forward above the spheno-parietal fenestra as the commissura orbito-parietalis. The front of this commissure merges into the ala orbitalis (fig. 5, *ao*), which shows no signs of undergoing absorption.

Viewed from the cerebral surface, the periotic bone shows a fossa acustica for the auditory nerve (fig. 5, *fa*), separate from the orifice for the facial nerve (*cf*), although in later stages of growth there is a shallow, common depression in the bone. The foramen perilymphaticum (*fp*) is a large opening at the back of the periotic leading into the foramen lacerum posterius, and the foramen endolymphaticum (*fe*) is a small orifice in an oval, crater-like mound in the postero-lateral part of the upper surface of the periotic. At the lateral extremity of the foramen lacerum posterius the periotic is unossified, and the cartilage is continuous with the unossified part of the exoccipital, and presents itself on the exterior, between the squamosal and exoccipital bones, in a back view of the skull (fig. 6). Except for this cartilage, the periotic consists of the labyrinthic portion only; the anterior and posterior extensions, which in the adult hold the bone in position, develop much later. Even in a 13½-feet fœtus of *Megaptera* the extensions are relatively shorter than they are in the adult (**25**, Plate 3, figs. 1, 2; **4**, Plate 9, fig. 11).

The ossification of the exoccipital cartilage, not yet begun in Skull X (fig. 2), has in Skull Y proceeded to about the same extent as is shown in the 14¾-inch fœtus of *Balænoptera borealis* described by SCHULTE (**28**, Plate 55, fig. 1). The width of the ossification, as seen in a back view, is about half the distance from the outer edge of the occipital condyle to the inner edge of the squamosal bone; in Skull Z its width is the full distance thus defined (fig. 6, *eo*). Even in Skull Z, however, the ossification does not extend into the condyles, which are wholly cartilaginous (fig. 5, *oc*). With regard to fig. 5, it is to be noted that, although the actual saw-cut freeing the upper part of the cranium of Skull Z is that indicated in fig. 7 by the dotted line AB, fig 5 is drawn as though the section had been taken lower down, through the foramen magnum.

The exoccipital bone does not yet reach the supraoccipital (fig. 6), and the whole of the margin of the foramen magnum is cartilaginous ; the lower extremity of the paroccipital process is still unossified (fig. 6, *po*). There is no separate foramen for the hypoglossal nerve in either X, Y or Z, but the nerve issues through the foramen lacerum posterius, together with the vagus-glossopharyngeus group ; HONIGMANN finds the same in his earlier fœtus of *Megaptera* (**20**, p. 82).

The two occipital condyles of Skull X, as already noted in the previous section of the paper, are feebly differentiated, and are relatively wider apart than they are in later stages of growth (*cf.* figs. 2, 6) ; and they do not extend so high up the sides of the foramen magnum. Except for the fact that they project to a small extent only, they present the appearance that one associates with the condyles of the mammalian skull generally. In Skull Z, however, the two condyles have already begun to acquire the " cetacean " character : a character due to the fact that the curvature of the two condyles, taken together, is that of a hemisphere.

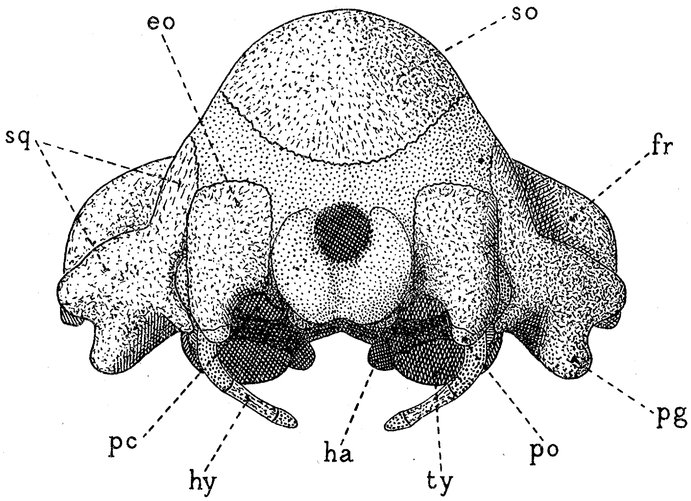

FIG. 6.—Back view of the skull of a fœtus of *Megaptera nodosa* measuring 27 inches, × 0·6.

eo, exoccipital ; *fr*, frontal ; *ha*, hamular process of the pterygoid ; *hy*, hyoid cornu or stylohyal ; *pc*, pars cochlearis of the auditory capsule ; *pg*, postglenoid process of the squamosal ; *po*, paroccipital process of the exoccipital ; *so*, supraoccipital ; *sq*, squamosal ; *ty*, tympanic.

The differences that occur in the occipital articulation of ordinary Mammals on the one hand, and of Sauropsida on the other, may be explained by the rotation of the head being effected mainly upon the occipital condyle in the latter, but about the odontoid peg of the axis vertebra in the former. In an ordinary Mammal the duplicity of the condyle permits of a nodding or up-and-down movement of the head, but not of a side-to-side movement, nor of a rotation of the head ; the side-to-side movement is effected by the flexure of the cervical vertebræ generally, and the axial rotation is mainly concentrated in the atlanto-epistropheal joint. In the Mystacocetes, however, the shortening up of the cervical vertebræ, and in some forms their fusion, effectually prevents both side-to-side movement and rotary movement, except in front of the atlas vertebra.

In those Whales in which the cervical vertebræ remain separate, it is evident, from the accessory articulation that exists between the atlas and the axis vertebra *above* the spinal cord, that any rotary movement about the odontoid, or about the epistropheal centrum that sometimes takes the place of the odontoid (see SMETS, **29**, p. 189), is of the slightest extent (DWIGHT, **8**, Plate 6, fig. 5, *c*). Owing to the fact, however, that the two occipital condyles, taken together, present the form of a hemisphere, fitting into a basin-shaped atlas vertebra*, the looseness of the marginal part of the synovial capsule permits of slight movements in all directions, up-and-down, side-to-side, and rotary.

That the coalescence of the two condyles in Whales is secondary is the view already taken by GAUPP (1908,† p. 522) and DE BURLET (**6**, III, pp. 124–5, and V, p. 3) upon embryological grounds, and it is supported by palæontological considerations. In *Prosqualodon,* for instance, as has been shown by ABEL (1912,‡ Plate 3), the condyles are like those of an ordinary Mammal, and are too wide apart to permit of any but a hinge-movement in an up-and-down direction. The syncondyly of modern Whales is thus to be regarded as a purely secondary feature, associated with the transfer of the rotary joint from the atlanto-epistropheal to the atlanto-occipital position.

On comparing the back views of Skulls X, Y and Z it is interesting to note how, as age increases, the supraoccipital mounts higher and higher until it conceals the parietals from behind (*cf.* figs. 2, 6). In a top view, also, the middle part of the supraoccipital is seen to be growing forward over the parietal bones (*cf.* figs. 3, 8); in an adult skull the forward growth has proceeded to such a degree that the supraoccipital nearly touches the frontal bones (**12**, Plate 3, fig. 2; **32**, Plate 32, fig. 1).

The parietal bones of Skull Y nearly meet one another on the vertex of the head; there is still a fairly large fontanelle between the hinder parts of the frontal bones, and in front of the parietals, but it is not nearly so large as in Skull X (fig. 3). The two parietal bones in Skull Z meet in a median suture (fig. 8), and their hinder parts are overlapped by the supraoccipital. There is no interparietal bones in *Megaptera.*

The frontal bones in Skull Z meet in a median suture, and the dorsal fontanelle is closed, although a certain amount of tough fibrous tissue still remains between the

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* GRAY, 'Proc. Zool. Soc.,' 1864, p. 208, fig. 5, *Megaptera.*

† GAUPP, E., "Ueber Entwickelung und Bau der beiden ersten Wirbel und der Kopfgelenke von *Echidna aculeata,*" 'Jena. Denkschr.,' 6, 2, (SEMON'S 'Zool. Forschungsreisen,' 3, 3), 1908, pp. 481–538, 1 plate, 20 text-figs.

‡ ABEL, O., 'Cetaceenstudien, III, Rekonstruktion des Schädels von *Prosqualodon australe* Lyd. aus dem Miozän Patagoniens," 'Sitzber. k. Akad. Wiss. Wien, Math.-naturw. Kl., 121, 1, 1–3, 1912, pp. 57–75, 3 plates, 1 text-fig.

postero-mesial corners of the frontals and the antero-mesial corners of the parietals (fig. 8). In the series of Skulls X, Y, Z the supraorbital process of the frontal shows a progressive outward (lateral) growth (*cf.* figs. 2, 6), which is greatly in excess of the antero-posterior growth (*cf.* figs. 3, 8); the series also demonstrates the late development of the antero-lateral process of the parietal that overlaps the frontal, and a correspondingly late development of the postero-mesial process of the maxilla that overlaps the frontal. The postorbital process of the frontal, at first slender, becomes more massive, and approaches nearer to the zygomatic process of the squamosal (*cf.* figs. 1, A, and 7), but even in Skull Z there is a mass of tough fibrous tissue intervening.

The nasal bones, at first in the form of rounded nodules embedded in loose connective tissue (figs. 1, B, and 3), increase in both vertical and antero-posterior directions, and in Skull Z already fit close up against the frontal bones. The nasal bones are wider than they would appear to be from an inspection of fig. 8, for their antero-external parts are overlapped by the premaxillæ. The frontal bones extend well beneath the nasals in Skull Z, although not to the same degree as in the 3-feet 11-inches fœtus of *Balænoptera borealis* (fig. 12). In Skull X the frontal suture is situated entirely behind the nasal bones (fig. 1, B), and the same relation obtains in Skull Y, where the suture is much longer; the forward extension of the frontals beneath the nasals, visible in Skull Z, is thus a late development of the skull. The curious antero-mesial point of the nasal bone, which appears to be a characteristic feature of the adult *Megaptera* (FLOWER, W. H., 'Proc. Zool. Soc.,' 1864, p. 390, fig. 3; TRUE, **32**, Plate 32), has not yet developed in Skull Z.

The premaxillary bones extend back as far as the hind ends of the nasal bones (fig. 8); they are widely divergent in the region of the blow-holes, and although they approach one another in front, they remain separated by the upper part of the rostral cartilage. The maxillæ increase rapidly in size in the series X, Y, Z; the antorbital process, unlike the postero-mesial process that overlaps the frontal, is an early development (*cf.* figs. 3, 4 and 8, 9). In a palatal view the two maxillæ do not meet, but are separated by the rostral cartilage and the vomerine bone (fig. 9); even in the adult skull the maxillæ do not meet beneath the vomer (TRUE, **32**, Plates 30, 33). The dental groove is widely open, and its margins are delicate and fragile (fig. 9).

The teeth of the upper jaw occur in the maxillæ solely; in Skull Y there are thirty-nine and thirty-five teeth in the right and left sides respectively; in Skull Z there are thirty-seven and forty-one. Double teeth are occasionally found, two teeth, one in advance of the other, being set upon the same base. In counting the teeth, two upon the same base are regarded as one tooth, but two teeth on separate, though closely adjacent bases, are counted as two teeth. Some of the hinder teeth in both Skull Y and Skull Z show traces of accessory cusps, but these are too small and too irregularly disposed to enable one to formulate any comparison between the teeth of *Megaptera* and those of Zeuglodonts; neither is it possible to identify the points as the "cones" of a typical tritubercular tooth. The teeth in Skull Z are not yet at their maximum development, and it would be interesting to study the hinder teeth of the upper jaw of an older fœtus, measuring about 38 or 40 inches. The tiny accessory cusps are figured by ESCHRICHT in the teeth of a 45-inch fœtus of *Megaptera** (**10**, Plate 4, fig. B, and p. 90). The teeth of this fœtus are already past their prime, and show evidences of absorption at the summits; in a $74\frac{1}{4}$-inch fœtus they have been completely absorbed (pp. 90–91).

The jugal bone does not differ greatly in the three skulls X, Y, Z (*cf.* figs. 1, A, and 7); it is curved, and in Y and Z is rather strap-like, and broadens inwards at its anterior end, where it is connected with the antorbital process of the maxilla (fig. 9); its posterior end is joined by fibrous tissue to the front of the zygomatic process of the squamosal.

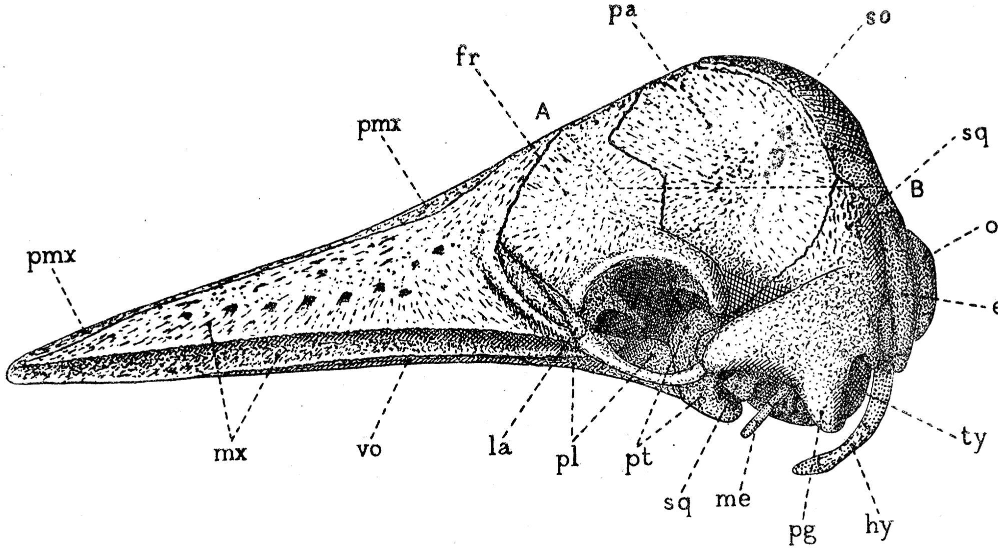

FIG. 7.—Skull of a fœtus of *Megaptera nodosa* measuring 27 inches, left side, × 0·6. The dotted line AB marks the saw-cut freeing the upper part of the cranium.

eo, exoccipital; *fr*, frontal; *hy*, hyoid cornu or stylohyal; *la*, lachrymal; *me*, MECKEL'S cartilage; *mx*, maxilla; *oc*, occipital condyle; *pa*, parietal; *pg*, postglenoid process of the squamosal; *pl*, palatine; *pmx*, premaxilla; *pt*, pterygoid; *so*, supraoccipital; *sq*, squamosal; *ty*, tympanic; *vo*, vomer.

A lachrymal bone cannot be recognised in Skulls X and Y; in Skull Z it is a rod-like, imperforate bone (fig. 7, *la*), thicker at its outer than at its mesial end, and lodged between the antorbital process of the frontal above and the antorbital process of the maxilla below. In a view of the front part of the orbital margin from behind, the outer end of the lachrymal is seen to be wedged in between the antorbital process of the frontal above and the front part of the jugal below.

The squamosal bone shows a marked increase in size as one reviews the Skulls X,

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* ESCHRICHT'S figures of the isolated teeth of *Megaptera* are drawn × 4, but OWEN, in his 'Odontography' (1840–45, Plate 87*a*, figs. 2–6), reproduces the figures and marks them as of natural size; the error is repeated in his 'Anatomy of Vertebrates,' 3, London, 8vo, 1868, p. 279, fig. 219.

Y, and Z, the most interesting feature being the rapid growth of the postglenoid process (*cf.* figs. 2 and 6, *pg*). This process, moreover, comes to occupy a more and more posterior position in the skull as age advances (*cf.* figs. 1, A, and 7), and in the adult it is situated almost in the same transverse plane as the exoccipital bones (4, Plate 9, fig. 1; Plates 10 and 11, fig. 1). The external auditory meatus passes immediately behind the postglenoid process. The zygomatic process of the squamosal increases slowly (*cf.* figs. 1, A, and 7) in marked contrast with the rapidly growing postglenoid process.

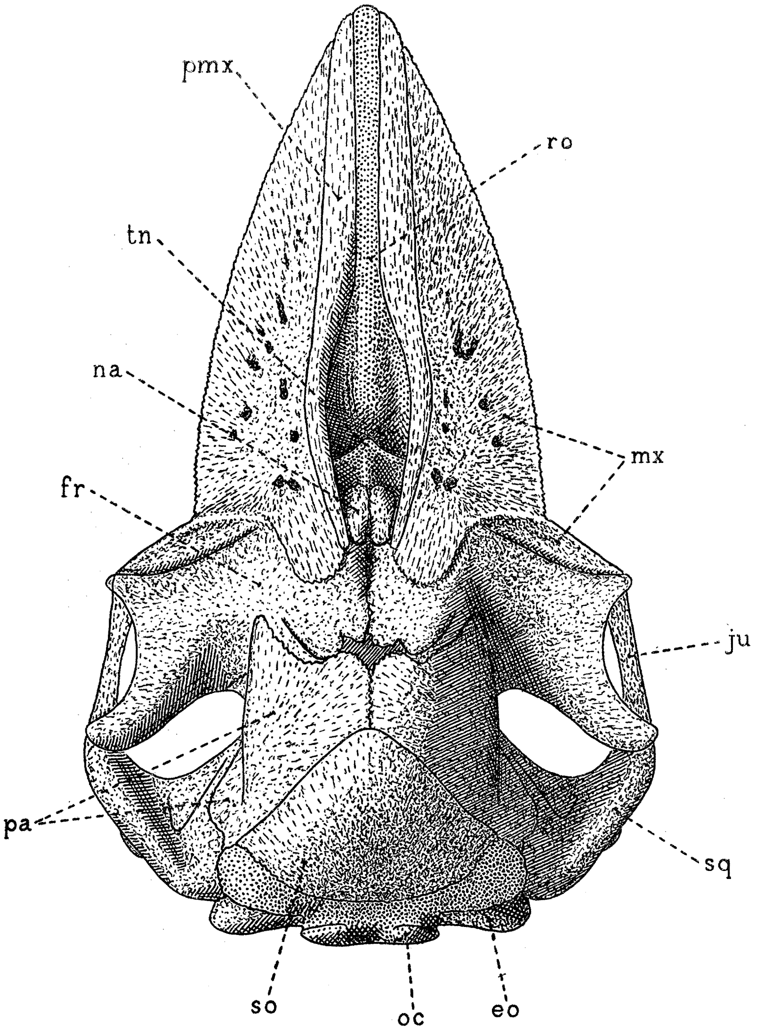

FIG. 8.—Upper view of the skull of a fœtus of *Megaptera nodosa* measuring 27 inches, × 0·6.
eo, exoccipital; *fr*, frontal; *ju*, jugal; *mx*, maxilla; *na*, nasal; *oc*, occipital condyle; *pa*, parietal; *pmx*, premaxilla; *ro*, rostral cartilage; *so*, supraoccipital; *sq*, squamosal; *tn*, tectum nasi.

The small conical process that passes mesially and ventrally from the hind edge of the squamosal to meet the posterior pedicle of the tympanic bone (Skull Z, figs. 7, 6) makes its first definite appearance in Skull Y, being scarcely recognisable in Skull X. The antero-dorsal edge of the squamous portion of the squamosal, which in Skull X has only just reached the parietal (fig. 1, A), meets that bone in a loose suture of considerable length in Skull Z (fig. 7), although the overlap that one associates with the squama occurs in the posterior part only. The relations of the bifid pterygoid process of the squamosal to the pterygoid bone and to the foramen ovale (fig. 15, B) have already been referred to in the previous section of the paper, describing Skull X, as also has the deep cleft in the bone that occurs between the pterygoid process and the squama.

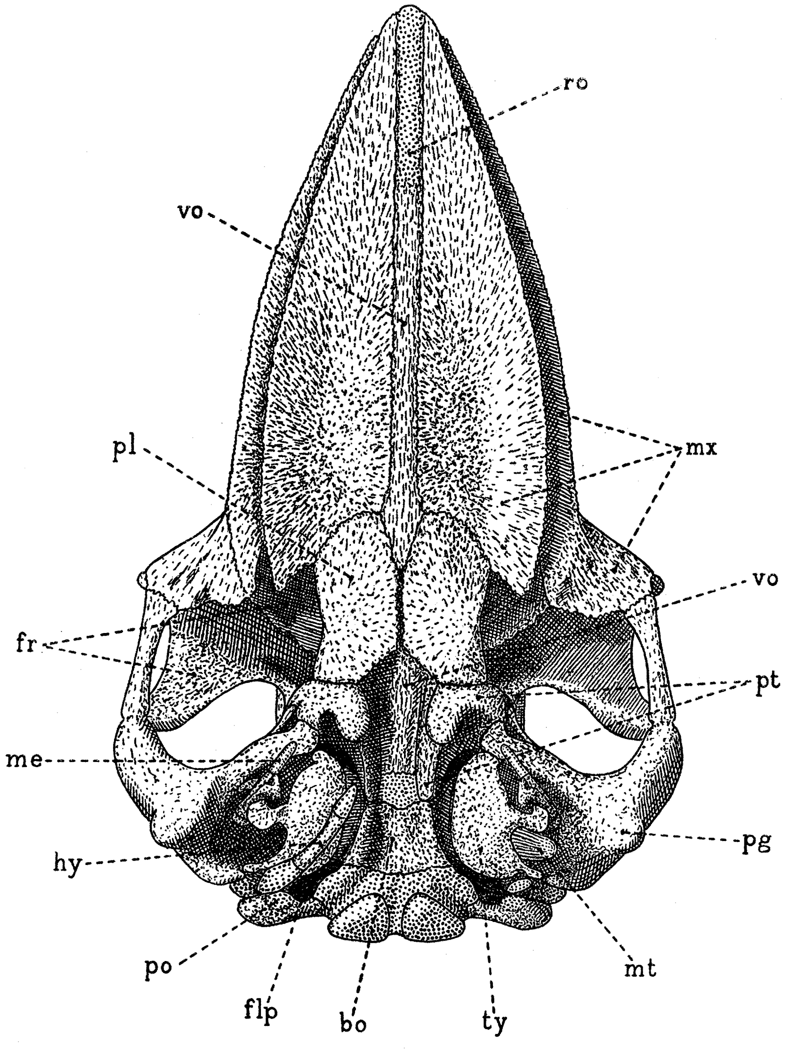

FIG. 9.—Palatal view of the skull of a fœtus of *Megaptera nodosa* measuring 27 inches, × 0·6.

bo, basioccipital; *flp*, foramen lacerum posterius or foramen jugulare; *fr*, frontal; *hy*, hyoid cornu or stylohyal; *me*, MECKEL'S cartilage; *mt*, thimble-shaped tympanic membrane; *mx*, maxilla; *pg*, postglenoid process of the squamosal; *pl*, palatine; *po*, paroccipital process of the exoccipital; *pt*, pterygoid; *ro*, rostral cartilage; *ty*, tympanic; *vo*, vomer.

Whereas in Skull X the squamosal bone does not present itself in a median bisection of the skull (fig. 1, B), owing to the abundance of cartilage in the lateral wall of the primordial cranium, and whereas the same remark holds good in the case of Skull Y, although the upper edge of the cartilage is much lower than before, in Skull Z the lamina supracapsularis has been completely absorbed, and the squamosal bone is visible, above the periotic, in a view from within.

The pterygoid bone is characterised by a prominent hamular process (figs. 6, 7, 9); the outer (ventro-external) face of the bone is overlapped by the palatine in front and by the bifid pterygoid process of the squamosal behind (fig. 15, B), and meets the parietal above. A portion of the front part of the pterygoid is visible in the cranial floor, in front of the alisphenoid bone (fig. 5, *pt*). The postero-mesial limb, on the under surface of the basicranial axis, forms a slight ridge, which is continued posteriorly by the paired ridge on the under surface of the basioccipital bone (fig. 9). The pterygoid bone is too complicated to describe adequately in words; that of Skull Z does not differ materially from the pterygoid of the fœtal *Balænoptera* (Skull S, fig. 14), and the reader is therefore referred to the figures and description of the latter in the next section of the paper.

In Skull Y the palatine bones are closer together than in Skull X (fig. 4, *pl*), but they are wider apart than in Skull Z (fig. 9, *pl*), and the vomer still shows between them. In Skull Z a fair amount of fibrous tissue persists between the palatine bones, and it is to be noted that even in the adult *Megaptera* the two palatines do not actually fuse in the middle line (TRUE, **32**, Plates 30, 33). The width of each palatine bone increases with age at a greater rate than the length (*cf.* figs. 4, 9).

In Skull X the anterior and posterior limits of the vomerine bone are difficult to determine, for the layer of fibrous tissue in which the bone is growing is tough, and the ossified part differs very little in texture from that in which ossification has not yet taken place; the posterior limit, however, may be said to occur at about the transverse level of the base of the hamular process of the pterygoid (fig. 4). In Skull Y the posterior limit is behind the transverse level of the free end of the hamular process, much the same as it is in Skull Z (fig. 9).

The anterior and posterior parts of the vomer of Skull Z are nearly flat, but a section taken through the middle of the length of the bone is curved, the form here being roughly that of a half-tube. In a transverse section taken through the palatine bones, the vomer presents the form of a V, with the lower edge of the V united with the fibrous tissue of the median suture of the palatine bones; the post-nasal passages occur externally to the sides of this V. It is probable that, in later stages of development, the region of contact, at the bottom of the V, extends in a vertical direction, so that the transverse section comes to take the form of a Y, as in *Balænoptera*; in fig. 12 the part of the bone marked *vo* is the median septum between the two post-nasal passages, the septum which in a transverse section would be represented by the lower part of the letter Y.

Although in the adult Mystacocete the vomerine bone extends far back, underlying even a part of the basioccipital, the cetacean skull seems to throw no light upon the vexed question whether the mammalian vomer is the equivalent of the reptilian parasphenoid. The credit for the suggested homology between these two bones is commonly attributed to BROOM, although in his first contribution to the literature of the subject, in 1903,* he points out that the equivalence had been previously adumbrated by BLAND SUTTON in 1884.†

What is not generally known, however, is that in 1885 SMETS, in his paper on the skull of a fœtal *Balænoptera*, had independently arrived at a similar conclusion, for he writes (**29**, p. 202): "L'homologie du vomer dans les vertébrés est très douteuse ; nous ne sommes pas loin de croire que le parasphénoïde de beaucoup de vertébrés inférieurs n'est que l'homologue du vomer. L'un et l'autre recouvrent la partie basilaire du crâne, en dedans des palatins et des ptérygoïdiens . . . . Les os décrits comme les vomers de ces vertébrés inférieurs peuvent avoir une autre signification."

The older view, that the mammalian vomer is the equivalent of the pair of vomers (BROOM'S prevomers) of the reptilian skull, is upheld by GAUPP (**14**, 1905, p. 850), and is supported by the paired origin of the vomer in *Echidna*, *Mus* and *Cavia* (*vide* WATSON, **34**, p. 357) and Man (KÖLLIKER, TOLDT, SPEE, FAWCETT, MACKLIN). TOEPLITZ‡ is a recent adherent to the view, on the evidence of the paired origin of the vomer in *Didelphys*, the two ossifications becoming subsequently united. WATSON,§ on the other hand, agrees with BROOM, although with a certain amount of reserve, and GREGORY|| agrees, but without conviction.

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* BROOM, R., "On the Mammalian and Reptilian Vomerine Bones," 'Proc. Linn. Soc. N.S. Wales,' 27, 1902, Part IV (April, 1903), pp. 545–560, 3 plates—"We are forced to conclude that the 'parasphenoid' of the snake is really the homologue of the mammalian vomer" (p. 555). See also BROOM, R., "On some Little-known Bones of the Mammalian Skull," 'Trans. S. African Phil. Soc.,' 16, 4, December, 1906, pp. 369-372 :—"In its relations and development it [the mammalian vomer] agrees exactly with the reptilian bone called parasphenoid" (p. 370). Also BROOM in 'Nature,' vol. 92, London, September, 1913, p. 7 :—a typically mammalian vomer in a newly-discovered *Dicynodon* "completely confirms the view . . . that the mammalian vomer is the reptilian parasphenoid." Also BROOM, R., "On the Origin of Mammals," 'Phil. Trans. Roy. Soc.,' 206, B, October, 1914, pp. 1–48, 7 plates—a search for the homologue of the mammalian vomer "seems to lead to the conclusion that it is represented in the lower forms by the median bone which is usually called parasphenoid" (p. 28).

† BLAND SUTTON, J., "Observations on the Parasphenoid, the Vomer, and the Palato-pterygoid Arcade," 'Proc. Zool. Soc.,' December, 1884, pp. 566–573, 2 plates.

‡ 'Zoologica,' 27, 3, 1920, p. 70.

§ WATSON, D. M. S., 'Bull. Geol. Soc. Amer.,' 28, December, 1917, p. 984 :—"The mode of origin of the mammalian vomer is much more like that of the reptilian parasphenoid than that of the reptilian vomer." Also WATSON, **34**, p. 365, No. 39 :—"The vomer of *Ornithorhynchus* has a very similar position to the rostral part of the parasphenoid of reptiles"; and (p. 385) :—"These facts seem to me to establish a case, too strong to be lightly set aside, for the homology of the os paradoxum [of *Ornithorhynchus*] with the reptilian prevomers, and of the mammalian vomer with the rostral part of the parasphenoid of reptiles ;" and (p. 360) :—"In the 'Therocephalian' *Lycosaurus* there is a large parasphenoid appearing on the palate in the exact region occupied by the mammalian vomer of Cynognathids ;" and (p. 360) :—"The whole of this evidence taken together seems to me to support BROOM'S view of the homology of the mammalian vomer, although it is not yet quite conclusive."

|| GREGORY, W. K., 'Bull. Geol. Soc. Amer.,' 28, December, 1917, p. 975 :—The parasphenoid of authors probably gave rise to the mammalian vomer, as held by BROOM.

The tympanic bone of Skull Y, although considerably larger than that of Skull X, is still of the same shape (*cf.* figs. 10, A, and 4), and consists of an obliquely crescentic plate, slightly concave on its dorsal surface, which forms the floor of the cavum tympanicum. The limb marked *sp* in fig. 10, A, lies ventral to the middle part of the malleus, and becomes later the sigmoid process, a process which in the Porpoise is relatively longer and narrower, and more S-shaped, than in the Mystacocetes (DENKER, 1902,* Plate 14, fig. 2, *p.s.*; BOENNINGHAUS,† 1904, p. 220, fig. G, *a*, *no.* 7). The limb marked *pp* is wedged in between the paroccipital process of the exoccipital and a small conical downgrowth of the squamosal, a downgrowth which is seen in figs. 6 and 7 of Skull Z. The limb lies immediately in front of the upper part of REICHERT'S cartilage, and develops later into the posterior pedicle, one of the two bony pedicles or pillars that in the adult unite the tympanic with the rest of the skull (LILLIE, **24**, p. 778). The tympanic membrane of Skull Y is still flat, and is attached, by about three-fourths of its margin, to the curved edge of bone around the area marked *tm* in fig. 10, A.

The main difference to be noticed in the tympanic bone of Skull Z, as compared with that of Skull Y, is in regard to the forward growth of the bone at the base of the sigmoid process (fig. 10, B); the sigmoid process is larger than before, but the margin of bone to which the tympanic membrane is attached is still much the same—the scale of enlargement of A and B is the same. The mesial edge of the bone (lower edge in figure B) is growing rapidly, and one finds just beyond the edge a number of small bony nodules which will later be incorporated in the edge as it spreads inwards (*i.e.*, mesially). The tympanic membrane of Skull Z is thimble-shaped (fig. 9, *mt*). The malleus is readily separable from the sigmoid process of the tympanic bone.

The tympanic bones of Skulls X, Y and Z form a well-graded series, and what is now wanted is another stage, or preferably two stages, between the tympanic of Skull Z and that of the 13½-feet fœtus figured by LILLIE (**25**, Plate 3, figs. 1–3), which leads on to the tympanic of the adult *Megaptera* (**25**, Plate 3, figs. 4, 5). The desired material not being available, the tympanic of Skull S, from a 6-feet 4-inch fœtus of *Balænoptera musculus*, may be employed to supply the deficiency. The tympanic of Skull R does not differ materially from this, except in its smaller size, and it is to be remembered that *B. borealis* is a smaller Whale than *B. musculus*.

The tympanic of Skull S shows a marked advance on that of Skull Z, and an intermediate stage would have been desirable, but the history of the essential

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[*] DENKER, A., "Zur Anatomie des Gehörorgans der Cetacea," 'Anat. Hefte,' 19, 2, Wiesbaden, May, 1902, pp. 421–448, 2 plates.

[†] BOENNINGHAUS, G., "Das Ohr des Zahnwales, zugleich ein Beitrag zur Theorie der Schalleitung,' 'Zool. Jahrb. Abth. Anat.,' 19, 2, Jena, February, 1904, pp. 189–360, 2 plates, 28 text-figs.

parts can be traced without difficulty. The sigmoid process and posterior pedicle (fig. 10, C, *sp*, *pp*) are readily recognised; the posterior edge of the former and the anterior edge of the latter, together with the free edge of the developing lip *pc*, give attachment to three-fourths of the margin of the tympanic membrane, which has the form of a thimble, much shorter in proportion to its width than it is in the adult. The remaining one-fourth of the margin is attached to the squamosal, in that region where it meets the periotic.

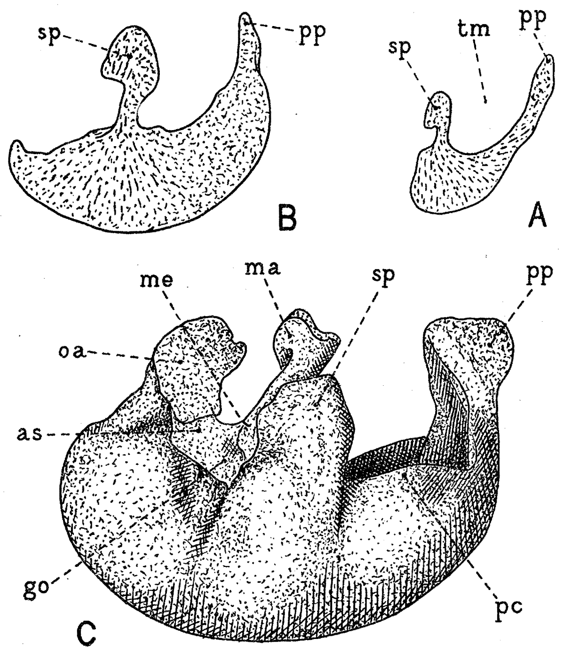

FIG. 10.—A, left tympanic bone (annulus tympanicus) of a fœtus of *Megaptera nodosa* measuring 16 inches, outer, *i.e.*, ventral view, × 1·2. B, tympanic bone of a fœtus of *Megaptera nodosa* measuring 27 inches, ventral view, × 1·2. C, tympanic bone and malleus of a fœtus of *Balænoptera musculus* 6 feet 4 inches, ventro-lateral view, × 0·9.

as, ascial process of the goniale, partly overlapped by the ossiculum accessorium; *go*, goniale, a membrane-bone of the processus anterior of the malleus; *ma*, head of the malleus; *me*, point of attachment of MECKEL'S cartilage to the malleus; *oa*, ossiculum accessorium, becoming later the anterior pedicle of the tympanic; *pc*, position in which arises later the posterior conical process; *pp*, posterior pedicle; *sp*, sigmoid, or anterior conical process; *tm*, position of tympanic membrane.

The processus anterior of the malleus is rigidly fixed to the front of the sigmoid process, and its membrane-bone, the goniale, extends forwards as a flattened, adze-like or ascial process (*as*). The cartilage-bone portion of the malleus terminates at the point *me*, where the axis is continued into the still persisting remnant of the Meckelian cartilage, not shown in the figure.

The anterior part of the tympanic has grown very considerably in comparison with the hinder part, so that the sigmoid process now comes to occupy the middle of the total length.* At the part that is destined to become the anterior pedicle is a separate flake of bone (*oa*), which seems to be the homologue of the ossiculum accessorium of the Lamb's skull. In the adult the anterior and posterior pedicles are co-ossified with the periotic bone, but they are at present free; the posterior pedicle touches the hinder part of the periotic, but the anterior pedicle is widely remote from that bone, and is kept in position by a fibrous union with the ventro-mesial surface of the processus falciformis of the squamosal bone. The tympanic bone has already become markedly bullate, and the involute dorso-mesial edge is much thickened; a portion of this edge is seen in the distance above the lip marked *pc* in fig. 10, C.

The term "sigmoid process" is adopted from BEAUREGARD (**3**, III, 1894, p. 393; Plate 11, figs. 1 and 3, *c*); the process marked *pc* in fig. 10, C, is the "apophyse conique postérieure" of BEAUREGARD (*ibid.*, p. 394), the "processus conicus posterior" of DENKER (*loc. cit.*, 1902, Plate 14, fig. 2, *p.c.p.*), the "processus medius bullæ" of BOENNINGHAUS (*loc. cit.*, 1904, p. 220, fig. G, *a*, No. 5), and HANKE (**18**, 1914, Plate 6, fig. 1, No. 5); it is at present merely a lip, but it projects much more in the adult. Its mode of growth is illustrated by HANKE in a series of diagrams (**18**, p. 509, fig. 7, *b*). The process is well shown in a figure of the tympanic bone of an adult Blue Whale given by TURNER (**33**, 1913, p. 15, fig. 3), which it is interesting to compare with the young tympanic of the same species shown in fig. 10, C, of the present paper; the sigmoid process is marked by TURNER the "lip-like process of the sinuous border with which the malleus is fused."

There is no endotympanic (metatympanic of WIŃCZA, **35**, 1896); the structure known as the tympanic bone in the Whale arises solely by the increase in size of the original annulus tympanicus; no part of it is preformed in cartilage. The relations of the late-developed, thick, inrolled edge to the rest of the bulla are well shown in the transverse sections of the bulla of *Balænoptera* given by BEAUREGARD (**3**, III, 1894, p. 393, fig. 7), and HANKE (**18**, 1914, p. 509, fig. 7, *a*).

The ossiculum accessorium mallei of Mammals is a structure of which more needs to be known; it was apparently first recorded in a new-born Sheep by VAN KAMPEN (**21**, 1905, p. 343, fig. 4, *o*), who found it as a small nodule on the course of the processus anterior of the malleus. WATSON (**34**, 1916, p. 361, and p. 365, No. 42), suggests that it may represent the reptilian surangular, the goniale being the prearticular, and the tympanic the angular of the mandibular ramus; he states that it occurs in the New World Edentates as well as in the Lamb.

In Skull S, of *Balænoptera*, there is a bone occupying the position of the ossiculum

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* It is interesting to note how accurately DORAN ('Trans. Linn. Soc.,' (2), 1, Zool., 7, 1878, p. 450) interpreted the parts, in spite of the absence of adequate material for studying the development of the Whale's tympanic. Concerning the sigmoid process he writes:—"This projection probably represents the anterior extremity of the annulus tympanicus of other mammals, the part in front being an extension of that ossification . . ."

as figured by VAN KAMPEN; it has the form of a plate, thicker in the middle than at the edges (fig. 10, C, *oa*), and is readily removable from the tympanic and from the ascial process (*as*) of the malleus. In texture it resembles the tympanic bone, but one can scarcely regard it as a dissociated or as a fractured portion of the tympanic, because the ascial process is wedged in between it and the tympanic. The ossiculum is not present in Skull R, nor in the *Megaptera* skulls.

The tympanic membrane, as already mentioned in the description of Skull X, is at first flat (fig. 4), and later becomes bulged outward, acquiring the form of a thimble (Skull Z, fig. 9, *mt*), and finally that of the finger of a glove, three or three and a half times as long as broad (LILLIE, **25**, p. 105). This outward bulge is characteristic of Mystacocetes; in Porpoises the tympanic membrane is slightly concave externally, *i.e.*, on the side towards the external auditory meatus.

LILLIE, in 1910 (**24**, p. 776), writes: "The tympanic membrane [of *Balænoptera*] seems to have escaped the notice of previous observers. It is highly modified and is a sac-like structure not unlike the finger of a glove." But the bulging of the tympanic membrane of Mystacocetes into the external auditory meatus was noted as far back as 1787 by HUNTER in *Balænoptera acuto-rostrata*, and has since been recorded by HOME (1812*), and BUCHANAN (1828†), in *Balæna mysticetus*, and by ESCHRICHT (**10**, 1849, p. 113, *t''*), and BEAUREGARD (**3**, III, 1894) in *Balænoptera acuto-rostrata*.

HUNTER (1787,‡ p. 434), writes that: "In the Piked Whale [*i.e.*, *Balænoptera acuto-rostrata*] the termination of the external opening, instead of being smooth and concave, is projecting, and returns into the meatus for above an inch in length, is firm in texture, with thick coats, is hollow on the inside, and its mouth communicating with the tympanum [*i.e.*, hollow tympanic bone]; one side being fixed to the malleus, similar to the tendinous process which goes from the inside of the membrana tympani in the others [*i.e.*, Bottle-nose Whale, Grampus, and Porpoise]."

HOME (*loc. cit.*, 1812, p. 84) found that in a young *Balæna mysticetus*, measuring 16 or 17 feet, the tympanic membrane projected an inch into the external meatus. He figures the ligament attached to the manubrium of the malleus (Plate 2), but he does not regard the fibrous tract into which it expands as being attached to the tympanic membrane; he says it is attached to the concavity of the tympanic bone. The tympanic membrane of *Balæna mysticetus*, as described by BUCHANAN (pp. 119–132, and Plates 5, 6, 7, 10), does not bulge to the same extent as in *Balænoptera* and *Megaptera*; it is hemispherical rather than of the form of a glove-

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* HOME, E., "An Account of some Peculiarities in the Structure of the Organ of Hearing in the *Balæna mysticetus* of Linnæus," 'Phil. Trans. Roy. Soc.,' 102, 1, 1812, pp. 83—89, 2 plates.

† BUCHANAN, T., 'Physiological Illustrations of the Organ of Hearing,' 8vo, London, 1828, pp. 160, 10 plates.

‡ HUNTER, J., "Observations on the Structure and Œconomy of Whales," 'Phil. Trans. Roy. Soc.,' 77, 2, 1787, pp. 371–450, 8 plates.

finger. Buchanan shows a process of the malleus embedded in the ligament, which he calls the "valvular process," but he erroneously interprets it as the processus gracilis.

Beauregard, in explaining his figures of the ear of *Balænoptera* (**3**, III, 1894, Plate 10, figs. 3 and 4, *t*), says that the ligament from the malleus "s'enfonce dans l'orifice *o* du sinus en doigt de gant, appelé membrane tympanique, dont on aperçoit en *t* l'extrémité convexe placée dans le conduit auditif externe *c*" (p. 412). From his use of the word "appelé" it would seem that he was not convinced of the correctness of the identification, but in his explanation of a figure of the isolated ear (Plate 11, fig. 3, and p. 413), he refers to *t* more definitely as "la membrane tympanique en doigt de gant," and on p. 395 he writes: "La situation et les relations de ce long diverticulum ne peuvent laisser de doute sur sa véritable nature. Il doit être homologué à la membrane tympanique des autres mammifères." Yet farther on (p. 397), he regards only a part of the glove-finger as the real tympanum: "Il semble probable que la paroi interne et supérieure seulement du doigt de gant qui la représente lui appartient en propre; elle se trouverait ainsi ramenée à une membrane très obliquement placée dans le conduit auditif externe. Tout le reste de la paroi du doigt de gant appartiendrait au sinus moyen" [of the Dolphin's ear, p. 388].

Hanke (**18**, 1914, pp. 494, 510) seems to accept the glove-finger as the tympanic membrane, yet in one place (p. 518, paragr. No. 8) he says that the outpushing does not represent the whole of the tympanic membrane, but only a part of it. He adds (p. 510, paragr. 3), that the membrane is at first concave externally, as in other Mammals; this is evidently in his 250-mm. fœtus of *Balænoptera acuto-rostrata*. Kernan (**22**, 1916, p. 492) finds the membrane to be slightly concave towards the inner surface in a fœtus of *Balænoptera borealis* measuring 375 mm.

From the study of the present three skulls of *Megaptera* (Skulls X, Y, Z), there seems to be no question that the thimble-shaped membrane of the 27-inch fœtus, and presumably the glove-finger membrane of the adult Whale, represents the whole of the tympanic membrane. It is to be borne in mind, however, in using the expressions thimble and glove-finger, that the edge is not transverse to the axis; the tympanic membrane of the adult is like a glove-finger that has been cut off obliquely.

The malleus of Skull X, as already pointed out in the preceding section of the paper, is large in comparison with the incus and stapes; the manubrium is short and stout, and its bluntly pointed extremity is attached by fibrous tissue to the middle of the dorsal surface of the tympanic membrane. The axis of the malleus, becoming later the processus anterior, passes insensibly into the Meckelian cartilage of the lower jaw (fig. 11, A).

Carte and Macalister were under the impression that it is the manubrium of the cetacean malleus that fuses with the tympanic bone (**7**, p. 254), but Dwight (**8**, 226), Doran (*infra*, 1878, p. 450), and Lillie (**24**, p. 779) consider that the part in question is the processus anterior. TURNER, writing as recently as 1913 (**33**, pp. 18–19), regards the homology of the parts of the cetacean malleus as still in doubt, and states that "the development of these processes [namely, that which is fused with the tympanic bone, and that to which the ligament of the glove-finger membrane is attached] requires to be studied before their morphology can be precisely determined." The study of the relations of the parts in Skulls X, Y, and Z makes it perfectly clear that it is the processus anterior (longus, gracilis, folianus), and not the manubrium, that co-ossifies with the tympanic bone. The fusion, nevertheless, has not yet taken place in Skull Z; it has in Skull S of *Balænoptera*, but not in Skull R.

The growth of the malleus of *Megaptera* is illustrated in three stages in fig. 11. The goniale arises as a thin flake of bone upon the surface of the cartilaginous axis of the malleus (A, *go*), and grows rapidly, first along the axis and afterwards independently of it. The outstanding part (*a* in B and C) bears a certain resemblance to the head of an adze, and for convenience of subsequent reference may be termed the "ascial process." In occurs in *Balænoptera* (fig. 10, C, *as*) as well as in *Megaptera*, and has been previously figured by HANKE (**18**, 1914, p. 515, fig. 10, No. 4), who terms it the "Verwachsungsstück des Processus folianus."

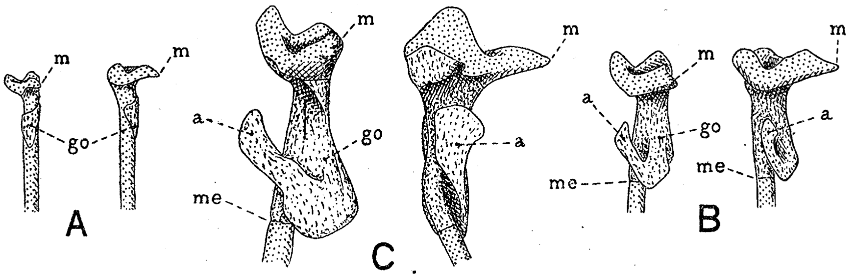

FIG. 11.—Right malleus of *Megaptera nodosa*. A, from a fœtus measuring 6 inches; B, from a 16-inch fœtus; C, from a 27-inch fœtus. The right-hand figure in each case shows the manubrium at its full length; the left-hand figure is drawn with the manubrium directed towards the observer, and consequently foreshortened. × 1·5.

a, ascial process of the goniale; *go*, goniale, a membrane-bone of the processus anterior of the malleus; *m*, extremity of the manubrium; *me*, extremity of the cartilage-bone of the malleus, where it continues into MECKEL's cartilage.

The cartilaginous axis of the malleus undergoes ossification, and in the region marked *me* in figs. B and C, where it is in a direct line with the Meckelian cartilage, the cartilage-bone is clearly distinguishable from the membrane-bone. Some authors write as though the processus anterior consists of membrane-bone solely, and this is particularly the case with those who use the term processus folianus in the sense of an exact equivalent of os goniale; but if one employs the term processus anterior as designating the forwardly directed limb of the malleus as a whole, it is clear that cartilage-bone enters largely into its composition.

The caput of the malleus is perforated in all three cases, and, judging from the work of BOENNINGHAUS (1904, p. 267*) on toothed Whales, and of HANKE (**18**, p. 515) on fœtal *Balænoptera*, it would seem that the foramen is traversed by the chorda tympani.

The orientation of the malleus changes during development; in all three skulls (X, Y, Z) the manubrium points mesially, horizontally, and slightly posteriorly; but the axis of the malleus, as also that of the MECKEL'S cartilage in front of it, slopes anteriorly, mesially, and ventrally in Skull X, whereas in Skull Z the axis of the malleus and of MECKEL'S cartilage slopes more ventrally and less mesially and anteriorly. In fig. 11, therefore, the malleus in the three stages of growth is represented as an isolated object, without reference to its orientation in the skull.

On the first appearance of the goniale, its position upon the cartilage of the malleus in mammals generally is fairly constant. The bone arises as a typical membrane-bone, although the ossification may spread later into the cartilage; it flanks the cartilaginous processus anterior, and is situated either upon the process itself, or in the bend that leads round to the manubrium. In Skull X of *Megaptera* (fig. 11, A) it occurs upon the process, much in the same position as in the Rabbit (VOIT, 1909,† Plate 41, fig. 9); in many other cases it begins to ossify nearer the caput, as in the Sheep (SALENSKY, 1880,‡ Plate 20, fig. 7), and in *Tatusia*, *Dasypus*, *Cholœpus*, *Manis*, *Erinaceus*, *Talpa* (PARKER, W. K., 'Phil. Trans,' vol. 176, 1, 1885 (1886); Plate 5, fig. 4; Plate 7, fig. 6; Plate 9, fig. 9; Plate 11, fig. 6; Plate 22, fig. 4; Plate 28, fig. 5).

The perforation of the bone by the chorda tympani was first noticed by DORAN (1878),§ and the observation has since been extended by GAUPP and others; the perforation is now known to occur in *Centetes*, *Ericulus* and *Gymnura* (DORAN), *Erinaceus* (DORAN, BONDY), *Tolypeutes* (BONDY), *Dasypus* (FUCHS), *Lepus* (VOIT), *Mus* (GAUPP, FUCHS), *Microtus* (FAWCETT), *Didelphys* (GAUPP, FUCHS, TOEPLITZ), *Perameles* and *Dasyurus* (GAUPP) and *Ornithorhynchus* (WILSON, WATSON). GAUPP lays stress upon the character as one of the means of establishing the homology between this membrane-bone, occurring on the processus anterior of the mammalian malleus, and the os goniale of the mandible of Reptiles and Amphibians (**16**, I, 1911).

The name "goniale," which is now in fairly general use, we owe to GAUPP, but the name "prearticular" of WILLISTON seems to have priority, and is preferred by some writers (*e.g.*, WATSON, **34**); KINGSLEY terms the bone the "antarticular" or

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* BOENNINGHAUS, G., "Das Ohr des Zahnwales, zugleich ein Beitrag zur Theorie der Schalleitung," 'Zool. Jahrb., Abth. Anat.,' 19, 2, Jena, February, 1904, pp. 189–360, 2 plates, 28 text-figs.

† VOIT, M., "Das Primordialcranium des Kaninchens unter Berücksichtigung der Deckknochen. Ein Beitrag zur Morphologie der Säugetierschädels," 'Anat. Hefte,' 1, 116 (38, 3), Wiesbaden, 1909, pp. 425–616, 16 plates.

‡ SALENSKY, W., "Beiträge zur Entwicklungsgeschichte der knorpeligen Gehörknöchelchen bei Säugethieren," 'Morph. Jahrb.,' 6, 3, Leipzig, 1880, pp. 415–432, 1 plate.

§ DORAN, A. H. G., "Morphology of the Mammalian *Ossicula auditus*," 'Trans. Linn. Soc.,' 2, 1, Zool., 7, August, 1878, pp. 371–497, 7 plates.

"dermarticular." By some writers it is called the "postsplenial," or the "postoperculare," since it occurs behind, *i.e.*, posterior to, the splenial (of OWEN), or operculare (of CUVIER). The bone is a membrane-bone, flanking the hinder part of the inner (mesial) face of the mandibular ramus, and is commonly fused with the articular, the cartilage-bone with which the quadrate bone articulates. In the Stegocephalian genus *Trimerorhachis* three flanking bones of the splenial series are present, there being a preangular (postsplenial or postoperculare) between the splenial in front and the prearticular behind (BROOM, 1913; WILLISTON, 1913).

The membrane-bone of the processus anterior of the mammalian malleus is regarded by PALMER (1913,* p. 515) as the homologue of the surangular, rather than of the prearticular of the reptilian mandible, because of its position on the cartilage, more to the outer side than to the mesial side. One must, however, consider its position in direct relation with the tilt of the auditory region as a whole. In the embryo of *Perameles* studied by PALMER the tympanic membrane is almost vertical (*loc. cit.*, p. 513) whereas in Skull X of *Megaptera* the membrane is horizontal (fig. 4). In Skull X, and in the *Megaptera* skull studied by HONIGMANN (**20**, p. 31, figs. 17, 18), the membrane-bone is on the dorso-mesial surface of the cartilage, while in *Perameles* (*loc. cit.*, figs. 1, 2) and *Didelphys* (TOEPLITZ,† 1920, p. 53, fig. 20; p. 25, fig. 8; p. 18, fig. 6) it is on the ventral surface; yet in all these cases the bone occurs in the same position relatively to the malleus itself, namely, on the concave surface that bends round into the manubrium. One must remember, nevertheless, that the tilt of the auditory region in embryonic Mammals is directly related to the degree of inflation of the brain-case; and the more primitive forms, such as the Marsupials, with their relatively smaller brain, are more strictly comparable with the Therapsida than are the higher Mammals, with their brain-distended cranium.

The stapes and incus of Skulls X and Y differ from those of Skull Z in their smaller size, but in no other respect. Even in Skull Z ossification has not begun, either in the incus or in the stapes. The stapes is movable in the fenestra ovalis, but it is difficult to isolate, owing to the footplate being a little larger than the free margin of the fenestra, a condition that appears to persist for life (STRUTHERS, **30**, 1889, p. 361). The perforation in the stapes is small and circular; the part where the stapedius muscle is attached does not project, as it does in some Mammals. The articular face by which the incus fits upon the malleus is saddle-shaped; the crus breve is so feebly differentiated as to be scarcely recognisable; the end of the crus longum is bent at right angles to the main portion of the incus, and there is no lenticulare between it and the stapes.

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* PALMER, R. W., "Note on the Lower Jaw and Ear Ossicles of a Fœtal *Perameles*," 'Anat. Anz.,' 43, 19–20, April, 1913, pp. 510–515, 4 text-figs.

† TOEPLITZ, C., "Bau und Entwicklung des Knorpelschädels von *Didelphys marsupialis*," 'Zoologica,' 27, 3, Stuttgart, 1920, pp. 1–84, 3 plates, 26 text-figs.

The mandibular ramus shows a progressive increase in size in the Skulls X, Y and Z; the lengths, measured along the curve, are 51, 117 and 190 mm. In Skull Y the part of the Meckelian cartilage that is continuous with the malleus (fig. 11, B) passes downward and forward on the mesial face of the hinder part of the mandibular ramus, and thins off (fig. 16, C), and, at the level of the coronoid process, passes into a longitudinally disposed tract of fibrous tissues flanking the periosteum.

At the level of the anterior end of the coronoid process the cartilage commences again, widens, and soon disappears in the longitudinal groove in the bone of the dentary. On opening up the groove it is seen that the continuation of the cartilage is ossified, and is recognisable as an ossified MECKEL'S cartilage for about 3 or 4 mm., but in front of this the bone is continuous with the dentary bone, and is indistinguishable from it. The front part of the cartilage, clearly defined in Skull X (fig. 1, C), seems in Skull Y to have been absorbed rather than ossified; a groove in the mesial face of the front part of the mandible marks the place where one would expect to find it, but there is here no trace either of cartilage or of cartilage-bone.

In Skull Z the Meckelian cartilage is greatly shortened up. The length of the still persisting part, *i.e.*, from the point marked *me* in fig. 11, C, to the natural, rounded, antero-ventral extremity of the cartilage, is about three-fifths of the length of the malleus (fig. 7). The mandibular groove, still visible in Y, has disappeared in Z. Dissection of the mandibular ramus fails to reveal any remnants of the Meckelian cartilage.

In the lower jaw of Skull Y there are thirty-six teeth on the right side and thirty-nine on the left. The front ten or twelve teeth, and the hindermost ten or twelve, are more closely set than those in the middle of the series. The lower front teeth lie obliquely, pointing more forward than upward; they are longer, finer and more sharply pointed than the front teeth of the upper jaw. In the lower jaw of Skull Z there are thirty-four teeth on the right side and thirty-seven on the left; they are larger and longer than the teeth of the upper jaw, and they have sharp, hooked points, resembling the spines of the bramble. The total number of teeth found in Skull X is 144, in Skull Y 149, and in Skull Z 149, but ESCHRICHT (**10**, p. 90) puts the total number of teeth in *Megaptera* fœtuses at 186.

The hyoid bar is of the same shape in Skulls Y and Z as in Skull X, although the transverse axis tends to become straighter as development proceeds; the increase in size may be gauged from the fact that fig. 16, A, representing the hyoid of Skull Z, is of the natural size, whereas fig. 1, D, of the hyoid of Skull X, is enlarged (× 1·8). There is no sign of bone in the hyoids of X and Y; but in Skull Z, the thyrohyals have begun to ossify, the bony part being about 11 mm. in length; there is as yet no sign of a basihyal. In the adult the three bones fuse into one, and the delimiting sutures disappear; a figure of the hyoid of an adult *Megaptera* is given by van Beneden and Gervais (**4**, Plate 9, fig. 7), and a description of one by Struthers (**30**, pp. 370, 371).

In the figure by van Beneden and Gervais the ends of the anterior cornua, or stylohyal bones, are represented as connected by ligament with the pair of cones that project forward from the basihyal, but the ligament is not yet present in Skulls X, Y and Z. Rudolphi, in his figure of the hyoid of an adult *Megaptera* (**27**, Plate 1, fig. 4) shows the stylohyals as if they were articulated with the lateral extremities of the thyrohyals, a mistake already noted by Eschricht (**10**, p. 126).

The thyrohyals of Odontocetes slope more backward than those of the Mystacocetes, and there is a definite attachment of the end of the anterior cornu to the front of the basihyal (*Phocœna*, Howes, G. B., 'Journ. Anat. Phys.,' 14, 4, July, 1880, Plate 29, fig. 10; Boenninghaus, G., 'Zool. Jahrb., Abth. Anat.,' 17, 1–2, Nov., 1902, p. 59, fig. S; *Platanista*, Anderson, J., 'Exped. Western Yunnan,' 1868, 1875, London 1878 (1879), Cetacea, Plate 40, fig. 20; *Grampus*, Danois, E., 'Arch. Zool. Expér.,' Paris (5), 8, 4, Sept., 1911, Plate 9, fig. 17).*

The anterior cornu of the hyoid (Reichert's or stylohyal cartilage) in Skull X is a curved rod of cartilage (figs. 1, A and B, 2, 4, *hy*), free at its anterior end, and confluent at its postero-dorsal end with the hinder part of the crista parotica of the auditory capsule. In Skull Y the cartilage shows the first indications of ossification; in Skull Z the bony part is sharply marked off from the cartilage. In figs. 6, 7 and 9 the anterior cornu (*hy*) is seen obliquely, and does not show its full length. The total length from the attached part to the free extremity, measured straight, and not following the curve, is 36 mm. The stylohyal bone is 16 mm. long, and 2·5 mm. thick in the middle of its length.

The stylohyal bone of Skull Z lies obliquely above (*i.e.*, dorsally to) the outer part of the bone of the hyoid bar. This would appear to be the natural position of the parts, and is in agreement with the relations found by Honigmann to subsist in an earlier fœtus of *Megaptera* (**20**, p. 26, fig. 11), but it is quite possible that, if the larynx be pulled backward, the anterior cornua may come to lie altogether in front of the hyoid bar, as is represented in fœtal specimens of *Balænoptera* by Eschricht (**10**, Plate 14, fig. 5), and Schulte (**28**, p. 484, fig. 7), in adult *Balænoptera* by Carte and Macalister (**7**, Plate 5, fig. 6), in adult *Megaptera* by van Beneden and Gervais (**4**, Plate 9, fig. 7), and in adult *Balæna* by Eschricht and Reinhardt (**11**, Plate 6, fig. 1).

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* This figure represents the hyoid of a fœtus, and shows three centres of ossification; oddly enough the author terms the median one the thyrohyal and the paired one the basihyal (p. 415).

SKULLS OF A 3-FEET 11-INCH FŒTUS OF *Balænoptera borealis* LESSON AND A 6-FEET 4-INCH FŒTUS OF *Balænoptera musculus* LINN.

These may be denoted Skulls R and S respectively. Skull R is from one of twin fœtuses, each measuring 3 feet 11 inches, of the Sei Whale or RUDOLPHI'S Rorqual, *Balænoptera borealis* LESSON, collected in June, 1912, off Collafirth, Shetland Isles, and received at the British Museum (Nat. Hist.) on July 5. The fœtus from which Skull S was prepared is that of a Blue Whale, *Balænoptera musculus* LINN., collected off Leith Harbour, South Georgia, on the Major G. E. H. Barrett-Hamilton Whaling Mission, 1913. Only the head was sent to the British Museum (Nat. Hist.); the length of the fœtus is not recorded, but it is computed to have been 6 feet 4 inches.

The length of Skull R, from condyles to the tip of the rostrum, is 11½ inches, or 292 mm.; that of Skull S is 19 inches, or 483 mm. The maximum breadth of the skull, taken across the zygomatic process of the squamosal, is in Skull R 6¼ inches, or 159 mm., in Skull S 12 inches, or 305 mm. The drawings reproduced as figs. 10, C, 12, 13, 15, A, and 16, B, were made from the freshly prepared skulls, before drying. It is not proposed to give complete descriptions of the skulls, but to restrict the account to features that appear to be of especial interest.

In Skulls R and S the occipital condyles are wholly cartilaginous; the lower parts of the two condyles are continuous in S but not in R; the basioccipital bone terminates posteriorly in a rounded projection in the middle of a cartilaginous mass, and from the skulls in their present dried condition it might seem as if the hemispherical pair of occipital condyles were supported by the basioccipital; but it is extremely probable that a study of later skulls will prove that the condyles are borne by the exoccipital bones solely (see SMETS, **29**, p. 191). It would not be altogether exceptional, however, if it were found that each condyle is formed partly of basioccipital bone, for it is well known that in the young Rabbit (about 3 weeks old) and in young *Echidna* (WEBER, M., 'Die Säugetiere,' 1904, Jena, p. 43, fig. 35, 3) the basioccipital bone contributes a fair proportion of the total condylar projection.

The dorso-lateral parts of the basioccipital touch the exoccipital bones, but farther back there is a great mass of cartilage intervening. The paired ventral ridges of the basioccipital are more prominent than they are in Skull Z of *Megaptera*; in fig. 12 the left one is seen below the median section of the basioccipital bone; its anterior end touches the hindermost part of the pterygoid bone. In Skull R the cartilage between the basioccipital and the basisphenoid is in the form of a thin plate (fig. 12), but in Skull S it is wedge-shaped, being 16 mm. thick above, and 3 mm. below.

The basisphenoid is well ossified in both R and S, and co-ossified with the alisphenoid, although in a 14¾-inch fœtus of *Balænoptera borealis*, SCHULTE finds that the incipient ossification of the ala temporalis is not yet continuous with the basisphenoidal centre of ossification, the intervening processus alaris being still cartilaginous (**28**, p. 476). Whereas in Skull R the connection between the alisphenoid and the lateral part of the basisphenoid, although fully ossified, is thin and readily broken, in Skull S the junction is bulky and massive. The carotid artery does not penetrate the bone, but runs in a groove at the side of the hinder part of the basisphenoid.

As has already been pointed out in describing the fœtal skull of *Megaptera*, the alisphenoid of Mystacocetes—possibly of Odontocetes also—is but the ossified ala temporalis; it is a cartilage-bone solely, without any addition of the tracts of membrane-bone that are so common in other Mammals. In a dorsal view of the cranial floor of Skulls R and S the alisphenoids project outward and forward from the basisphenoid, but not upward; and the parts are very similar to those figured by ESCHRICHT and GERVAIS in fœtal *Balæna* (**13**, Plate 2, fig. 1, G and E; **17**, Plate 4, fig. 3), and by GERVAIS in a young (not fœtal) *Balænoptera acuto-rostrata* (**17**, Plate 4, fig. 4, A). ESCHRICHT shows the same parts in a figure of *Balænoptera acuto-rostrata* (fœtus, $6\frac{1}{2}$ feet); he marks the notch behind the alisphenoid for the passage of the third division of the trigeminal nerve, but he terms it the foramen lacerum anticum (**10**, Plate 13, fig. 1, *x*).

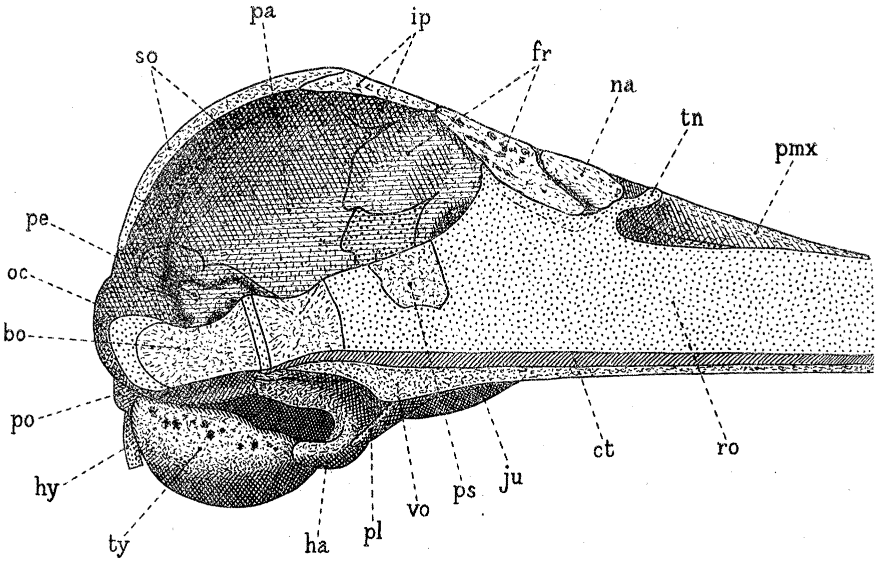

FIG. 12.—Left half of bisected skull of a fœtus of *Balænoptera borealis* measuring 3 feet 11 inches, × 0·5. The front part of the snout is omitted.

bo, basioccipital; *ct*, thick layer of connective tissue between the vomer and the rostral cartilage; *fr*, frontal; *ha*, hamular process of the pterygoid; *hy*, hyoid cornu or stylohyal cartilage, cut short; *ip*, interparietal; *ju*, jugal; *na*, nasal; *oc*, occipital condyle; *pa*, parietal; *pe*, periotic; *pl*, hind edge of the palatine; *pmx*, premaxilla; *po*, paroccipital process; *ps*, presphenoid; *ro*, rostral cartilage; *so*, supraoccipital; *tn*, extremity of the tectum nasi; *ty*, tympanic; *vo*, vomer.

The dorsal view of the basisphenoid–alisphenoid complex in Skulls R and S bears a close resemblance to that in PARKER's sixth developmental stage of the Pig,* the main difference being that the alisphenoids slope outward and forward in Skulls R and S, and outward and backward in the Pig. BROOM writes (1909,† p. 210), that "there is good reason to believe that it is this cartilage [the alisphenoid cartilage of embryonic Mammals] that PARKER, in his work on the Pig's skull, took for the palato-pterygoid." But, whatever may be said as to the supposed origin in cartilage of PARKER's external pterygoid plate (*epg* in figs. 2 and 3, Plate 32), which the present writer regards as the membrane-bone portion of the definitive alisphenoid of the Pig (Plate 35, figs. 2 and 10, *epg*), there can be no doubt that PARKER correctly identified the alisphenoid cartilage in the embryos that he was studying (*e.g.*, *al* in Plate 30, fig. 4, and p. 301); his palato-pterygoid is something distinct from this (*e.g.*, *ppg* in figs. 2 and 5, Plate 28).

The presphenoid in Skulls R and S is a median bone, the ossification of which has reached the upper surface of the cartilage, but is still remote from the lower surface (fig. 12, *ps*), it which respects it resembles the presphenoid of a fœtus of *Balænoptera physalus* (= *musculus* auctt.), measuring 1180 mm. studied by KÜKENTHAL (**23**, II, Plate 21, fig. 6, and p. 319, text-fig. 47), and that of a fœtus of *Balænoptera musculus* (= *sibbaldii*, GRAY), with a skull-length of 400 mm., studied by SMETS (**29**, Plate 196, and p. 199, text-fig. 4). In ESCHRICHT's $6\frac{1}{2}$-feet fœtus of *Balænoptera acuto-rostrata* the ossification of the presphenoid has reached the lower surface of the cartilage, and is visible from below on removal of the vomerine bone (**10**, Plate 13, fig. 2).

Although in both Skulls R and S the presphenoid, when viewed from above, has in its hinder border a median notch into which the basicranial cartilage extends, there is no reason for believing that the presphenoid arose from a paired centre of ossification. SCHULTE, in his $14\frac{3}{4}$-inch fœtus of *Balænoptera borealis*, finds that the presphenoid has a pair of small centres of ossification not yet united in the middle line (**28**, p. 482), and, since he bisected the skull, there can be no doubt about the absence of the ossification in the median plane (Plate 56, fig. 2).

It is interesting to note in this connection that there are two published figures of the cranial floor of young *Balæna*, in which a tract of cartilage intervenes between the two bones, *Balæna japonica*, fœtus, 1·6 m., ESCHRICHT, **13**, Plate 2, fig. 1; *Balæna antipodum*, fœtus, about 1 metre, GERVAIS, **17**, Plate 4, fig. 3, and p. 108. The bones visible are regarded by the authors as orbitosphenoids (alæ parvæ or petites ailes), but it is quite possible that they are the right and left parts of a median presphenoid, appearing to be separate in consequence of a dorsally placed median tract of cartilage which does not ossify until later. On this interpretation the orbitosphenoids proper would be merely the parts of bone immediately adjacent to the optic foramina, a conclusion that is supported by the smallness of the orbitosphenoid bones

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* 'Phil. Trans. Roy. Soc.,' 164, 1, 1874, Plate 35, fig. 4.

† BROOM, R., 'Proc. Linn. Soc. N.S. Wales,' 34, 2, September, 1909.

in the skulls now under consideration, Skulls R and S, and Skull Z (fig. 5). It is only by the inspection of a median section of the basicranial axis that one can state definitely whether the developing presphenoid is median or paired.

In a young (not fœtal) *Balænoptera acuto-rostrata*, measuring about 3 metres, the basioccipital, basisphenoid and presphenoid, although in close contact, are all distinct (GERVAIS, **17**, Plate 4, figs. 4 and 4 *a*), but in a slightly older specimen of the same species, measuring 5·8 metres, the basisphenoid is united with the basioccipital, although separate from the presphenoid.* It would seem that even in adult Mystacocete Whales the presphenoid remains separate from the basisphenoid (**17**, Plate 4, figs. 5, 6, 7 ; **4**, Plate 10, figs. 2, 10).

WEBER, in the figure mentioned in the previous paragraph, marks the combined basisphenoid and basioccipital bones the basioccipital. The presphenoid he regards as the combined pterygoid and presphenoid ; but the pterygoid bone would be posterior to the palatine bone, as he shows in his text-fig. 412 of *Balæna*; and, further, the part of the bone upon which the letter *p* is written, in his fig. 418, is more likely to be pterygoid than palatine. The pituitary depression in Mystacocetes is very shallow and scarcely recognisable as a hollow, and it occurs above the basisphenoid bone (fig. 12) ; the depression that WEBER marks "Hypophysis-Grube" (*fh*) in the presphenoid bone is evidently the transverse groove that runs between the right and left optic foramina.

In both R and S there is a considerable tract of the ala orbitalis still remaining, seen in fig. 12 above the presphenoid ossification, and below and behind the frontal bone. The front part of the presphenoid cartilage continues forward imperceptibly into the rostral cartilage, and it is not possible to define the limit between the basicranial cartilage and the cartilage of the olfactory capsule, either in a median section of the skull or in a ventral view after removal of the palatine and vomerine bones.

In both Skulls R and S the orbitosphenoid is a small bone in the lower part of the ala orbitalis, with a curved mesial edge, which forms the external boundary of the optic foramen. In Skull R the two ends of the bone are not yet co-ossified with the presphenoid, but in Skull S the front part is fused with the presphenoid, although the hinder junction is still cartilaginous. The orbitosphenoid is not seen in fig. 12, since it occurs at a low level and is concealed by the presphenoid. In a younger fœtus of *Balænoptera borealis* (14¾ inches) SCHULTE finds that the tænia metoptica, forming the hind border of the optic foramen, is partially absorbed, so that the foramen is confluent with the sphenoidal fissure (**28**, p. 481, and Plate 56, fig. 2) ; but this is not so in Skull R.

The orbitosphenoid develops to a very small extent in the Mystacocetes, and although, on the whole, a view of the cranial floor of Skull S bears a close resemblance

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* WEBER, M., 'Die Säugetiere,' 1904, Jena, p. 563, text-fig. 418.

to the corresponding view of PARKER'S sixth stage of the Pig,* yet the orbitosphenoid in the former is very small in comparison with the other parts. The difference is probably related to the late development of the orbitosphenoid in the Whale, for in the Pig† the two orbitosphenoid bones have already attained a fair size before the presphenoid cartilage begins to ossify.‡ A similar discrepancy is to be noted in the relative growth of the alisphenoid; in Skull Y of *Megaptera* it has been shown that a basisphenoidal centre of ossification is present, although the ala temporalis is entirely cartilaginous; and in SCHULTE'S fœtus of *Balænoptera borealis* the ossification in the ala temporalis has only just begun, although that in the basisphenoid is fairly advanced (**28**, p. 476); but in the Pig, Parker shows (*ibid.*, p. 317) that the alisphenoids ossify rather earlier than the basisphenoid: in PARKER'S Plate 33, fig. 11, the bones are marked respectively *ab. s.* and *c. s.*, but reference to the text shows that the lettering was evidently intended to be *al. s.* and *b. s.*

No part of the olfactory capsule shows any signs of ossification in Skulls R and S; the rostral cartilage grows to an enormous size later on, but remains unossified even in the adult, and, consequently, in the skulls found in museums there is, above the vomer and between the maxillary bones, a great space that was formerly occupied by this mass of cartilage. The rostral cartilage is to be regarded as the enlarged lower part of the mesethmoid; the septum nasi itself, between the two nasal passages, is not exceptionally thick. In comparing the figure of the longitudinal section of Skull R (fig. 12) with that of Skull X of *Megaptera* (fig. 1, B), it should be borne in mind that the latter skull is cut a little to the left of the median plane of the head, so that the left nasal cavity is exposed. Fig. 12 represents a strictly median section and passes through the middle of the septum nasi.

In his description of a 14¾-inch fœtus of *Balænoptera borealis* SCHULTE states that the lateral ethmoid, *i.e.*, the part lateral to the cribriform plate, is ossified (**28**, p. 483), although his figure (Plate 56, fig. 2) does not show any indications of the bony part. In Skull R, from a 3-feet 11-inches fœtus of the same species of *Balænoptera*, there is no sign of ossification in the ethmoid cartilage. It has already been suggested, in dealing with Skull Y of *Megaptera*, that SCHULTE'S "ectethmoid" bone is really a part of the frontal. In fig. 12 of the present paper the depression in which the cribriform plate lies is indicated by the dark shading between the frontal bone and the ridge of the mesethmoid cartilage that terminates in front in the spina mesethmoidea, situated ventrally to the middle of the length of the suture between the two frontal bones.

The periotic bone in both R and S consists of the labyrinthic portion only, the

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* 'Phil. Trans. Roy. Soc.,' 164, 1, 1874, Plate 35, fig. 4.

† Also in a bisected skull of *Zebra grevyi* at the British Museum (Natural History). The skull is that of a three-months' fœtus, and in its present dried condition is 122 mm. long; the presphenoid cartilage between the two orbitosphenoid bones is unossified.

‡ PARKER, *ibid.*, p. 314, and Plate 34, figs. 5 and 6, Stage 4.

great extensions—pro-otic and opisthotic of LILLIE (**24**, p, 778), pre-otic and opisthotic of TURNER (**33**), processus anterior petrosi and processus posterior petrosi of HANKE (**18**, p. 505)—not having yet developed. The isolated periotic bone of R, in its present dried condition, is smaller and more rounded than that of S, but in other respects the two agree with one another and with the periotic of Skull Z, described in the previous section of the paper. But in R and S the anterior margin of the canalis facialis is ossified, whereas in Skull Z it is still cartilaginous; and the rounding off of the front part of the periotic in R and S, and its separation from adjacent cartilage, may be taken as an indication that the commissura prefacialis, or at all events a part of it, is to be regarded as belonging to the auditory capsule.

The hinder process of the periotic in the adult *Balænoptera* is longer than the anterior, and is wedged in between the squamosal and the exoccipital without, however, fusing with either; and in the present skulls there is a tract of unossified cartilage occupying this position. The anterior process in the adult is lodged in a cavity in the squamosal bone near the front of the tympanic, but the growth of the process has not yet commenced in Skulls R and S.

In fig. 12 the part of the periotic bone actually indicated by the letters *pe* is the orifice of the endolymphatic duct; situated posteroventrally to it is the foramen perilymphaticum, opening backward; situated anteroventrally to it, above the edge of the basioccipital, are seen the upper halves of the depressions for the facial and auditory nerves. The facial nerve runs backward, skirting the dorso-external border of the fenestra ovalis, in a groove that represents the Fallopian canal of other Mammals, and emerges by the stylomastoid foramen, behind the upper end of the stylohyal cartilage. In comparing fig. 12 with SCHULTE's figure of a longitudinal section of the skull of an earlier fœtus of the same species of *Balænoptera* (**28**, Plate 56, fig. 2), it must be borne in mind that the half-skull in his figure is tilted over towards the observer, and in consequence more of the auditory capsule is seen than in fig. 12 of this paper.

In a back view of the skull it is seen that the exoccipital bone is in a rather more advanced stage of ossification in S than in R, and in S it has a long, thin, dorsolateral process which is wanting in R; the external edge of this process fits against the upper part of the posterior edge of the squamosal. The occipital cartilage persists to a large extent between the exoccipital and supraoccipital bones, and a tract of this cartilage runs up some considerable distance behind the posterior edge of the parietal, both on the outside of the skull, and on the inside (fig. 12). The inner face of the exoccipital bone (traversed by the dotted line *pe* in fig. 12) is less extensive than the outer or posterior face.

There is no separate foramen for the hypoglossal nerve, but the nerve issues through the hinder part of the foramen lacerum posterius, being feebly separated from the glossopharyngeus, vagus and accessorius by a strand of fibrous tissue. This is in agreement with the findings of SCHULTE in *Balænoptera borealis* (**28**, pp. 474, 481;

375-mm. fœtus) and ESCHRICHT in *Balænoptera acuto-rostrata* (**10**, p. 118; 9-inch fœtus), and CARTE and MACALISTER in an adult of the latter species (**7**, p. 207); but DE BURLET figures a special notch at the back of the foramen lacerum posterius for the emergence of the hypoglossal nerve in *Balænoptera acuto-rostrata* (**6**, III, p. 126, Plate 6; 105-mm. fœtus), and remarks that in one adult skull of *Balænoptera physalus* he found separate condylar foramina, although they were wanting in another skull of that species (**6**, III, p. 127).

The foramen magnum is comparatively small and circular in outline. The tract of cartilage between the lower edge of the supraoccipital bone and the upper border of the foramen magnum is about 14 mm. high in both R and S. The supraoccipital is concavo-convex, and its slanting antero-lateral edges meet the parietals, and overlap them to a slight extent, in both R and S, but the relations of the front edge of the supraoccipital are different in the two skulls.

In Skull R an interparietal bone is present, and the two parietals do not meet one another in the median plane of the head; the interparietal is overlapped by the supraoccipital behind (fig. 12), and by the parietals at the sides (fig. 13, A); it scarcely reaches the frontal bones anteriorly, there being still a fair amount of fibrous tissue between the bones. In Skull S there is no interparietal bone, and the two parietal bones meet, except for a small tract of fibrous tissue (fig. 13, B), the relations of the parietals to one another and to the overlapping supraoccipital being much the same as in young *Megaptera* (figs. 3, 8).

Seeing that Skulls R and S are from animals of different species, *Balænoptera borealis* and *B. musculus* respectively, efforts were made to ascertain whether the presence of an interparietal and the separation of the parietals in the former, and the absence of interparietal and the meeting of the parietals in the latter, might be regarded as a reliable specific difference. Skull R is from one of twin fœtuses, and an examination of the other fœtus proves the similarity in the relations of the parts of the cranial vertex in the two; and in a younger fœtus of the same species, measuring 14¾ inches, SCHULTE shows a separate interparietal, distinct from, and overlapped by, the supraoccipital (**28**, Plate 54, fig. 1).

Skull S is from a 6-feet 4-inch fœtus of the Blue Whale, *Balænoptera musculus*, and by good fortune an 8-feet fœtus of the same species was available for study. The fœtus bears the British Museum (Nat. Hist.) Register Number 6.19.3.14; loc. South Georgia; length of head from condyles to tip of snout—23½ inches. The dried calvarium of this agrees exactly with that of Skull S, except in being slightly larger. Viewed from within and from without, the two parietals are seen to meet in an irregular suture, and there is no trace of an interparietal. Owing to the supraoccipital overlapping the parietal bones, the parietal suture is more extensive on the inner or cerebral surface than externally.

Thus far the evidence is in favour of the conditions delineated in fig. 13, A and B, being truly representative of the species *Balænoptera borealis* and *Balænoptera* *musculus* respectively, but SMETS, in his description of a skull of a fœtal Blue Whale (*Balænoptera sibbaldii* GRAY = *B. musculus* LINN.), records the presence of a small interparietal. The skull is smaller than Skull S, the lengths of the two being respectively 15¾ inches (400 mm.) and 19 inches (483 mm.); and SMETS's Whale is a northern form (loc., Vadsö, Lapland), whereas Skull S is from South Georgia, in the South Atlantic Ocean. The interparietal is nearly circular (**29**, p. 192, fig. 1), thin at the edge and thick in the middle. The two parietal bones do not quite meet beneath the front of the supraoccipital; they overlap the posterolateral parts of the interparietal, and the frontal bones are overlapped by the front of the interparietal.

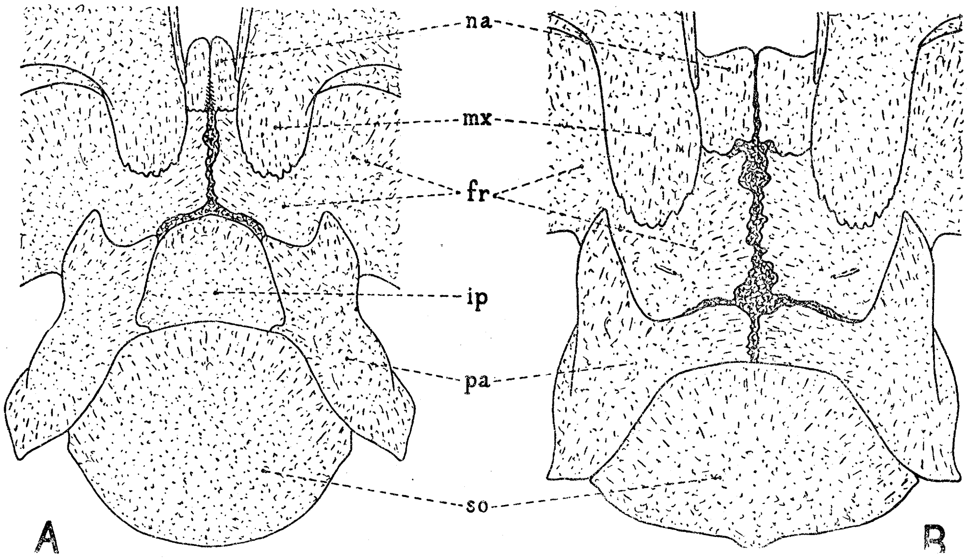

FIG. 13.—Cranial vertex of two species of *Balænoptera*. A, from a fœtus of *B. borealis* measuring 3 feet 11 inches; B, from a fœtus of *B. musculus* measuring 6 feet 4 inches. The parietal bones are separated by an interparietal in A, but not in B. A is × 0·5, B is × 0·45.

fr, frontal; *ip*, interparietal; *mx*, maxilla; *na*, nasal; *pa*, parietal; *so*, supraoccipital.

An interparietal is present in *Balænoptera acuto-rostrata;* in a 9-inch fœtus of this species ESCHRICHT shows it separate from the supraoccipital (**10**, Plate 11, figs. 1–3), but in a 6½-feet fœtus the interparietal is fused with the supraoccipital (Plate 10, fig. 1). CARTE and MACALISTER, writing of the skull of an adult of the species, consider that there is an interparietal combined with the supraoccipital (**7**, p. 206).

Except in the respects just noted, and in certain differences in the alisphenoid region noted elsewhere, the relations of the parietals to the surrounding bones are the same in Skulls R and S. The forwardly directed point of the parietal (fig. 13, A and B) overlaps the frontal bone, which in this region is very thick.

The supraorbital process of the frontal is already massive, and the channel for the passage of the optic nerve comparatively reduced. The antero-mesial part of the frontal that is overlapped by the maxilla presents a curious lamellated or plicated appearance, the lamellæ being set longitudinally, and interlocking with corresponding lamellæ of the maxillary bone.

It is of particular interest to note how the slope of the suture between the two frontal bones changes as age advances. In SCHULTE'S 14¾-inch (375 mm.) fœtus of *Balænoptera borealis* it is only the antero-ventral parts of the frontal bones that meet, and the suture is nearly vertical (**28**, Plate 56, fig. 2), although less strictly vertical than in Skull X of *Megaptera* (fig. 1, B); the suture is also nearly vertical in KÜKENTHAL'S 1180-mm. fœtus of *Balænoptera physalus* (*musculus* auctt.; **23**, Plate 21, fig. 6). In Skull R of *Balænoptera borealis*, 1194-mm. fœtus, the suture is complete, except for a little intervening fibrous tissue (fig. 13, A), and is already more horizontal than vertical (fig. 12); and the frontal bones now extend well beneath the nasal bones. The subsequent increase in the vertical dimension of the suture is well illustrated in WEBER'S figure of the skull of a young (not fœtal, 5·8 metre long) specimen of *Balænoptera acuto-rostrata*, the height of the suture being roughly one-half of the length.*

The nasal bones are nodular, and are overlapped to a slight degree externally by the premaxillæ. In Skull S each nasal has a shallow, vertical groove in front, but this is not present in Skull R.

The premaxillæ are long and narrow, with a slight sigmoid curve; they extend farther forward than the maxillæ, but not as far forward as the anterior extremity of the rostral cartilage. They are separated from one another by the rostral cartilage, the interval between the front portions in Skull S being about 7 mm. wide. The dental groove of the maxilla is not continued into the premaxilla.

The maxilla is a large bone, slightly concave on its palatal aspect; the mesial edges of the ventral surfaces are in Skull S separated by an interval of 6 mm., in which the vomer presents itself; but the vomer terminates at a distance of 85 mm. from the tip of the rostral cartilage, and in this region the front portions of the maxillæ are divaricated and separated by a width of cartilage not less than 30 mm. The dental groove is very deep, with delicate, fragile edges, and shows as yet no signs of closing up. In Skull S the teeth in each maxilla number 47; they are past their prime, and show signs of absorption, particularly at the summit, so that the remnants are in the form of rings. No records appear to have been kept of the teeth of Skull R.

The jugal is a thin, curved bone, broader in front than behind; the hinder part is loosely connected by fibrous tissue with the ventro-mesial face of the extremity of the zygomatic process of the squamosal bone; the anterior end underlies the lachrymal, and is connected by fibrous tissue with the ventral edge of the antorbital process of the maxilla. The lachrymal bone is imperforate, and situated beneath the

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* 'Die Säugetiere,' 1904, Jena, p. 563, fig. 418.

external part of the antorbital process of the frontal. The isolated lachrymal of Skull S is 30 mm. long, 10 mm. wide, and 5 mm. thick.

The squamosal bone is thick and massive, with a roughly conical zygomatic process, and a postglenoid process which increases rapidly in size, and slopes more backward, as age advances; in a 9-inch fœtus of *Balænoptera acuto-rostrata* it is vertical (**10**, Plate 11, fig, 3, A); it slopes backward slightly in a 14¾-inch fœtus of *Balænoptera borealis* (**28**, Plate 55, fig. 2, No. 14) and still more backwardly in Skulls R and S.

The squamous part of the bone that meets the parietal is thick, and is loosely joined to the parietal bone, edge to edge; the postero-dorsal part is cleft, however, and receives the postero-ventral corner of the parietal in such a manner that the squamosal may be said to overlap the parietal both inside and outside.

The relations of the pterygoid process of the squamosal to the pterygoid bone are shown in fig. 15, A; the process is bifid, and its notch combines with a notch, or groove, at the back of the pterygoid to form the foramen ovale, which, as ESCHRICHT (**10**, p. 120) and BEAUREGARD (**3**, I, p. 202) have shown in *Balænoptera acuto-rostrata*, transmits the lower division of the trigeminal nerve. The name processus falciformis applied to the ventral limb of the fork may not seem very appropriate, but it is a term first used in the Odontocetes, for a process which is sickle-shaped; in those forms the processus falciformis does not extend forward to the pterygoid, as it does in Mystacocetes, but passes directly inward, following the course of the anterior surface of the periotic bone (**3**, I, pp. 217, 202).

In Skull R the upper limb of the pterygoid process is longer than the lower (fig. 15, A); in Skull S the processus falciformis is the longer. Between the squama, or part that meets the parietal, and the bifid pterygoid process of the squamosal bone is a deep, narrow cleft, which is of regular occurrence, and persists in the adults of both *Balænoptera* and *Megaptera* (**30**, p. 317).

Although there is a general impression that in Whales the squamosal bone does not participate in the constitution of the cranial wall, *i.e.*, is not visible from within (*e.g.*, WIEDERSHEIM, R., 'Vergl. Anat. Wirbeltiere,' Ed. 7, Jena, 1909, p. 163, footnote), it is to be noted that in Skull R a fair amount of the bone can be seen in the cerebral surface of the cranial wall; in fig. 12 the squamosal shows as a notched bone between the periotic and the parietal. BEAUREGARD, moreover, has pointed out that, while in the Dolphin and Cachalot the squamosal is entirely eliminated from the inner face of the cranial wall, in two species of *Balænoptera* he recognised it in an internal view of the Skull (**3**, I, pp. 199, 217). And ESCHRICHT shows a portion of the squamosal bone persisting in the inner surface of the skull in *Balæna japonica* (5¼-feet fœtus; **13**, Plate 2, fig. 2, T).

The pterygoid bone in Skulls R and S is readily isolated; viewed from above (fig. 14, C) it shows the shallow groove (*al*) in which the alisphenoid bone lies, and the deeper and narrower channel—seen also in the side view, fig. 14, B, V3—for the mandibular division of the trigeminal nerve. The hamular process (*ha*) is a conspicuous feature, as also is the large pterygoid fossa (*f*), roughly hemispherical in shape. The channel marked *on* in A is the lateral part of the roof of the oro-nasal passage. A large portion of the ventro-external surface of the pterygoid bone is flanked by the palatine (*cf.* fig. 15, A); the posterior point of the bone is situated just in front of the paired ventral ridge of the basioccipital (fig. 12).

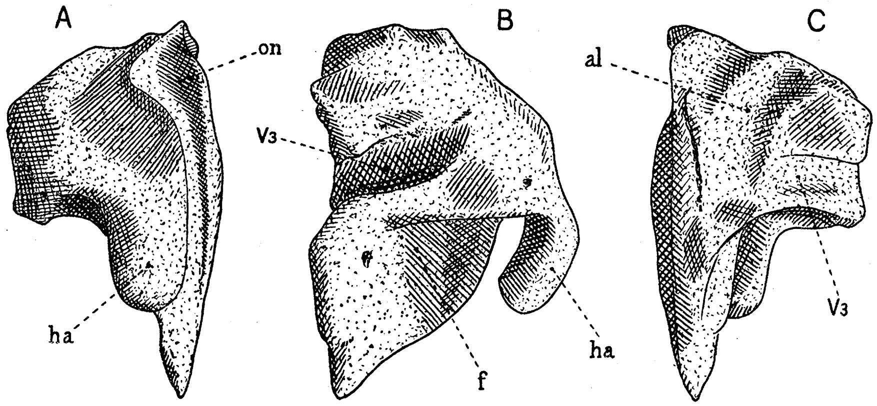

FIG. 14.—Right pterygoid bone of a fœtus of *Balænoptera musculus* measuring 6 feet 4 inches. A, ventral view; B, external view; C, dorsal view. × 0·7. In each figure the anterior end of the bone is uppermost.

al, groove for alisphenoid bone; *f*, pterygoid fossa; *ha*, hamular process; *on*, roof of oro-nasal passage; V_3, groove for mandibular nerve.

LILLIE, in describing certain parts of the skull of adult specimens of *Balænoptera* (**24**, 1910, p. 778), gives an account of the air-containing pterygoid fossa, and states that the pterygoid and alisphenoid bones are fused together; but the particular tract of bone that he marks *Al* in his text-figure 71 is clearly the outer limb of the pterygoid bone, meeting at its postero-external edge the pterygoid process of the squamosal, in the middle of the front edge of which is the foramen ovale, although he does not show it. And, further, what he terms the "pterygoid plate of the alisphenoid" in the text-figure is clearly the hamular process of the pterygoid itself.

In his interpretation of these bones (pterygoid and alisphenoid) LILLIE was evidently influenced unduly by DWIGHT, to whose paper on a skeleton of the Common Rorqual (*Balænoptera physalus* LINN. = *B. musculus* auctt.) he frequently refers, and by CARTE and MACALISTER, who had previously published an account of the anatomy of the Lesser Rorqual, *Balænoptera acuto-rostrata*, LACÉP. (= *B. rostrata* auctt.).

CARTE and MACALISTER (**7**, 1868, p. 208, par. 2) speak of "the alisphenoid or pterygoid bone," and elsewhere refer to the bone indifferently, calling it "alisphenoid" in some places (p. 208, line 6 up; p. 209, lines 7 and 8 down, and line 14 up; p. 211, line 21 up) and "pterygoid" in others (p. 207, line 2 up; p. 208, lines 12 and 19 down; p. 210, top line). The exposed part of the alisphenoid proper they term "a small portion of the basisphenoid" (p. 207, line 5 up; p. 209, line 9 down, and line 17 up).

DWIGHT does the same; the pterygoid bone he usually calls the "alisphenoid" (**8**, 1872, p. 207, line 17 down, and line 11 up; p. 208, lines 13 and 22 down), but in some places he speaks of it as the "pterygoid" (p. 207, line 2 down, and line 13 up; p. 209), apparently restricting the latter term to the ventral portions, the whole bone being the "alisphenoid." The alisphenoid bone proper he refers to as "the small interposed scale of the basisphenoid" that occurs in the temporal fossa "between the alisphenoid below and the parietal above" (p. 207, line 4 up; p. 208, line 22 down). Compare *al* in fig. 15, A (*Balænoptera borealis*), of the present paper. The word "scale" in the quotation above is misleading; the part that is seen is the oblique extremity of a fairly solid alisphenoid bone that stands out transversely from the basisphenoid.

BEAUREGARD, again, writing of the skull of *Balænoptera acuto-rostrata* (*B. rostrata*, **3**, 1893, p. 202), states that the two parts of the forked antero-internal limb of the squamosal, above and below the foramen ovale, fuse in front with the alisphenoid. Reference to fig. 15, A, of the present paper shows that the union is with the pterygoid, not the alisphenoid. And HANKE (**18**, 1914, p. 504) accepts the interpretation of BEAUREGARD, and says that the periotic lies in a space bounded in front by the alisphenoid; reference to fig. 9 of the present paper shows that the bone in question is the pterygoid.

The present writer considers that the term "alisphenoid" in Mammals should be applied to the cartilage-bone that develops from the ala temporalis of the primordial cranium, together with such membrane-bone as is immediately related to it. This seems to be the view of most modern writers on the mammalian skull. ESDAILE (1916,* p. 464) remarks that the alisphenoid is partly a cartilage-bone and partly a membrane-bone in *Perameles*, *Trichosurus*, *Dasyurus*, and *Macropus*; but the construction of the alisphenoid bone in this manner is not by any means confined to Marsupials, it may be demonstrated in the bisected skull of a new-born Pig, the outline of the ossified ala temporalis being clearly discernible to the naked eye against the outer scale of membrane-bone with which it is co-ossified. In the Whales, however, the applied membrane-bone seems to be entirely wanting.

The alisphenoid bone of Whales is a relatively small component of the cranial wall; it is but the ossified ala temporalis, which has not spread upward and downward, and consequently has nothing comparable with the great wing and the external pterygoid plate familiar to students of human anatomy. The erroneous interpretation of the Whale's pterygoid by LILLIE was probably due to the fact that CARTE, MACALISTER and DWIGHT, being medical men, confused the air-containing pterygoid fossa of the Whale with the pterygoid fossa of Man, a space between the pterygoid bone on the inner side

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* ESDAILE, P. C., "On the Structure and Development of the Skull and Laryngeal Cartilages of *Perameles*," 'Phil. Trans. Roy. Soc.,' B, 207, May, 1916, pp. 439–479, 6 plates, 2 text-figs.

and the descending part of the alisphenoid on the outer side, parts known to the human anatomist as the internal pterygoid plate and external pterygoid plate respectively. The fossa in the Whale is contained in the pterygoid bone solely. FLOWER, although an anatomist with a medical training, avoided the error, and applied the name pterygoid to the whole bone, without any suggestion of there being an alisphenoid component in the outer and upper parts of it.* ESCHRICHT also used the word pterygoid in this sense (**10**, 1849, Plates 9, 10, 11 ; $u =$ os pterygoideum).

It is unusual in Mammals for the squamosal to extend so far forward as to reach the pterygoid ; the Whales are exceptional in this respect, as they also are in having the foramen ovale in the form of a cleft between the squamosal and the pterygoid. VAN KAMPEN (**21**, 1905, p. 649) correctly interprets the parts, and says that the pterygoid bone has pushed its way in between the alisphenoid and the squamosal, and that the air-containing pterygoid fossa is bounded, in its front part, by the pterygoid solely :—"Zwischen Alisphenoid und Processus falciformis hat sich das Pterygoid hineingedrängt; es enthält eine weite Höhle, welche eine Verlängerung nach vorn bildet von der Mulde, worin das Petro-tympanicum liegt."

DWIGHT observes (**8**, 1872, pp. 207–8) that in his *Balænoptera musculus* (*i.e.*, *B. physalus* LINN.) the parietal bone meets the pterygoid (his alisphenoid) in front of the alisphenoid (his basisphenoid scale); also that the basisphenoid scale does not touch the squamosal bone behind, as, according to CARTE and MACALISTER (**7**, 1868, p. 207), it does in *B. rostrata* (*i.e.*, *B. acuto-rostrata* LACÉP.).

STRUTHERS identifies the pterygoid in the same way that FLOWER does (**30**, 1889, p. 317) :—"The lower part [of the temporal, *i.e.*, squamosal] articulates with the pterygoid." He gives a minute description of the pterygoid bone in *Megaptera* and *Balænoptera musculus* (*i.e.*, *B. physalus* LINN.), but in the absence of illustrations the account is rather difficult to follow. "The sphenoid bone," he continues, "shows itself on the surface here [*i.e.*, in the orbit] in *B. musculus*, but not in *Megaptera.* In *B. musculus* it . . . . articulates posteriorly with the temporal bone, above with the parietal, below with the pterygoid . . . The parietal is thus cut off from reaching any part of the pterygoid, by the interposition of the sphenoid, in contrast with the condition in *Megaptera.*" In a footnote he adds that in *B. borealis* the parietal meets the pterygoid behind the sphenoid, and prevents the temporal from meeting the sphenoid ; and in *B. rostrata* the parietal meets the pterygoid in front of the sphenoid, but not behind it.

It might seem from this that, if the relations of the exposed part of the alisphenoid to the surrounding bones are sufficiently constant, there is here a means of distinguishing the skulls of the various species of *Balænoptera* ; and in this connection the figures given by MÜLLER some years earlier (1863,† Plate 3, figs. 5, 6, 8) are of

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[*] "Delphinidæ," 'Proc. Zool. Soc.,' 1883, p. 472.

[†] MÜLLER, A., "Ueber das Bruchstück vom Schädel eines Finnwales, *Balænoptera syncondylus*," 'Schriften d. k. Phys.-oek. Ges. Königsberg,' 4, 1, Jahrg. 1863, pp. 38–78, 3 plates.

interest, for he shows the surroundings of the "ala magna ossis sphenoidei" in *B. rostrata, B. laticeps* and *B. musculus* (*i.e., B. acuto-rostrata* LACÉP., *B. borealis* LESSON, and *B. physalus* LINN.

In the skull of the fœtus of *Balænoptera borealis* considered in the present paper (fig. 15, A) the parietal bone meets the pterygoid behind the alisphenoid, but not in front of it, for the anterodorsal part of the pterygoid passes sharply inwards, and escapes the anteroventral corner of the parietal. In the fœtal *Megaptera* (fig. 15, B) the alisphenoid does not show itself in the orbito-temporal region, and judging from the account given by STRUTHERS, quoted above, and the figure given by MÜLLER (1863, Plate 3, fig. 7) the condition persists for life.

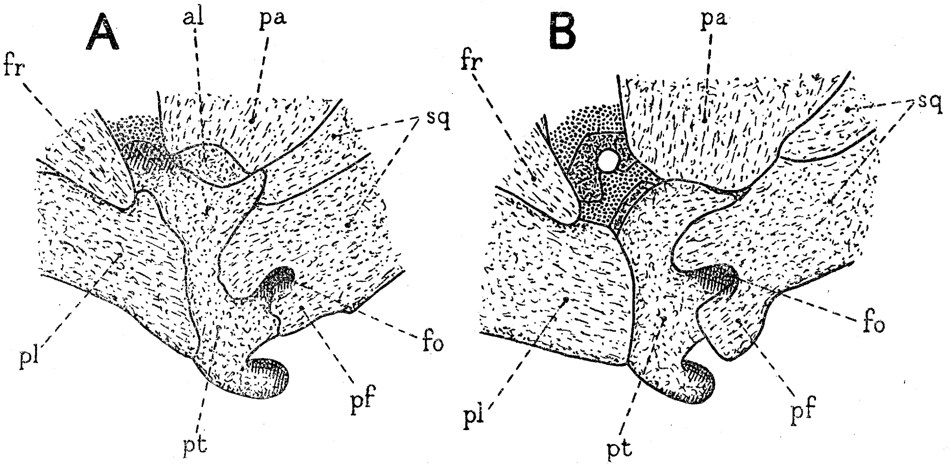

FIG. 15.—Left pterygoid bone and adjacent parts, antero-ventro-lateral view. A, from a fœtus of *Balænoptera borealis* measuring 3 feet 11 inches, for comparison with Schulte's figure (**28**, Plate 55, fig. 2); B, from a fœtus of *Megaptera nodosa* measuring 27 inches. B is of natural size, A is slightly less (× 0·9).

al, outer end of the alisphenoid; *fo*, foramen ovale; *fr*, palatine process of the frontal; *pa*, lower border of the parietal; *pf*, processus falciformis of the squamosal; *pl*, hinder part of the palatine; *pt*, pterygoid; *sq*, upper and lower parts of the inner limb of the squamosal, separated by a fissure.

In his very careful and detailed description of the skull of a fœtus of *Balænoptera borealis* measuring 375 mm. SCHULTE distinguishes two parts of the pterygoid bone, separated by a suture; these parts are the internal and external pterygoid respectively (**28**, 1916, Plate 54, fig. 2; Plate 55, fig. 2). The internal pterygoid, he remarks (p. 476), is situated between the palatine bone and the external pterygoid, and has a narrow dorsal process which joins the frontal; the external pterygoid is suturally united with the squamosal and the internal pterygoid. The external pterygoid, he continues (p. 477), is a massive bone of irregular pyramidal shape; by its summit it joins the as yet cartilaginous processus alaris of the basisphenoid. "It thus conforms literally to the definition of the external pterygoid, being a descending process of the alisphenoid, and ossifying from a centre common to it and the processus ascendens"; nevertheless, he draws a suture between the ala temporalis and the external pterygoid.

The hamular process occurs on the internal pterygoid bone, and the suture between the internal and external pterygoids is situated external to the base of the process; the foramen ovale lies behind the external pterygoid and above the processus falciformis of the squamosal bone (p. 477, Plate 54, fig. 2).

In the skull of *Balænoptera borealis* now under consideration (Skull R) there is no trace of the suture described by SCHULTE; it is true that the skull is much larger, its length being 11½ inches, whereas that of SCHULTE'S measures only 4 inches, and it might be argued that the suture has closed and disappeared; but it is significant that no such suture is shown in ESCHRICHT'S figure of a much younger skull of *Balænoptera acuto-rostrata* (**10**, Plate 11, fig. 2), where one might expect to find it, in spite of the species not being the same. Neither is there any suggestion of the suture in the three skulls of *Megaptera* considered in the present paper (Skulls X, Y, Z).

In Skull R the height of the exposed part of the pterygoid—*i.e.*, the measurement taken in a circumferential direction around the skull—is much greater than its anteroposterior length (fig. 15, A); in SCHULTE'S specimen the pterygoid, counting external and internal pterygoids together, is considerably longer than high (**28**, Plate 55, fig. 2). In Skull R the palatine process of the frontal, in the antero-internal part of the orbital cavity (fig. 15, A, *fr*), touches the front part of the pterygoid and the upper part of the palatine bone; in SCHULTE'S specimen, judging from his lateral view (Plate 55, fig. 2), it crosses over the external pterygoid in order to join the internal pterygoid; the relations of the process to the palatine bone are not very clear. In the fœtal *Megaptera* (Skull Z) the upper part of the pterygoid does not extend forward to reach the palatine process of the frontal bone (fig. 15, B).

The suture between the internal and external pterygoids is figured so definitely by SCHULTE, and is shown so symmetrically on the right and left sides (Plate 54, fig. 2), and is described in such minute detail (pp. 476, 477) that it is scarcely likely that the author mistook a fracture for a suture; the skull may possibly be aberrant in this respect. On the other hand, I cannot help thinking, as the result of a comparison of Skull R with his side view (Plate 55, fig. 2), that SCHULTE has erroneously interpreted some portions of the palatine bone as parts of his two pterygoid bones. The parts to which, in his figure, the indicating lines lead from the numerals 40 and 41 (internal and external pterygoids) are in my opinion two parts of the left palatine bone.

In his figures of the primordial cranium of Cetacea, DE BURLET (1913, 1914*) marks the pterygoid bone as "parasphenoid," a new departure that is also followed by SCHREIBER (1916,† figs. H, V, W, Y), VOIT ('Anat. Hefte,' 38, 3, 1909, p. 501)

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* DE BURLET, **6**, I, text-figs. 14, 15, 16, 23; **6**, II, text-figs. 16, 17, 18 (in text-fig. 19 he marks it "pterygoid"); **6**, III, text.-figs. 19, 20, 21, 23.

† SCHREIBER, K., "Zur Entwicklungsgeschichte des Walschädels; Das Primordialcranium eines Embryos von *Globiocephalus melas* (13·3 cm.)," 'Zool. Jahrb., Abth. Anat.,' 39, 2, 1916, pp. 201–236, 4 plates, 25 text-figs.

and HONIGMANN (**20**, 1917, pp. 28, 33, and Plates 1, 2). This practice, in the opinion of the present writer, is unfortunate, for whatever the merits of the case may be, the time is not yet ripe for a whole-hearted acceptance of the thesis set forth by GAUPP (1905,* and **14**, p. 837) that the bone commonly known as the pterygoid in the skull of *Echidna* is the homologue of the reptilian pterygoid, whereas the new bone that he had discovered in advance of it is the same as the ordinary mammalian pterygoid, and, as he contends, the equivalent of the crus transversum ossis parasphenoidei of the Reptile's skull.†

This view has been contested by FUCHS (1910‡), who brings evidence to show that the bone newly discovered by GAUPP in the skull of *Echidna* is in reality a dissociated portion of the pars perpendicularis ossis palatini. Although GAUPP in his rejoinder (**15**, 1910, pp. 354 *et seq.*), claims that there is no foundation for FUCHS' view, and adheres to and elaborates his original thesis, yet it is to be noted that GREGORY (1910,§ p. 120), approaching the subject from a palæontological standpoint, maintains the equivalence of the mammalian pterygoid, through that of the Cynodonts, with the reptilian pterygoid, and expresses himself (p. 150) as unconvinced, from a comparison of fœtal Monotremes and of fœtal Edentates and Insectivores, that the pterygoids of Monotremes have any different homology and derivation from those of placental Mammals.

WATSON, also, writing in 1916, is an adherent of the earlier view. He is of opinion that it is the mammalian-pterygoid, not the Echidna-pterygoid, that is homologous with the reptilian pterygoid (**34**, pp. 351, 364), the Echidna-pterygoid being the equivalent of the posterior process of the epipterygoid of the Cynognathid

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* GAUPP, E., "Neue Deutungen auf dem Gebiete der Lehre vom Säugetierschädel," 'Anat. Anz.,' 27, 12–13, August, 1905, pp. 273–310, 9 text-figs.

† That the newly-discovered "Säuger-pterygoid" of *Echidna* is the equivalent of the pterygoid of other Mammals is supported by EDGEWORTH'S study of the developing muscular system (' Quart. Journ. Micro. Sci.,' 59, 4, February, 1914, pp. 592–597). The "Echidna-pterygoid" and the "Säuger-pterygoid" are together present in *Ornithorhynchus* as well as in *Echidna* (BROOM, 'Phil. Trans.,' B, 206, October, 1914, p. 26; WATSON, **34**, 1916, p. 363, No. 24), and in two Edentates, *Tatu* and *Tamandua* (BROOM, *ibid.*), and traces of the Echidna-pterygoid are recorded by BROOM (*ibid.*) in a Marsupial, *Petrogale*. LUBOSCH (1908, 'Semon's Forschungsreisen,' 4, 6, p. 527) suggests that the pterygoid bone in *Manis* and the Xenarthra may be homologous with the Echidna-pterygoid, or, alternatively, that it represents a fusion of a mammalian-pterygoid (parabasale) with an Echidna-pterygoid; but EDGEWORTH (*loc. cit.*, p. 595) disagrees. It would be interesting in this connection to inquire into the origin and homology of the bone that PARKER described as the "mesopterygoid." It is situated behind the pterygoid, but it does not appear to be an Echidna-pterygoid, its anterior end being situated on the mesial side of the hamular process of the ordinary pterygoid (*e.g. Galeopterus*, 'Phil. Trans.,' 176, 1, 1885 (1886), Plate 39, fig. 1).

‡ FUCHS, H., "Ueber das Pterygoid, Palatinum und Parasphenoid der Quadrupeden," 'Anat. Anz.,' 36, 2–4, March, 1910, pp. 33–95, 45 text-figs.

§ GREGORY, W. K., "The Orders of Mammals," 'Bull. Amer. Mus. Nat. Hist.,' 27, February, 1910, pp. 1–524, 32 text-figs.

skull, and the tympanic wing of the alisphenoid of Marsupials (pp. 353, 364). KESTEVEN, moreover, goes farther, and applies to the Echidna-pterygoid the name alisphenoid (1918,* pp. 464–465).

Even if it be firmly established that the mammalian pterygoids represent lateral parts of the reptilian parasphenoid, it does not follow that it is convenient, or calculated to facilitate the study of the vertebrate skull in the future, to apply to them the name parasphenoid, as DE BURLET and HONIGMANN have done. To carry out this principle logically, one would need, as BROOM points out,† to call the quadrate bone of the Reptile, Bird and Fish the "incus," seeing that the homology between the two bones is now generally accepted, and that owing to the study of human anatomy having preceded to a large extent that of comparative anatomy, the term "incus" can claim priority over "quadrate."

In Skulls R and S the vomer is long and trough-like; it is largest in the region of the palatine bones, where its transverse section has the form of the letter Y; in fig. 12 the part marked *vo* is the median partition between the two postnasal passages. The palatine process of the frontal bone (*fr* in fig. 15, A) has, on its inner (mesial) part, a definite articulation with the upper extremity of the Y, the articular surface of the vomer being deeply concave.

As one passes backward, the lower, vertical part of the Y shortens, and the upper oblique lamellæ become narrower, and together terminate posteriorly in an almost flat plate beneath the front portion of the basioccipital bone. As one passes forward from the point marked *vo* in fig. 12 the vertical part of the Y diminishes and disappears, and the oblique upper lamellæ increase and become more vertical. A section of the vomer taken through the part of the skull shown at the right-hand end of fig. 12, where the front of the beak is cut away, is in the form of a great U, in the trough of which is lodged the lower part of the rostral cartilage, separated from the bone by a fairly thick layer of soft connective tissue (*ct*).

The palatine bone has the form of a curved, oblong plate, wider behind than in front; the postero-external corner curves up into a vertical plate, feebly developed in Skull R (fig. 15, A), but large and hook-like in Skull S. The front part of the palatine lies ventrally to the vomer; its antero-external edge is thick, and lies dorso-mesially to the palatal part of the maxilla; the hind edge is ventral to the front part of the pterygoid, and the hooked vertical process lies on the external face of the pterygoid.

The tympanic bone of *Balænoptera* has already been discussed in the preceding section of the paper, in conjunction with the younger tympanics of *Megaptera*. The malleus is separable from the tympanic bone in Skull R, but not in Skull S; according to HANKE (**18**, p. 515) the malleus is not yet fused with the tympanic in

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* KESTEVEN, H. L., "The Homology of the Mammalian Alisphenoid and of the Echidna-Pterygoid," 'Journ. Anat.,' 52, 4, London, July, 1918, pp. 449–466, 10 text-figs.

† BROOM, R., 'Bull. Geol. Soc. Amer.,' 28, December, 1917, p. 976.

a 720-mm. fœtus of *Balænoptera musculus*. In Skulls R and S the malleus is well ossified, only the articular face of the caput being cartilaginous; the remnant of MECKEL'S cartilage is relatively larger in R than in S.

The stapes of Skull S is well ossified, but the end that articulates with the incus is still cartilaginous; the stapes has a depression on each side, but no perforation. The incus is ossified, although the greater portion of the crus longum is still cartilaginous, and there is a thick cap of cartilage on the face that fits upon the caput of the malleus. The incus and stapes of Skull R differ from those of Skull S mainly in being less completely ossified.

The mandibular rami of Skulls R and S were not measured before drying; in their present dried state the respective lengths, measured along the curve, are 265 and 425 mm. Except in size, they bear a close resemblance; the dental groove is still well marked, and the mandibular foramen, for the third division of the trigeminal nerve, is relatively very large, in Skull S being large enough to admit one's fifth finger.

The hyoid bar of Skull S is almost straight (fig. 16, B), with thyrohyal bones measuring 40 mm., and with a basihyal ossification in the form of an elliptical plate. The anterior processes of the hyoid of adult specimens of *Balænoptera* are longer than those of *Megaptera* (STRUTHERS, **30**, p. 370), and the difference is already apparent in the fœtal specimens now under consideration (fig. 16, B and A).

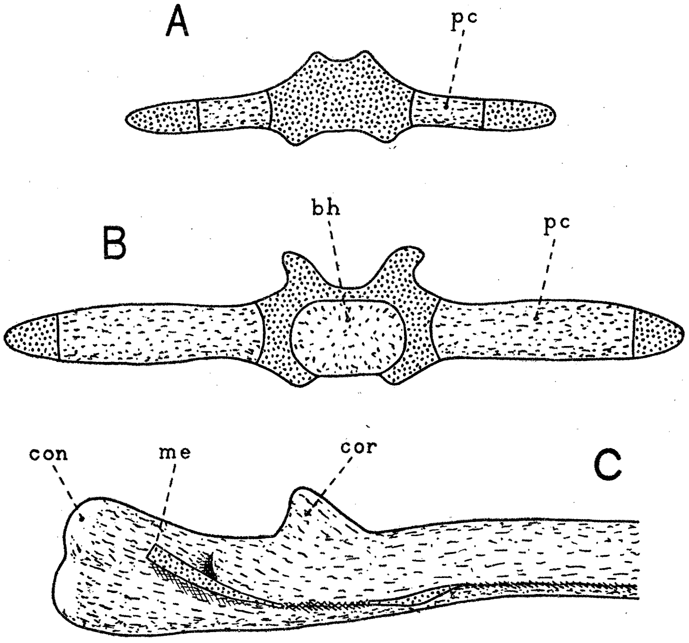

FIG. 16.—A, hyoid bar of a fœtus of *Megaptera nodosa* measuring 27 inches, natural size. B, hyoid bar of a fœtus of *Balænoptera musculus* measuring 6 feet 4 inches, × 0·66. C, hinder part of left ramus of mandible of a fœtus of *Megaptera nodosa* measuring 16 inches, × 1·33.

bh, basihyal; *con*, condyle of mandible; *cor*, coronoid process; *me*, MECKEL'S cartilage, cut across at the point marked; *pc*, posterior cornu or thyrohyal, Figures of the hyoid of adult *Balænoptera* are given by RUDOLPHI (**26**, Plate 4, fig. 1), CARTE and MACALISTER (**7**, Plate 5, figs. 4, 6; Plate 6, fig. 3) and DELAGE ('Arch. Zool. Expér.' (2), 3 *bis*, 1885, Plate 17, fig. 5).

The anterior cornu of the hyoid of Skull S has a total length of 125 mm., the stylohyal bone in it being 45 mm. long; there is no tympanohyal bone. In the figure of the hyoid of an adult *Balæna* given by ESCHRICHT and REINHARDT (*loc. cit.*) there is shown a ligamentous tract between the stylohyal bone and the anterior process of the basihyal, but in that of *Balænoptera* by CARTE and MACALISTER the parts are drawn as though they were closely approximated in life; DELAGE puts the parts in close association, but expresses his doubts as to the accuracy of such juxtaposition (*loc. cit.*, p. 57). A ligament is shown in SCHULTE's figure of the hyoid of a fœtus (**28**, p. 484, fig. 7). Oddly enough, although the animal is a fœtus of *Balænoptera borealis*, not more than 375 mm. (= $14\frac{3}{4}$ inches) in length, and although the stylohyals are wholly cartilaginous, the author observes that the hyoid bar is well ossified, and shows no sutures between its component parts (**28**, p. 483). The hyoid of Skull R, from a 3-feet 11-inch fœtus of *Balænoptera borealis*, is not accessible for study, but it probably does not differ materially from that of *Balænoptera musculus* shown in fig. 16, B.

SUMMARY.

Five skulls are described—three of *Megaptera nodosa*, from fœtuses measuring 6 inches, 16 inches and 27 inches, one of *Balænoptera borealis*, from a fœtus measuring 3 feet 11 inches, and one of *Balænoptera musculus*, from a fœtus measuring 6 feet 4 inches.

The presence of an interparietal bone in some Whales, and the meeting of the parietal bones in a median suture in others, is discussed, and the value of these characters in taxonomy is discounted (pp. 256, 257).

Syncondyly in Whales is regarded as associated with the suppression of the atlanto-epistropheal joint (pp. 232, 233).

There is no separate foramen for the hypoglossal nerve (pp. 232, 255).

The periotic bone shows no separate centres of ossification, but a diffuse, endochondral, granular deposit (p. 231).

The orbitosphenoid ossifies independently of the presphenoid (pp. 229, 253).

The confusion that has arisen regarding the pterygoid and alisphenoid bones of Whales is discussed; the confusion is attributable to a spurious resemblance existing between the air-containing pterygoid fossa of Whales and the pterygoid fossa of the skull of an ordinary Mammal (pp. 260–262).

In Whales there is no "external pterygoid plate" of alisphenoidal origin; the alisphenoid bone is the ossified ala temporalis solely, with no additional plates of membrane-bone (pp. 229, 251, 261).

The present inquiry fails to confirm SCHULTE's observation of the division of the pterygoid bone into external and internal pterygoids (pp. 263, 264).

The suggestion of homology between the reptilian parasphenoid and the mammalian vomer was made by SMETS in 1885 independently of BLAND SUTTON's remarks in 1884 (p. 239).

The growth of the malleus is described, and the homologies of the processes, regarded as still in doubt by TURNER in 1913, are elucidated (pp. 244–246).

The growth of the tympanic bone, and the relations of the great bulla to the primary annulus tympanicus, are explained (pp. 240–242).

The inflation of the tympanic membrane, claimed by LILLIE in 1910 as a new discovery, is shown to have been recorded several times previously in the literature of the subject (pp. 243, 244).

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