THE BRAIN OF THE ARCHÆOCETI.¹

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So far as I have been able to ascertain, nothing whatever is known of the form of the brain or, more strictly, of the cranial cavity in the Archæoceti. Hence no apology is needed for presenting even this imperfect account of two cranial casts representative of this sub-order, which have come into my hands.

Among the Eocene remains found in the Fayûm region of the Egyptian desert by Mr. H. J. L. BEADNELL and Dr. CHARLES W. ANDREWS, in 1901, there was a broken skull of *Zeuglodon*,² from which it was possible to obtain a mold, representing the form of the greater part of the dorsal and lateral aspects of the brain. A plaster cast was made in the British Museum at the instance of Dr. ANDREWS, who kindly placed it at my disposal for description.

In the following winter (1902), Mr. BEADNELL found in the same locality a natural cranial cast of the same size and general form as the artificial cast of *Zeuglodon*. It is obvious at a glance, if the two specimens be placed side by side, that the natural mold belongs to some member of the Archæoceti,

¹ These notes were originally intended for the Report on the Survey of the Fayûm, to be issued by the Egyptian Survey Department, and are now published separately with the permission of the Under Secretary of State for Public Works and Captain H. G. LYONS, Director-General of the Survey Department.

² C. W. ANDREWS, "Extinct Vertebrates from Egypt," Part II. (Extracted from the 'Geological Magazine,' N. S., Decade IV, vol. 8, 1901, p. 437,—*Zeuglodon Osiris*, Dames'.)

but whether to the same species or even genus as the other specimen must at present remain an open question.

Mr. BEADNELL kindly placed this specimen at my disposal.

The size and relative proportions of the different parts are almost identical in the two casts. Nevertheless, there are a considerable number of differences, some features being displayed in one and not in the other, and *vice versa*. Many of these differences are obviously due to the imperfections of the casts, and especially to the failure of the plaster mold to represent the true form of the brain. But there are several peculiarities of the natural cast—such, for example, as the form of the caudal part of the cerebellum and the shape of the cerebral hemispheres—which are difficult to reconcile with the artificial mold, even if we admit that the inner face of the cranium (from which the latter was made) is damaged or imperfectly cleaned. The differences, nevertheless, are sufficiently pronounced to indicate a generic distinction between the two specimens; and in this connection it is interesting to recall a statement made by Dr. ANDREWS in his first reference to *Zeuglodon*, as “including apparently DAMES’ *Z. Osiris*, and perhaps a second species.”¹ It would, however, be very unwise, because it would serve no useful purpose, and possibly lead to error, to found a new genus or even a new species on the evidence of this natural cranial cast, when our source of information concerning the known genus (*Zeuglodon*) is as unsatisfactory as that obtainable from the artificial one about to be described. More especially so, when it is remembered that in the case of the only indisputable facts (*i. e.*, size and general form) the two casts are agreed. I shall therefore merely describe and attempt to explain the meaning of the form of the two specimens, and leave the question of the specific identity open for future research.

The general appearance of the brain is extraordinarily peculiar (figs. 1 and 2). The shape of the anterior part of the natural cast (fig. 1, *a* and *b*) closely resembles the cerebrum of

¹ ‘Geological Magazine,’ September, 1901, p. 401.

a Lizard greatly magnified. An anterior prismatic stalk (*a*), representing the pedunculi olfactorii, suddenly expands into a plump, broad, smooth mass (*b*), showing the form of the chief part of the cerebrum. The maximum breadth of the two hemispheres (fig. 1, *b*) is 95 mm.; the greatest length of each (mea-

FIG. 1.—Dorsal aspect of the natural cast described in the text. Two-ninths natural size. *a*, olfactory peduncles; *b*, cerebral hemisphere; *c*, *d*, cerebellum; *e*, *e'*, fragments of skull.

sured in front from the point where the ventral surface of the olfactory peduncles appear to expand into the chief mass of the hemisphere) is 47 mm.; and the maximum depth is 54 mm. Each cerebral hemisphere (exclusive of the olfactory peduncle) is slightly broader than it is long.

The two olfactory peduncles are represented in the natural cast by a single prismatic process. This extends forward for a distance of 37 mm. (measured along the dorsal edge) in front of the point where the expansion to form the hemispheres com-

mences; and, as the peduncles are broken across there, it is not possible to estimate their total length or the shape and size of the olfactory bulbs.

The coronal section formed by its anterior (broken) surface gives an isosceles triangle with a base measuring 8.5 mm. and sides of 10 mm. each. It expands as it passes backward, so that at its junction with the rest of the hemisphere its sides are each 19 mm. and its base 16 mm. in length.

FIG. 2.—Dorsal aspect of the artificial cranial cast of *Zeuglodon*. Two-ninths natural size. *a*, *b*, *c*, *d*, as in fig. 1. *a*, the dorsal rostrum, and *b'*, an irregular boss on the cerebral hemisphere. (These are probably due to imperfections in the cranium.)

In the artificial cast (fig. 2) all that represents this extensive olfactory stalk is an irregular rostrum with two small boss-like projections, one above the other (*a* and *a'*). The cerebral hemispheres in the natural cast have a broad base, from which

the sides extend upward toward the narrow dorsal surface with a gradual slope. In the artificial cast, however, the lateral parts of the hemispheres seem to be expanded into full rounded swellings.

Then, again, the antero-posterior diameter of the hemisphere is much shorter (being about 13 mm. less) than it is in the natural cast, although the breadth of the two specimens is approximately the same. It may be that the anterior parts of the skull, from which the artificial cast was made, are so damaged that little reliance can be placed upon the mold as an indication of the exact form of the brain. In fact, if this artificial cast even approximates to the form of the brain, it is quite certain that it did not belong to the same genus as the animal from which the natural cast was derived.

In other words, as we know that the artificial cast belonged to *Zuglodon*, the probability is that the natural cast furnishes the first evidence of some hitherto undescribed genus of Archæoceti.

Behind the part *b*, which I have just described as the cerebrum, there is (in the natural cast) a large, irregular mass of a very peculiar shape, not exactly comparable to the condition occurring in any other brain known to me.

Immediately behind the hemispheres (*b*) there is a great transverse bar (*c*) measuring 125 mm. in the transverse direction—*i.e.*, extending on each side 15 mm. beyond the lateral margin of the cerebrum (*b*).

Each lateral extremity of this mass (*c*) is expanded to form a large buttress. In the natural cast these buttress-like masses are practically vertical, and of uniform thickness; whereas in the artificial cast they are obliquely-placed, and expanded ventrally. In the natural cast the mesial continuation of these thick lateral masses (each of which measures 30 mm. antero-posteriorly) becomes reduced to a bridge measuring only 5 or 6 mm. [the exact figure cannot be stated, because a piece of bone (fig. 1, *e*) partially covers this region].

In the deep concavity behind the narrow bridge of the area *c* (in the natural cast) two rounded, irregular, walnut-like bosses

project, one on each side of the middle line (fig. 1, *d*). Each of these is 26 mm. in diameter, and is placed so obliquely that its surface looks almost directly backward. Shallow but clearly defined furrows separate these two bodies from each other and from the area *c*. In the artificial cast there is only a very faintly-marked indication of these bodies (fig. 2, *d*).

At a first glance it might seem that they represent the whole cerebellum, in which case *c* would be part of the cerebrum! But careful examination of the natural cast renders such an interpretation highly improbable, and comparison with the artificial cast seems to finally establish the belief that the whole of the region marked *c* forms part of the cerebellum.

It is extraordinarily difficult to accurately interpret this peculiar form of cerebellum. A comparison with other primitive types of cerebellum¹ points to the probability that the lateral buttresses of the mass *c* represent the floccular lobes, and that the walnut-like mass (*d*) represents the cerebellar lobule which I have called "area C" (*op. cit.*, 'Catalogue,' p. 211). If it be objected that the lateral buttress-like mass is much too extensive to be entirely "floccular," attention may be called to the fact that in the large aquatic Sirenia, which have retained an exceedingly primitive type of brain, the floccular lobes are enormous in comparison with those of other mammals (*op. cit.*, 'Catalogue,' p. 346).

It would perhaps be difficult to find elsewhere in the mammalia a greater contrast than that presented by the smooth, reptilian-like cerebral hemispheres of these casts and the highly complicated, ultra-mammalian neopallium of the recent whales, both Odontoceti and Mystacoceti.² And yet, if we inquire into the nature of the factors which have molded the form and determined the size of the various parts of the brain in Eocene times and at the present, the contrast between the brain of *Zeuglodon* and the modern Cetacea loses much of its significance.

¹ Compare, for example ('Catalogue of the Royal College of Surgeons,' 2nd edition, vol. 2, 1902), Armadillo (p. 211), Tapir (p. 311), Manatee (p. 346).

² *Vide* 'Catalogue of the Royal College of Surgeons,' *op. cit.*, pp. 348—359.

ance, and becomes much less peculiar, even though it may not be wholly explained.

In most Eocene mammals the cerebral hemispheres were exceedingly diminutive in comparison with those of their modern descendants and successors. Moreover, the bulk of the primitive mammalian hemisphere was composed of those parts (hippocampus and lobus pyriformis), which are pre-eminently olfactory; in other words, the neopallium (*i.e.*, that part of the pallium which is neither hippocampus nor pyriform lobe) is especially insignificant. It is a well-known fact that the sense of smell loses much of its importance in mammals of aquatic habits (*e.g.*, *Ornithorhynchus*, the Sirenia, the Pinnipedia, and especially the Cetacea), and in these animals the olfactory parts of the brain dwindle to very small proportions. In the Odontoceti the olfactory bulb and its peduncle actually disappear. The Archæoceti, therefore, are subject to two factors, which will account in some measure for their small cerebrum. For, in addition to the smallness of the brain to which most Eocene mammals are subject, there is their aquatic mode of life. This causes a reduction in size of just those portions of the pallium which form the greater part of the Eocene hemispheres.

In the modern Cetacea the neopallium attains to the greatest absolute size which it ever reaches in any mammal. This fact cannot, however, be considered fatal to the belief in the close affinity of the Archæoceti and the Cetacea, because the extraordinary dissimilarity between the brains in the two sub-orders is such as we know to have been produced by the operation of well-recognised causes in the long lapse of time which separates the dawn of the Tertiary period from the present day. In all mammals which lead a life "in the open" it has become a condition of their survival that the neopallium must increase in size in each successive generation: failing this, the creature must either adopt a "retired and safe mode of life" or become extinct. Numerous examples might be quoted in support of this hypothesis. But the case of the Sirenia shows us how little we really know of the factors which

determine the size of the brain. These creatures began the struggle for existence in Eocene times with relatively large brains, in spite of their aquatic mode of life; and they have been succeeded by generations of descendants whose latest progeny at the present day have a brain-equipment only slightly superior to their earlier Tertiary ancestors (*vide* Catalogue, *op. cit.* p. 344, *et seq.*). Even if we admit that the modern Manatees and Dugongs lead an eminently safe and retired life, which is in marked contrast to the venturesome and "open" life of the whales and porpoises, much still remains to be satisfactorily explained.

Perhaps the most striking feature of the brain of *Zeuglodon* is the extreme disproportion between the size of the enormous cerebellum and the diminutive cerebrum. In this respect the fossil brain presents a most marked contrast to that of all recent mammals, and especially to that of the Cetacea. This relatively great size of the cerebellum is not peculiar to the Archæoceti, but is common to other extinct mammals of large size. In my memoir on the brain in the Edentata¹ the difficulty presented itself of adequately explaining a similar phenomenon in *Glyptodon*; and it must be born in mind, in even attempting to do this, (1) that the obtrusive greatness of the cerebellum presents itself only in large mammals and not in lowlier vertebrates, and (2) that the size of the cerebellum is not proportionate to that of the cerebrum. In the case of *Glyptodon* I four years ago attempted to explain these facts in this manner.

The development of the neopallium in mammals opens up the possibility of the performance of many more complex muscular acts than are possible in the Amphibia or Reptilia; these acts require a co-ordinating mechanism, the size of which will be largely determined by the bulk of the muscular masses, the actions of which are to be harmonised, and the extent of the sensory surfaces which send into the cerebellum streams of controlling impulses. A large cerebellum is being demanded by a

¹ "The Brain in the Edentata," 'Linnean Society's Trans.,' 2nd series, Zoology, vol. 7, part 7, 1899, p. 381.

large mammalian body, even if the cerebrum is small. I cannot offer any more satisfactory explanation of the magnitude of the cerebellum in *Zeuglodon* than this.

It is clear from the foregoing that the extraordinarily great contrast in the appearance of the brain of the Archæoceti and that of the Cetacea cannot be urged as a reason against their kinship, when it is remembered that the operation of known factors is quite sufficient to explain the transformation of the one type into the other in the time which has separated the Eocene period from the present.

Having disposed of these negative arguments, we may consider the positive evidence for Cetacean affinity in the brain of *Zeuglodon*.

The shape of the cerebrum, and especially its relatively great breadth, is peculiar. In fact, this form of hemisphere rarely or never occurs among mammals, other than the Cetacea. I have elsewhere¹ attempted to explain the shortness of the Cetacean hemispheres by the fact that the abortion of the basal (olfactory) parts of the cerebrum limits their longitudinal extension. This, however, is not the whole explanation, because in many microsmatic Sirenia (*Halicore*), and Pinnipedia (*Otaria*, *Phoca*), the hemispheres are not especially broad. The disproportionate breadth seems, in fact, to be to some extent a characteristic of the Cetacea; and, in this respect, *Zeuglodon* agrees with them.

The peculiar elongation of the olfactory peduncles beyond the anterior extremities of the hemispheres is rarely found in mammals, though it is common enough in Reptiles and the Ichthyopsida. In fact, the exact parallel to the condition found in *Zeuglodon* occurs among recent mammals only in the Cetacea.² An analogous condition is found in the extinct Lemuroid *Megaladapis* [described by FORSYTH MAJOR (*op. cit.*)] and some *Amblyopoda*.

¹ 'Catalogue of the College of Surgeons,' *op. cit.*, p. 350.

² Full references to this are given by FORSYTH MAJOR, "On the Brains of Two Sub-Fossil Malagasy Lemuroids," 'Roy. Soc. Proc.' vol. 62, 1897, p. 48, second footnote.

It is not without interest to note that the two outstanding features of the cerebral hemispheres of the Archæoceti, even if their value as indices of kinship be slight, both find their nearest parallel in Cetacea. There are no characters of the brain of the modern Cetacea which can be regarded as certainly distinctive, if we put aside such features as the extreme dwindling of the olfactory apparatus, and the enormous development of the neopallium. Both must be regarded as late acquisitions, not to be expected in an Eocene mammal. Under these circumstances these slight points of positive evidence of the relationship of the Archæoceti and Cetacea must be allowed some value, as reinforcing the testimony of the skeletal parts.

If we seek to institute closer comparisons between the brain of *Zeuglodon* and of the Odontoceti and Mystacoceti with a view to the determination of its relationships, we are not unnaturally doomed to disappointment. It might, perhaps, be supposed by some anatomists that the absence of an olfactory bulb in the Odontoceti might point to a closer affinity of *Zeuglodon* to the Mystacoceti, in which a small olfactory apparatus is retained. But there is every indication that the olfactory apparatus of the Odontoceti has become aborted quite recently.

FIG. 3.—Ventral aspect of brain of an early fetus of *Monodon*. Natural size. *a. d.*, locus perforatus (area deserti); *b. o.*, bulbus olfactorius; *l. p.*, lobus pyramidalis.

Thus in a specimen of the embryonic brain of the Narwhal (*Monodon*), which was given to me some years ago by Professor HOWES, the remains of the olfactory bulb (fig. 3, *b. o.*) are still

quite visible as a small umbilicate area in part of the "desert region" of BROCA (fig 3, *a.d.*), wherefore it follows that in the early embryo the olfactory bulb and peduncle develop as in all other mammals. Moreover, in all Odontoceti traces of the pyriform lobe are found even in the adult; and in the brain of *Kogia greyi* the rhinal fissure and the typical (macroscopically only) pyriform lobe are retained in a form as clearly defined as that of any macrosmatic mammal (fig. 4). Professor HASWELL, in describing this brain¹ emphasises the fact that "the most re-

FIG. 4.—Ventral aspect of left hemisphere of *Kogia greyi*. Reduced approximately one-half. *a.d.*, corpus striatum (area desert); *b.o.*, place occupied by bulbous olfactorius in foetus; *f.r.a.*, fissura rhinalis anterior; *f.r.p.*, fissura rhinalis posterior; *l.p.*, lobus pyriformis.

markable feature of the [basal] region, and perhaps of the whole brain, is in the great depth of the ectorhinal fissure, a feature marking off the present form very strongly from *Delphinus*" (p. 438). Since his illustrations do not properly delineate this interesting conformation, Professor HASWELL

¹ W. A. HASWELL, "On the Brain of Grey's Whale (*Kogia greyi*)," 'Linnean Society of New South Wales Proc.,' vol. 8, 1883 (publ. 1884), pp. 437-439, pl. XXI.

kindly permitted me to examine his specimen; and Mr. J. P. HILL has made me an excellent photograph (of its ventral surface), roughly reproduced the accompanying drawing (fig. 4). It shows the complete and quite-typical rhinal fissure and the characteristic pyriform lobe. In its anterior part the rhinal fissure is fully a centimeter deep.

The exact reproduction of these characters of the rhinencephalon in an adult anosmatic Cetacean, and the presence of the olfactory bulb in the foetal Narwhal, show that these toothed Cetaceans were certainly (and probably quite recently) derived from ancestors presenting the normal mammalian type of olfactory apparatus. The absence of the olfactory bulb and peduncle in the Odontoceti cannot, therefore, be considered a just reason for adopting the utterly improbable suggestion of a nearer affinity of the Archæoceti to the Mystacoceti than to the Odontoceti.

Estimated by the amount of sand which it displaced, the bulk of the natural cast (including that of a considerable quantity of matrix attached to the base of the brain and some small fragments of bone) is 410 c.c. If the necessary corrections and estimations be made from this gross cubic capacity, the weight of the brain in the Archæoceti must have been considerably less than 400 grammes, and perhaps nearer 300, as against that of the recent Cetacea, which ranges from 455 grammes in *Kogia* (HASWELL) to 4,700 grammes in *Balænoptera* (GULDBERG).