TWO ENDOCRANIAL CASTS OF CETACEANS FROM THE OLIGOCENE OF NEW ZEALAND

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ABSTRACT. Two natural endocranial casts of Cetaceans from the Oligocene of New Zealand are described. No skeletal remains are associated with either of them. The larger closely resembles published figures of endocranial casts of Archaeocetes except in that its cerebellum is small and normal instead of being of immense size. The cerebral hemispheres are small, especially anteriorly, and apparently had an olfactory region. The smaller specimen more closely approaches the condition seen in Recent specimens. The cerebral hemispheres have no olfactory region and are rounded anteriorly, but they are far less swollen. The two specimens afford intermediate stages between the brain of the primitive mammal and that of the Recent Odontocete. It is suggested that the immense and unique cerebellum described previously in the brain of Archaeocetes might conceivably be a misinterpretation of a large vascular plexus.

IN the collection of the Otago Museum, Dunedin, New Zealand, are two natural endocranial casts belonging to Cetaceans from the Early Tertiary. The larger one (No. C.48.70) has no data attached to it, while the smaller (No. C.34.7) was collected at Milburn, Otago. There seems no doubt but that both are of Oligocene age. They were mentioned in a paper dealing with *Prosqualodon hamiltoni* by Benham, who pointed out that the larger one is roughly similar in size to the cranial cavity of the skull of this Squalodont, though the skull is not well enough preserved for any of the details to be compared. The only literature on the endocranial casts of cetaceans available has been the papers of Elliot Smith and of Dart on the brains of Archaeocetes. Dart also figures and discusses an endocranial cast of *Prosqualodon davidi* from the Miocene of Tasmania. The present specimens are so unlike those in the literature that it seems desirable that they should be described, and I am indebted to the Director of the Otago Museum for permission to do so.

The larger specimen (Fig. 1), as preserved, is 145 mm. long, 148 mm. wide and 89 mm. high, and it has a volume of approximately 670 cc. It is broken off transversely at the anterior end and obliquely in the region of the medulla, while a portion is missing on the right side. The rest of the surface is well preserved and the impressions of many bloodvessels are clearly visible. The broken surface at the anterior end forms a roughly equilateral triangle with sides about 50 mm. long. The dorsal angle runs back for some 35 mm. as a sharp ridge, the cerebral hemispheres swelling gently on either side.

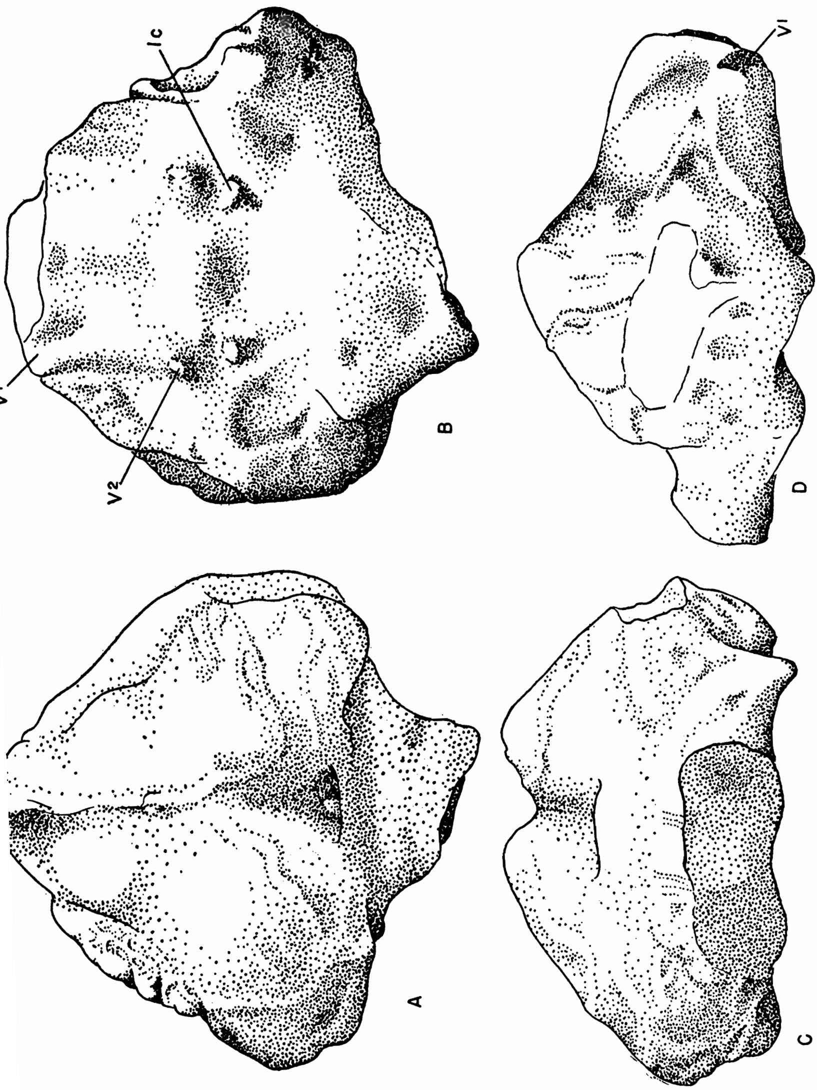

Fig. 1. Natural endocranial cast of Oligocene Cetacean from New Zealand. Larger specimen, No. C.48.70. Actual length 145 mm. A. Dorsal side. B. Ventral side. C. Posterior side. D. Right side. I.C. Internal carotid. V.1. Maxillary branch of trigeminal nerve. V.2. Mandibular branch of trigeminal nerve.

Indications of the sagittal sinus are visible in the middle line posterior to the ridge, and it extends into a deep V-shaped groove between the posterior regions of the cerebral hemispheres, which rise on each side into rather sharp conical projections. Still more posteriorly the median groove widens out into a triangular depression bounded behind by a sharp transverse ridge. This depression presumably indicates the position of the tentorium cerebelli.

The cerebral hemispheres are low and narrow anteriorly, but expand rapidly both sideways and upwards towards their posterior ends. A shallow lateral depression separates a slight anterior swelling from the high conical region behind. The surface of the posterior half, as far forward as the highest peak, is covered with a network of bloodvessels, some of which are indicated in the figures. The best marked is a vessel which takes a curving course outwards from the sagittal sinus, passing posterior to the peak of the cerebral hemisphere. A larger, but less clearly defined vessel, runs from the region of the ridge behind the tentorial depression anteriorly round the lateral corner of the cerebral hemisphere. The details on the sides of the cast are not clear. Lying alongside the anterior half of the cerebral hemisphere is an irregular mass which seems to be composed of bloodvessels and appears to be connected with the posterior cerebral vessel and below with a large vessel which emerges between the cerebral hemisphere and cerebellum. This irregular mass is separated medially from the cerebral hemisphere by a groove, and is divided into three lobes by two oblique dorso-ventral grooves. Small fragments of bone still adhere to the cast in these grooves. The anterior end of the lateral irregular mass is broken off and lies adjacent to the corner of the anterior triangle as a small triangle about 10 x 15 mm.

The posterior region of the cast is broken off obliquely and only extends some 45 mm. behind the transverse ridge. From the ridge the dorsal surface sweeps smoothly down with only a slight transverse swelling and a few fine longitudinal bloodvessels. The cerebellar region extends obliquely downwards and forwards under the overhanging posterior edge of the cerebral hemisphere.

The ventral surface of the cast is broad and flat, its most conspicuous feature being a low transverse swelling slightly anterior to the middle. Posterior to the ends of this are small elevations apparently showing the positions of the internal carotid foramina, and lateral to these the large bloodvessels come from the groove between the cerebellum and cerebral hemispheres and turn outwards towards the lateral irregular mass of bloodvessels. Smaller vessels appear from the same groove and also run laterally. Lateral to the ends of the transverse swelling are elevations probably representing the foramina for the mandibular branch of the trigeminal nerve, while the maxillary branch and the optic nerve appear to run forward at the lower corner of the anterior triangle.

Two artificial endocranial casts of Recent Odontocetes were available for comparison, one of *Lagenorhynchus obscurus* and the other of *Cephalorhynchus hectori* (fig. 2, E & F). A number of striking differences are at once apparent. In the fossil the main axis is straight while in the Recent specimens the anterior half is bent upwards at an angle of roughly 40°. The flatness of the ventral surface of the fossil is the more noticeable in that the lateral lobes of the cerebellum hardly extend below the ventral surface, while in the Recent casts they are much larger and more rounded and extend 15-20 mm. below it. The whole of the Recent cerebral hemisphere is more rounded and the anterior end is without the prismatic appearance of the fossil, while there is no sign of the lateral irregular mass of bloodvessels. Apart from these differences the fossil and Recent casts are easily comparable and the cerebral bloodvessels have the same course. The vessel emerging between the base of the cerebral hemisphere and the ventral anterior corner of the cerebellum runs round the back of the cerebral hemisphere on to the cerebellum near the tentorium and thence round to the ventral side of the medulla, while the middle cerebral vessel runs round over the apex of the cerebral hemisphere to the sagittal sinus. On the ventral surface, the internal carotid foramen and that for the mandibular branch of the trigeminal nerve are similarly situated.

The differences between the size and shape of the cerebral hemispheres and cerebellum in the fossil and the Recent specimens are such as one would expect in comparing the brains of Oligocene and Recent members of the same group of mammals. The difference at the anterior end seems to be due to the loss of the olfactory sense in the Recent Odontocete and perhaps also to the telescoping of the skull.

On comparing the fossil cast with the figures given by Elliot Smith and Dart of the endocranial casts of *Archaeocetes*, a very strong general resemblance is at once apparent. The cerebral hemispheres of the Archaeocete are low and rounded anteriorly, and there is a dorsal ridge leading to a prismatic anterior end, formed by the olfactory peduncles and anterior nerves. On each side is an irregular mass, interpreted by Dart as a huge Gasserian ganglion covered by middle cerebral vessels. The posterior part of the Archaeocete cast rises to a peak, superficially much as does the present specimen.

The peculiarity of the Archaeocete brain lies in the cerebellum. This is an irregular transverse mass rising high above the cerebral hemispheres and extending down the sides in what are referred to by Dart as the parafloccular lobes. To quote Elliot Smith, "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." Much discussion has centered on the size of the cerebellum, and its relation to the systematic position of the Archaeocetes and their mode of life.

As pointed out above, if this information had not been available no difficulty would have been experienced in comparing the specimen with the Recent casts, its cerebellum being quite similar though relatively smaller (fig. 2). In view of the published information about the Archaeocete cerebellum and the close similarity in shape between the Archaeocete cast and the present one, a close reëxamination was made. There seems no doubt but that the whole of the anterior portion of the cast represents the cerebral hemispheres. A smooth continuous surface is visible with no trace of a transverse tentorium in front of the highest part, while there is one posteriorly, exactly as in Recent specimens. The elevated portions are separated by a deep sagittal groove as one would expect if they are cerebral hemispheres but not if they are cerebellum, and this is also visible in some of Dart's figures. The relations of the bloodvessels are also exactly as in the Recent specimens.

Unfortunately nothing is known of the origin of this specimen and Archaeocetes, Squalodonts and Cetotheres are all present in the Early Tertiary of New Zealand. The skull of *Prosqualodon hectori* is not sufficiently well preserved to show what was the shape of its brain, and the endocranial cast of

Prosqualodon davidi figured by Dart is quite unlike the present specimen. The balance of evidence, except for the condition of the cerebellum, seems to point to the present cast belonging to an Archaeocete. If it could be shown that the cerebellum of the Archaeocete was in reality a small normal one, the his-

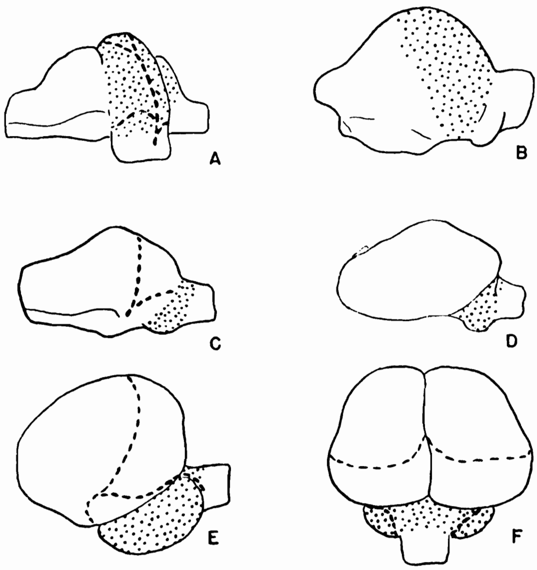

Fig. 2. Diagrams of endocranial casts of Cetaceans reduced to approximately the same size. Cerebellar region dotted, bloodvessels in broken lines. A. Left side of *Zeuglodon osiris* (bloodvessel from *Prozeuglodon atrox*), after Dart. Middle Eocene. B. Left side of *Prosqualodon davidi*, after Dart. Miocene. C. Left side of larger specimen. Oligocene. D. Left side of smaller specimen. Oligocene. E. Left side of *Cephalorhynchus hectori*. Recent. F. Dorsal side of *Cephalorhynchus hectori*. Recent.

tory of the Cetacean brain would be much simplified and the present specimens would fit readily into it. It is of course impossible to determine anything definite without examination of the specimens, but several points in the published figures and descriptions suggest that an alternative explanation is conceivable. The peculiarity of the Archaeocete structure is exemplified by Elliot Smith's statement, "behind the part which I have just described as the cerebrum there is a large irregular mass of a very peculiar shape, not exactly comparable with the condition occurring in any other brain known to me." Close examination, however, convinced him that it formed part of the cerebellum. Examination of Dart's figures shows that this region has a very irregular surface, due to the presence of either numerous small sulci or of bloodvessels. In some specimens there is a deep sagittal groove. It seems possible that this mass represents, not an immense anterior development of the cerebellum, but one of the retia mirabilia which are known to occur in Recent Cetaceans. Ommanney, describing these structures in the cervical region of *Balaenoptera* states that "up to the foramen magnum the neural canal is filled with a plexus, which is entirely venous, embracing the spinal cord and entering the skull through the foramen magnum to form a vascular mass against the hinder surface of the brain." In support of this suggestion is the fact that the corresponding region of the present specimen is covered with the impressions of bloodvessels, though not so thickly as to obscure the outline of the cerebral hemispheres. In Dart's figure of *Prozeuglodon atrox* the transverse sulcus anterior to this mass is very slight, while a bloodvessel runs over its apex very much as one does over the cerebral hemisphere of the Recent cast and of the present specimen. Further support to the vascular theory is the statement by Kellogg that the vertebrarterial foramina in the cervical vertebrae of *Basilosaurus cetoides* are very large, and that the main arterial supply to the brain of Recent Odontocetes is by this route.

The smaller specimen (fig. 3) is 88 mm. long, 89 mm. wide and 50 mm. high, and is asymmetrical, being strongly skewed over to the right. Its volume is approximately 200 cc. The cerebral hemispheres are low anteriorly, rising to a rounded elevation behind, the highest part being much less acutely pointed than in the larger specimen. The surface is smooth and without bloodvessels except for a few small ones entering the sagittal sinus. The anterior ends of the cerebral hemispheres are rounded and between them is a striking hexagonal projection whose concave anterior face contains traces of bone. No comparable depression was observed in several Recent porpoise skulls, and the shape of this part of the cast is quite unlike that of the larger one. Dart figures a conical anterior projection on the cast of *Prosqualodon davidi*, which he refers to as the olfactory peduncle. On the left side is a large mass somewhat ridged on its surface in a way suggestive of bloodvessels. There are traces of bone in the groove between this mass and the cerebral hemisphere. No transverse tentorial depression is visible posterior to the cerebral hemispheres and the details of the posterior region are obscure.

The ventral surface is well preserved as a smooth undulating surface, all approximately in one plane. In the centre are several elevations and depressions, the largest apparently

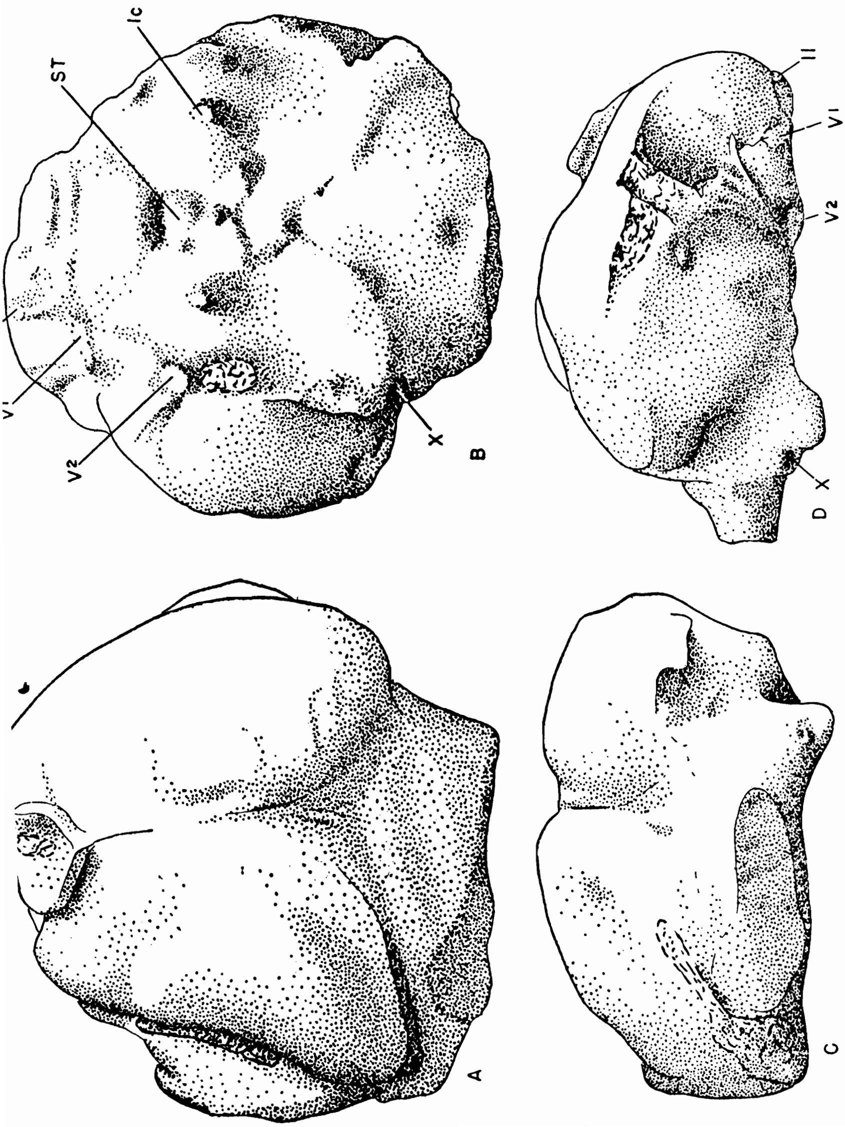

Fig. 3. Natural endocranial cast of Oligocene Cetacean from New Zealand. Smaller specimen, No. C.34.7. Actual length 88 mm. A. Dorsal side. B. Ventral side. C. Posterior side. D. Right Side. S.T. Stella turcica. I.C. Internal carotid. II. Optic nerve. V.1. Maxilllary branch of trigeminal nerve. V.2. Mandibular branch of trigeminal nerve. X. Vagus nerve.

representing the sella turcica, and laterally there are elevations indicating the carotid foramina. Postero-laterally there is the elevation below the cerebellum and on its posterior surface is the impression of a foramen, possibly that for the vagus nerve. Anterior to this elevation is a deep depression containing fragments of bone on the right side of the cast, and anteriorly again are two elevations apparently representing the foramina for the mandibular and maxillary branches of the trigeminal nerve. At the anterior end on the right side can be detected what is probably the foramen for the optic nerve. The arrangement of these features is not unlike that seen on Recent endocranial casts, though in these they are more crowded together.

The smaller cast seems to represent a brain more closely resembling that of a Recent Odontocete than does the larger one. It differs from the Recent endocranial cast in being flat on the ventral surface, in having a relatively smaller cerebellum and very much less expanded cerebral hemispheres. It differs from the larger cast principally in the more rounded cerebral hemispheres especially at the anterior end where the cast is not drawn out into the prismatic anterior region. A remarkable feature is its very small size, 200 cc., and it seems likely that it belonged to a young individual. All the known New Zealand Odontocetes of camparable geological age are considerably larger, and according to Dart the volume of the endocranial cast of *Prosqualodon davidi* from the Miocene of Tasmania, is approximately 750 cc. Dart comments on the fact that this volume is slightly less than that of the endocranial cast of the Eocene *Zeuglodon intermedius*. He maintains that this is sufficient, in accordance with the "law of increasing brain weight" put forward by Marsh, to show that the Zeuglodont cannot have been ancestral to the Squalodont, but that the ancestor must have had a brain capacity very much less. Edinger, however, as a result of a study of the phylogeny of the horse brain, criticizes Marsh's law.

The larger specimen is interesting in the light of Edinger's findings in connection with the evolution of the horse brain. She showed that in *Eohippus*, where the skeletal characteristics already clearly foreshadowed the line of descent leading to the horse, the brain was completely unspecialized and comparable with only the most primitive of living mammals, such as the opossum *Didelphys*. As she says, "the outstanding characters of the skeleton place *Eohippus* with the Equidae; the osteologist can see the future horse in this Lower Eocene form. The brain connects *Eohippus* only with the past. The ancestral brain, an unspecialized mammalian brain, was held over in the Equid body. No features of this brain signal the future." The cerebral hemisphere of the larger cast almost resemble those of *Eohippus*, though more expanded posteriorly so that the mid brain and cerebellum are less conspicuous. Assuming that the larger cast belongs to an Archaeocete, it is tempting to speculate as to whether the specialization of the bodies of these whales for aquatic life had taken place while the skull and especially the brain remained in a primitive condition. In the Odontocete, telescoping of the skull, loss of olfactory sense and enlargement of the cerebral hemispheres seems to have already taken place by Oligocene times, to judge from the smaller specimen, while in Recent times the cerebral hemispheres and cerebellum are greatly enlarged and exhibit the greatest degree of convolution of any brain. It is clearly recognized, however, that this interpretation of the present specimens does not fit in with those of Elliot Smith and Dart for the Archaeocete and Squalodont endocranial casts at their disposal, and further material must be awaited.

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