OBSERVATIONS ON ENDOCRANIAL CASTS OF RECENT AND FOSSIL CETACEANS

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INTRODUCTION

The problems of the ancestry of the modern whales (Odontoceti and Mysticeti) and especially that of their relationship to the extinct cetaceans of the Eocene and Oligocene (Archeoceti) as well as the Miocene Squalodonts, is still very much a matter of controversy, largely because of the lack of intermediate types which might serve to bridge the morphological gaps between the three groups. Dart (1923), on the basis of an examination of a series of endocranial casts, concluded that the Archeocetes cannot be regarded as being on the direct line of cetacean evolution because of certain specializations manifest in the brain, viz. enormous hypertrophy of the trigeminal apparatus and cerebellum. This interpretation of the casts and the widespread conclusions concerning the manner of life, probable habitat and relationships of the Archeocetes which are based on it have been given considerable weight by palaeontologists, e.g. Kellogg (1928, 1936), Flynn (1947), and the most recent writer on this subject—Edinger (1955)—after an examination of the actual casts has reached conclusions concerning the form of the brain which do not differ significantly from those arrived at by Dart. If these authors' views be accepted, then the Archeocete brain must be regarded as presenting an arrangement unique among mammals almost to the point of being grotesque. There is no *a priori* reason why this should not be so, but the form of the brain as read by Dart (1923), Edinger (1955), and others from the endocranial cast is so peculiar that (bearing in mind the highly equivocal nature of the information which can be derived from such material) it is difficult to accept it on neurological grounds, unless it can definitely be shown that no other interpretation is possible.

Marples (1949), as a result of a study of two endocranial casts of very doubtful horizon but which he considered probably belonged to Archeocetes, has tentatively suggested that the alleged immense cerebellum of the Archeocetes might be a misinterpretation of a large vascular plexus of a nature similar to the intra-cranial retia mirabilia which are such a characteristic feature of modern cetaceans. It cannot be known for certain whether or not the Archeocetes possessed such structures, although in view of their complete adaptation to an aquatic life it is at least possible, if not probable, that they did, since such structures are common to all living cetaceans. If so, obviously the presence of retia will be reflected in the endocranial cast, making it a very misleading representation of the brain.

It is evident from figures published (e.g. by Gervais, 1871) that the endocranial cast in modern cetaceans, with well-developed retia, presents but a poor caricature of the form of the brain. However, precise information is lacking as to the type and situation of such distortion of the cast (considered as a reasonable replica of the brain) which might be directly attributed to the presence of retia and other intracranial vascular structures. Accordingly, it was considered of some interest to examine this question more fully in order to determine whether or not, in living cetaceans, the appearances of whose brains are well known, the presence of retia can alter the form and proportions of the brain as reflected in the endocranial cast, in such a manner as to suggest either presence or absence of similar structures in the Archeocetes. This may enable one to assess their role as factors contributing to the alleged bizarre appearance of the 'brain' in this group, and perhaps substantiate Marples's (1949) suggestion from a different viewpoint.

MATERIALS AND METHODS

Apart from illustrations of brains and casts published by other authors, and referred to in the text, the following material was examined.

(1) Brain and endocranial cast of foetal fin-whale (*Balaenoptera physalus*) 14 ft. long, of an estimated (using Walmsley's, 1938, curve of growth during gestation) age of 10–11 months.

(2) Brain and endocranial cast of adult common porpoise (*Phocaena phocaena*). These were not from the same specimen.

(3) Endocranial cast of common dolphin (*Delphinus delphis*).

(4) In addition, well fixed and undistorted brains of the adult fin-whale (*Balaenoptera physalus*) and humpback whale (*Megaptera novaeangliae*) were available, and through the kindness of the Museum authorities access was had to the series of Archeocete skulls and endocranial casts housed in the British Museum.

OBSERVATIONS

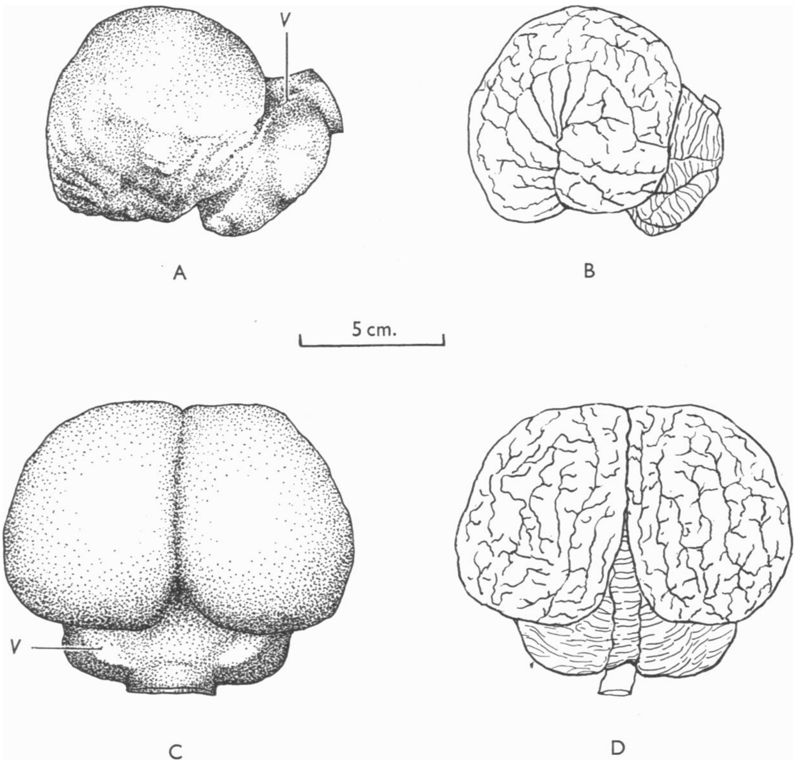
It is not intended here to make a very detailed and point-for-point comparison between casts and brains. The main interest is to determine to what extent the cast reflects the form, arrangement and proportions of the major subdivisions of the brain, and how far its shape is determined by the presence of vascular or other tissues, apart from the brain, within the cranial cavity.

Odontoceti

It can be seen from Text-fig. 1 that there is a close correspondence between the endocranial cast and the brain in the porpoise. The cast gives a reasonable idea of the brain and of the general proportions and mutual relations of the cerebrum and cerebellum. These remarks apply equally to the endocranial cast of *Delphinus* (not illustrated), and judging from figures of similar casts of other recent Odontocetes such as those of *Cephalorhynchus hectori* and *Pontoporia blainvillii* published by Marples (1949) and Dal Piaz (1905) respectively, this would appear to be a general finding as far as the smaller Odontoceti are concerned.

On closer examination certain differences become apparent. Whereas there is very little distortion of the cerebral hemisphere in the cast and while the approximate position of the lateral fissure can be readily determined, it is evident when one compares the superior view of cast and brain (C and D, Text-fig. 1) that considerably less of the 'cerebellum' is visible from this aspect in the former. This is due to the presence of retial tissue in relation to the posterior end of the cerebral hemisphere and above the bony tentorium. An exactly comparable state of affairs is evident from Dal Piaz's (1905) photograph of a similar view of the endocranial cast of *Pontoporia*; even less of the cerebellar portion can be seen than in the present instance.

When viewed from above (Text-fig. 1 C, D) the cerebellar portion of the cast can be seen to consist of three portions, two rounded lateral parts and a large elevated central portion continuous with the cast of the foramen magnum. A ridge caused by



Text-fig. 1. Lateral and dorsal views of endocranial cast (A and C) and brain (B and D) of common porpoise (*Phocaena phocaena*). *V*, cast of blood vessel.

a blood vessel (*V*) limits this latter portion on either side. Comparison with the corresponding view of the brain shows that these three parts bear very little relation to the actual disposition of the vermis and lateral lobes of the cerebellum.

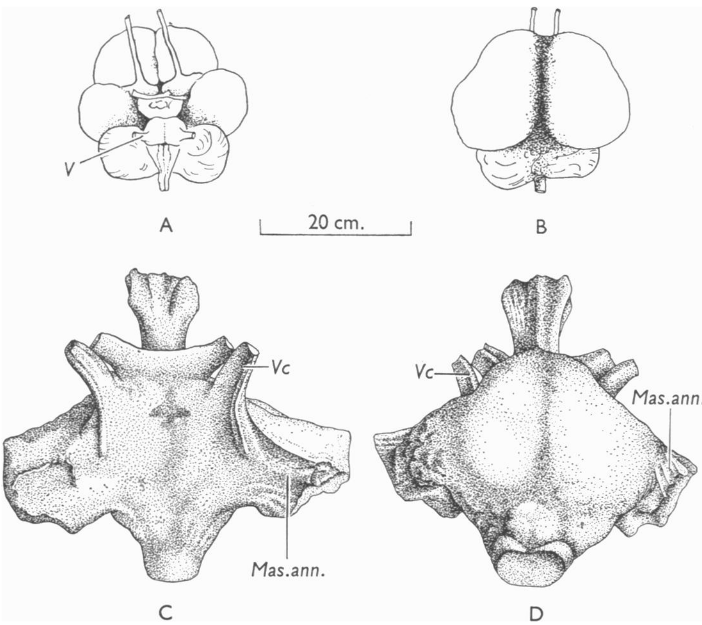
From the lateral aspect (Text-fig. 1 A, B) it is evident that the antero-posterior diameter of the cerebellar region of the cast is considerably greater than in the brain and, more important (since the two are not from the same specimen), that it is also greater in relation to the corresponding diameter of the cerebral hemisphere. The vertical diameter is also greater in the cast.

A close comparison between the cerebellar region of the cast and the actual cerebellum leads to the conclusion that no information of any value concerning the fissural pattern and morphological subdivisions of the latter can be gained from a study of the cast. In fact it may be positively misleading. This is only to be expected since the cerebellum is nowhere in direct contact with the skull, and even if it were, the lips of the cerebellar fissures are so close together that one would not expect to find any significant impressions on the inner table.

One might fairly conclude from these observations that considering the amount and distribution of the retial tissue in the smaller Odontoceti, it is surprising how good an impression of the general proportions and shape of the brain can be obtained from the endocranial cast. There is some distortion tending towards enlargement of the posterior pole of the cerebral hemisphere and of the various dimensions of the cerebellum. Details of cerebellar morphology are not reflected in the cast. It is probable that these remarks would not apply in like measure to the larger Odontocetes such as the sperm whale, in which the retial tissue is much more strongly developed.

Mysticeti

Gervais, who worked only with the skeleton, published (1871) some excellent illustrations of endocranial casts from a series of Mysticetes. C and D, Text-fig. 2, are drawn from ventral and dorsal views respectively of Gervais's cast of *Megaptera*,



Text-fig. 2. A and B: outlines of ventral and dorsal aspects respectively of a brain of the humpback whale (*Megaptera novaeangliae*) drawn from photographs. C and D: corresponding views respectively of endocranial cast of same after Gervais (1871). *Mas. ann.*, masses annexes, *V*, trigeminal nerve; *Vc*, cast of ophthalmic nerve and accompanying rete.

and above them (Text-fig. 2 A, B) are outlines traced from photographs of a brain from the same species in our possession. The figures show in a striking manner how inadequate and distorted an impression of the size and form of the brain can be gained from the endocranial cast of a typical Mysticete.

It will be noted that the form and limits of the cerebrum and cerebellum cannot be inferred from the cast, and that extending laterally on either side from the approximate region of confluence of the two are large masses, the 'masses annexes' of Gervais (1871), which have no counterpart in the brain, and which represent the mass of retial and vascular tissue surrounding the cerebellum and accompanying certain of the cranial nerves on their passage towards exit from the skull. There is a great disparity between the actual size of the trigeminal nerve and the apparent counterpart of the only one of its branches (*Vc*) which can be identified in the cast, due again to the fact that in the living animal the branches of this nerve are accompanied in their intra-cranial course by considerable masses of retial tissue. The actual size of the olfactory peduncles bears little relation to that of the central pedunculated mass which projects from the anterior end of the cast, and which represents the olfactory fossa, of which the peduncles and bulbs occupy only a very small part.

All of these features, with minor differences of degree in different species, are visible in other casts illustrated by Gervais.

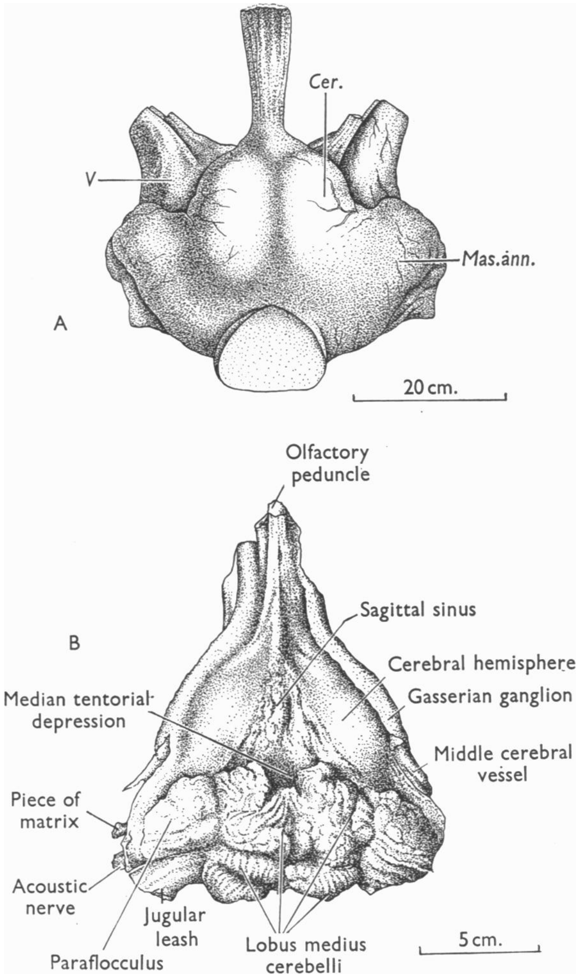
Comparison of Mysticete and Archeocete endocranial casts

So far as the endocranial casts are concerned it was at once clear (bearing in mind the time factor and the differences in the form of the skull) that the Archeocete resembles the Mysticete far more closely than the Odontocete. Now the two main features which characterize the Archeocete brain, according to Dart (1923) and those who accept his interpretations, are the enormous size of the trigeminal apparatus, and the marked extension of the cerebellum, particularly in a lateral direction. Since, as has been shown in the previous section, the presence of retia can account for a marked exaggeration in the size of the trigeminal nerve and its branches, as well as a marked lateral extension opposite the cerebro-cerebellar junctional area in the endocranial cast of recent cetaceans, it is obviously of interest to compare examples of recent and fossil casts. It is possible that what are appearances of a similar order might have the same underlying causes.

In Text-figs. 3 and 4, dorsal and lateral views respectively of the endocranial casts of two Archeocetes as interpreted by Dart are figured together with a similar view of casts of two modern cetaceans as figured by Gervais (1871).

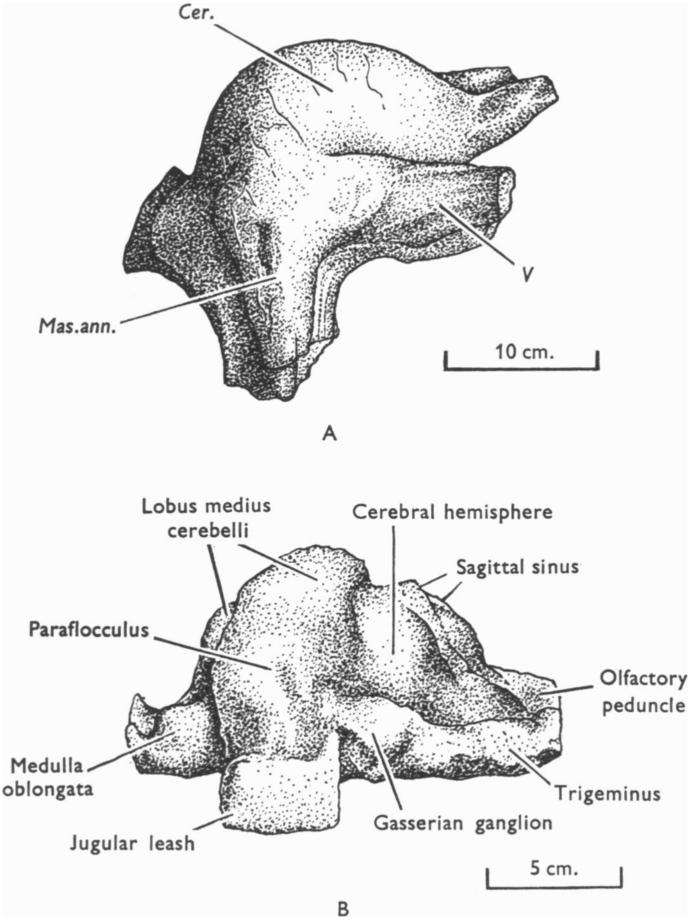
In each the general position of the cast of the cerebral hemisphere can be made out, as well as a mass which extends in a forward direction alongside it. In the Archeocete this is regarded by Dart as representing an enormous trigeminal ganglion and nerve, while in the recent cetacean we have seen that the structure which occupies a corresponding position, although associated with this nerve, bears little relation to its actual size, and represents mainly the cast of a large amount of retial tissue which accompanies the nerve and its branches.

Directly posterior to this 'trigeminal' mass in both Archeocete and the modern cetaceans, the cast is considerably widened, due in the former, according to Dart, to an enormous hypertrophy of the cerebellum, and of the 'paraflocculus' in particular. The corresponding portion of the cast in modern cetaceans is largely a cast of retial and vascular tissue (masses annexes of Gervais) surrounding the cerebellum and accompanying the more posterior cranial nerves (Text-fig. 3A). It may be noted in passing that Dart labels as 'medulla oblongata' the cast of the foramen magnum in the Archeocete, and he concluded that this portion of the brain was widened due to hypertrophy of the 'tuberculum quinti' (spinal nucleus and tract of the trigeminal).



Text-fig. 3. A: dorsal view of endocranial cast of *Balaena mysticetus* after Gervais (1871). *Cer.*, cerebral hemisphere; *Mas. ann.*, masses annexes; *V*, cast of space occupied by retial tissue surrounding trigeminal nerve. B: dorsal view of endocranial cast of the Archeocete *Zeuglodon sensitivus* after Dart (1923) brought up to approximately the same overall size as A. Dart's labelling unchanged.

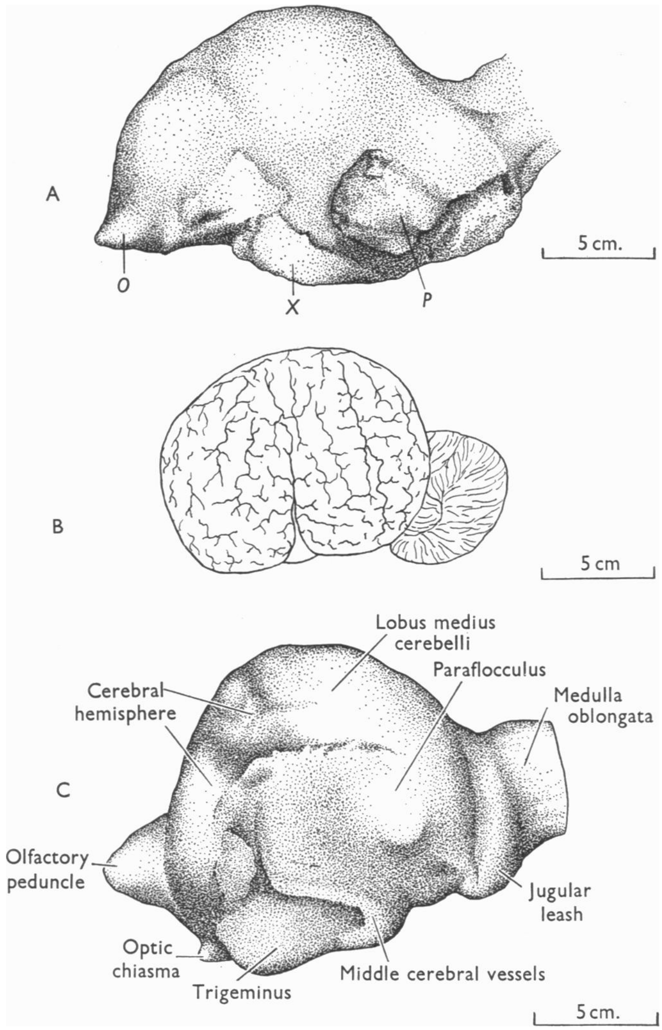
From this brief comparison it is evident that appearances of a similar order to those which are known to be due to the presence of retia in certain modern cetaceans occur in corresponding situations in the endocranial casts of Archeocetes. Since the latter were also cetaceans and fully adapted to an aquatic environment, a strong suspicion is aroused that they may also have possessed retia and that the features of the casts which have been interpreted as an enormous development of the cerebellum and trigeminal apparatus may be accounted for by this.



Text-fig. 4. A: lateral view of endocranial cast of *Balaenoptera rostrata* after Gervais (1871). Abbreviations as in Text-fig. 3A. B: lateral view of endocranial cast of the Archeocete *Zeuglodon Osiris* after Dart (1923) brought to approximately the same size as A. Identifications according to Dart.

Comparison of endocranial casts of foetal fin-whale and Prosqualodon

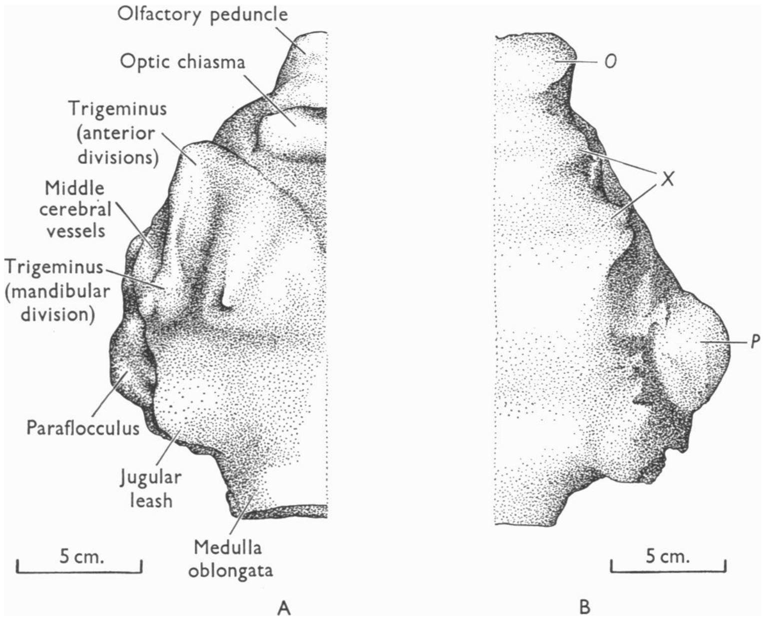
Lateral and ventral views of the endocranial cast of a foetal fin-whale are illustrated in Text-figs. 5A and 6B. Partly owing to the lesser development of the retia in foetal stages it is not so extraordinary in shape as the adult casts figured by Gervais (1871). Taking this cast by itself it is not difficult to see a general resemblance to a mammalian brain; it could plausibly be suggested that the anterior projection (*O*) represented a fairly large olfactory bulb, and that the lateral projection from the posterior end (*P*) was evidence for the presence of a very large flocculus, or paraflocculus, or both. A comparison with an outline of the actual brain from this specimen (Fig. 5B) shows how false any such interpretation would be. The apparent



Text-fig. 5. A: lateral aspect of endocranial cast of foetal fin-whale (*Balaenoptera physalus*). The letters indicate structures referred to in the text (p. 538). B: lateral aspect of the brain from the same specimen drawn from a photograph. C: lateral aspect of endocranial cast of *Prosqualodon davidi* Flynn after Dart (1923) brought to approximately the same size as A. Dart's labelling unchanged.

olfactory bulb is the cast of the olfactory fossa (Pl. 1, fig. 1) lying anterior to the brain, and which, as is evident from Pl. 1, fig. 2, bears little relation to the actual size or shape of the olfactory peduncle, while the projection (*P*) in the cast has no counterpart whatsoever in the brain. It is obvious that the presence of the retia and other endocranial structures apart from the brain has so modified the shape of the cranial cavity that it yields virtually no reliable information about the morphology of the brain, and is in fact seriously misleading if used for this purpose.

The endocranial cast of *Prosqualodon*, illustrated by Dart (1923), is rather similar in shape to that of the foetal fin-whale (see Text-figs. 5C and 6A, outlines traced from Dart's figs. 21 and 18 respectively, orientated similarly to the cast from the foetal fin-whale). One notes a similar precerebral projection which is taken to represent a nipple-like olfactory bulb, from which identification certain far-reaching conclusions were drawn. It is certain that this projection represents the cast of the



Text-fig. 6. A: ventral aspect of right half of endocranial cast of *Prosqualodon davidi* Flynn after Dart (1923) brought to approximately the same size as B. Identifications according to Dart. B: similar view of left half of endocranial cast of foetal fin-whale (*Balaenoptera physalus*). The structures labelled are referred to in the text (p. 540).

'olfactory fossa' figured by Flynn (1947; Text-fig. 4) and there is no evidence that it represents the actual size or manner of attachment of the bulb in *Prosqualodon*. Again, the structure confidently labelled 'paraflocculus' by Dart bears a striking resemblance in shape and position to the structure *P* in the foetal cast, which, as is evident, does not represent any part of the brain but rather the cast of a space occupied by vascular tissue. Finally, there is present in the foetal cast a prominence (*X*, Text-fig. 6B), similar in situation to the 'trigeminus' of Dart, which can again be accounted for by the presence of intra-cranial vascular tissue. One might legitimately conclude from the above that in some respects the skull of *Prosqualodon* is more like the foetal than adult stages of the skull of modern Mysticetes, a conclusion which could be tested by reference to the actual bones. One might also suggest that the similarity between the casts is at least partly due to the presence of retial tissue within the cranial cavity of both animals, as is certainly the case in the one living to-day. This suggestion must remain a speculation so far as *Prosqualodon* is concerned, but it is far more in line with what one would expect to find within a cetacean skull than the almost incredible hypertrophy of the cerebellum and trigeminal apparatus which Dart's interpretation necessitates. It might, of course, be argued that *Prosqualodon* should be compared with the Odontocete rather than that with a Mysticete cetacean, and again, though less striking, there is some similarity in the casts (compare Text-figs. 1A and 5C). It has already been shown that the Odontocete cast gives a fair but by no means perfect representation of the brain, but this does not help Dart's interpretation. If the similarity means anything it is that the Squalodont brain may have resembled that of a modern Odontocete (Text-fig. 1B) and not that it possessed a cerebellum considerably larger than the cerebral hemisphere, and a trigeminal apparatus of large proportions.

DISCUSSION

One may summarize the present findings by stating that the endocranial cast of the smaller Odontocetes gives a reasonable picture of the form of the brain, but with distortion of the cerebellar region, while in the Mysticetes in general, the cast is little less than a poor and misleading caricature. This difference is mainly accounted for by the exuberance of intra-cranial retial tissue in the latter group as compared with the former. The possibility that the Archeocetes and *Prosqualodon* possessed retia (as do all modern cetaceans) is strongly suggested by certain similarities which can be demonstrated to exist between their endocasts and those of modern Mysticetes.

This being so, it is possible that certain features of the Archeocete endocast—as suggested by Marples (1949)—may be due to the presence of retia. It is clear from Dart's (1923) and Edinger's (1955) writings that no weight was given to this consideration, and that they regarded the endocast as a replica of the brain. As Edinger (1955, p. 39) states 'a palaeoneurologist calls cerebral hemisphere the endocast of the osseous chamber which once lodged the hemisphere', and on this basis both authors regarded the posterior part of the cast as representing an enormous cerebellum. Elliot Smith (1903) and Stromer (1908) had previously reached a similar conclusion. Dart (1923), in addition, emphasized an enormous trigeminal hypertrophy in the Archeocetes and to a lesser extent in *Prosqualodon*. As pointed out in the introduction, this conception of the form of the Archeocete brain is not an easy one to accept on neurological grounds, and it is desirable to examine critically the evidence on which it is based.

The whole foundation of Dart's theory of the trigeminal specialization of the Archeocetes rests upon his interpretation of the size and situation of the trigeminal ganglion. This he takes to be the relatively large mass lying alongside the cerebral hemisphere, and which, he says, it almost rivals in size. He does not advance any convincing reasons in support of this interpretation, but accepts it without further argument as a fact, and elevates it to the status of a first premise to which he relates many other of the unusual features of the cast. For example, the marked breadth of the ventral aspect of the cast of *Zeuglodon sensitivus* in the general region of the medulla oblongata is alleged to be due to expansion of the 'tuberculum quinti', the upper portion of which is stated to form a bulge on the cast postero-medial to the 'Gasserian ganglion'. The precise situation of this bulge is doubtful since it is not labelled in any of the figures. A study of the actual cast shows two bulges in this general situation but there is nothing about either of them as regards situation and appearance which can even remotely justify regarding it as being produced by the 'tuberculum quinti' in preference to anything else.

It would not be difficult to suggest alternative explanations to account for the appearance of Dart's 'Gasserian ganglion'; for instance, it may well be due to the presence of retial tissue associated with the branches of the trigeminal nerve such as is found in modern cetaceans. Both interpretations are of necessity speculative, but whereas the one involves the acceptance (on highly questionable evidence) of a degree of hypertrophy of the trigeminal apparatus which has been seen in no other mammal, living or extinct, the other has the support of similar appearances in the endocasts of modern representatives of the same order, which undoubtedly result from the presence of retial tissue.

Perhaps the most extraordinary feature of the Archeocete endocranial cast is the massive expansion laterally and upwards of the posterior end. On the basis of its position and on theoretical grounds Elliot Smith (1903), Stromer (1908), Dart (1923) and Edinger (1955) regard almost the whole of this mass as representing the actual size of the cerebellum. Dart, in referring to the natural cast of *Z. sensitivus*, says that it 'reproduces very faithfully the convolutional pattern of the cerebellum', and proceeds to identify a 'lobus medius', a 'paraflocculus' and a 'lobulus simplex'. Examination of the actual cast reveals these elevations, but cannot by itself justify their identification. The only justification for the label 'paraflocculus' (in which is apparently included the flocculus) is its postero-lateral position in the cast, and the theoretical consideration that in all marine mammals this part of the cerebellum, which was thought to be concerned with equilibration, might be expected to be enlarged. This postulated association between 'equilibration' and the paraflocculus has not been borne out by subsequent anatomical and experimental studies (see Brodal, 1954). Now we have seen in modern cetaceans, Odontocete and Mysticete alike, that no information of any value concerning the morphological subdivisions of the cerebellum can be obtained from the endocast, and indeed, this applies to mammals in general as a glance at a number of casts will show. There is no reason therefore for the identification which has been made, apart from the theoretical expectation that an aquatic mammal would have a large cerebellum with particularly well-developed paraflocculi. If the theoretical expectation had been the opposite of this, the cast could have been interpretated in at least an equally plausible manner.

That theoretical expectations have been the main influence in making interpretations is even more evident in the case of *Prosqualodon*. Here again a huge cerebellum is recognized, although in this instance with even less justification than in the Archeocete cast, since, to judge from his figure (1923, text-fig. 18) there is little to indicate even an approximate line of subdivision between cerebrum and cerebellum. The cast from a foetal fin-whale shows that a brain of an entirely different form to that postulated for *Prosqualodon* can be associated with a very similar endocranial cast. In the fin-whale the differences between cast and brain can be attributed to the presence of retia (much less developed than in the adult) and, since they are such as to make the cast closely resemble that of *Prosqualodon*, it is quite possible that retia were present in this animal as well and to a large extent determined the form of the endocranial cast.

The neurological considerations which have led Dart and others (e.g. Edinger, 1955) to justify their interpretation of the features of the casts merit some discussion. As previously indicated, both these authors considered that the Archeocetes must have possessed a large cerebellum because of the needs of 'equilibration', a consideration partly based upon the fact that modern marine mammals have large cerebella. Enlargement of the cerebellum, however, can result from a number of causes other than the need for equilibration. Structures directly concerned with equilibration in Cetacea such as the vestibular apparatus and the vestibular division of the 8th nerve are small. The flocculo-nodular lobe of the cerebellum, the part which receives direct vestibular fibres, is manifestly atrophic (Jansen, 1953), and the great size of the modern cetacean cerebellum is due mainly to enlargement of the paraflocculus.

It is now generally agreed that the large paraflocculus of modern cetaceans is associated with connexions from the upper levels of the brain stem or cerebral hemisphere (Brodal & Jansen, 1954). Dow (1942) found action potentials in the paraflocculus following stimulation of the cerebral cortex, and Wilson (1933) estimates that 60% of the ponto-cerebellar fibres pass to the paraflocculus in the blue whale. Bearing these facts in mind, it seems that the enlargement of the paraflocculus of cetaceans should be associated with the enlargement of the cerebral hemispheres (certainly a characteristic of all modern representatives) rather than with any paramount need for equilibration. According to Dart and others, the cerebral hemisphere and pons are small in the Archaeocetes. If one accepts these small cerebral hemispheres and pons it is difficult to associate them with an enormously hypertrophied cerebellum.

Dart also postulates that the bulk of the trigeminal fibres ended in the cerebellum, on the basis of his theory that in the zeuglodonts 'equilibration' was subserved by this nerve, and it is in this manner that he associated the alleged enormous development of trigeminus and cerebellum. The suggestion that the trigeminus could take over equilibratory function is purely speculative and direct trigemino-cerebellar fibres are known to be very few in mammals (Brodal, 1954). If they were preponderant in the zeuglodonts then this is just another instance of an almost incredible uniqueness of the neurological make-up of these animals.

A considerable part of current palaeontological opinion concerning the manner of life, affinities and relationships of the Archeocetes is at least partly based on the interpretation of endocranial casts. As a result of the present investigation and discussion one is led to conclude that these casts are unlikely to have reproduced with any degree of accuracy the form of the brain. One could probably go so far as to state that conclusions based upon them are probably worthless, and that far from contributing anything of value towards solving the problems of the morphology of the cetacean brain they are more likely to have clouded the issue. One cannot say that the Archeocete brain was necessarily similar to that of other mammals living at the same time; on general grounds it is likely that it already possessed specializations which may or may not have resembled those of the modern cetacean brain;

one can say, however, that the view that it differed so radically in particular ways from all other mammalian brains is based on highly questionable evidence and improbable speculation. This view, reached from a different approach agrees with that advanced by Marples (1949), whose paper directly led to this investigation.

If, as has been suggested here, the Archeocete casts are to be rejected as misleading, it is pertinent to inquire what one's attitude should be towards the more recent fossil cetacean casts which have been described. As regards *Prosqualodon* (Miocene) it would seem evident that Dart's (1923) interpretation is unlikely to be correct. Marples (1949) compared vascular impressions which he states can be identified on the cast with those evident on casts from recent Odontocetes, and concluded that the cerebrum was larger, and the cerebellum smaller and more ventrally placed. This much more likely interpretation, must, however, in the absence of further evidence, remain no more than a suggestion incapable of being fully proven. Indeed, it is probable that the cast of *Prosqualodon* is no more likely to yield information of value than are the Archeocete casts. As regards the more recent Miocene casts such as that of *Cyrtodelphis sulcatus* (Dal Piaz, 1905) the position is somewhat different. The form of this cast bears a reasonably good resemblance to that of a mammalian brain, and although many of Dal Piaz's more detailed identifications are open to question, his general conclusions by no means stretch credulity unduly. In fact, it is likely that what has been said (p. 541) concerning the casts of the modern smaller Odontocetes should apply equally in this instance, i.e. that the cast probably gives a reasonably true impression of the general proportions of the major parts of the brain with some distortion of detail. It may be noted in passing that the 'cerebellar' portion of this cast bears a close resemblance in shape to the corresponding region of the cast of the porpoise, a fact which strongly suggests the presence of retial tissue in this situation in the former.

It is interesting to note that in the case of both recent and fossil cetaceans, endocranial casts of two types are encountered. On the one hand are those of the Archeocetes, *Prosqualodon*, modern Mysticetes, and the sperm whale, which give a very poor impression of the form of the brain, and on the other the casts of the Miocene Odontocetes and the smaller modern Odontocetes from which a less distorted impression may be gained. It will be noted that this grouping cuts across both time and taxonomy, and that casts of both types are encountered among fossil as well as recent cetaceans. Since the differences in the case of the latter can be attributed to varying degrees of development of the intracranial vascular structures, it is conceivable that a similar state of affairs might have obtained in the fossils, and thus account for the more bizarre appearance of some of the casts without implying an extraordinary development of certain parts of the brain. Even among the Archeocetes as a group, marked differences in appearance occur. These have been interpreted by Dart (1923) as indicating progressive trigeminal specialization and degeneration. Might they not be equally well accounted for by attributing them to differences in the degree of development of retial tissue in different members of the group?

SUMMARY

1. Endocranial casts of living cetaceans can at best give only a very general impression of the form and proportions of the brain. Where retia mirabilia are particularly well developed, e.g. as in Mysticeti, such casts are positively misleading if regarded as reasonable replicas of the brain.

2. Certain features common to the endocranial casts of the Archeocetes (as well as *Prosqualodon*) and those of recent Mysticetes, strongly suggest the presence of retia in the former group. It is suggested therefore that these casts are unlikely to be of any assistance towards elucidating the true form of the Archeocete and Squalodont brains, and that previous views concerning the size of the cerebellum and trigeminal apparatus in these forms are highly speculative and based upon inadequate evidence. Certain neurological considerations would appear to reinforce this view.

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REFERENCES

Brodal, A. (1954). Afferent cerebellar connections. In *Aspects of Cerebellar Anatomy*, by Jansen, J. and Brodal, A. Oslo: Johan Grundt Tanum Forlag.

Brodal, A. & Jansen, J. (1954). Structural organisation of the cerebellum. In *Aspects of Cerebellar Anatomy*, by Jansen, J. and Brodal, A. Oslo: Johan Grundt Tanum Forlag.

Dal Piaz, G. (1905). Sugli Avanzi di *Cyrtodelphis sulcatus* dell' arenaria di Belluno. Pt. 2. *Palaeontogr. ital.* **11**, 253–280.

Dart, R. A. (1923). The brain of the *Zeuglodontidae*. *Proc. zool. Soc. Lond.* pp. 615–654.

Dow, R. S. (1942). Cerebellar action potentials in response to stimulation of the cerebral cortex in monkeys and cats. *J. Neurophysiol.* **5**, 121–136.

Edinger, T. (1955). Hearing and smell in cetacean history. *Mschr. Psychiat. Neurol.* **129**, 37–58.

Elliot Smith, G. E. (1903). The brain of the *Archeoceti*. *Proc. Roy. Soc.* **71**, 322–331.

Flynn, T. T. (1947). Description of *Prosqualodon davidi* Flynn, a fossil cetacean from Tasmania. With a note on the microscopic tooth structure by T. Thornton Carter. *Trans. zool. Soc. Lond.* **26**, 153–197.

Gervais, P. (1871). Remarques sur l'Anatomie des Cétacés de la division des Balénidés. *Arch. Mus. Hist. nat. Paris*, **7**, 65–146.

Jansen, J. (1953). Studies on the cetacean brain. The gross anatomy of the rhomboncephalon of the fin-whale (*Balaenoptera physalus*, L.). *Hvalråd. Skr.* **37**, 1–35.

Kellogg, R. (1928). The history of whales—their adaptation to life in the water. *Quart. Rev. Biol.* **3**, 29–76, 174–208.

Kellogg, R. (1936). A review of the Archaeoceti. *Publ. Carneg. Instn*, **482**, 1–366.

Marples, B. J. (1949). Two endocranial casts of cetaceans from the Oligocene of New Zealand. *Amer. J. Sci.* **247**, 463–471.

Stromer, E. (1908). Die Archaeoceti des ägyptischen Eozäns. *Beitr. Paläont. Geol. Öst.-Ung.* **21**, 106–177.

Walmsley, R. (1938). Some observations on the vascular system of a female fetal finback. *Publ. Carneg. Instn*, **496**, 107–178.

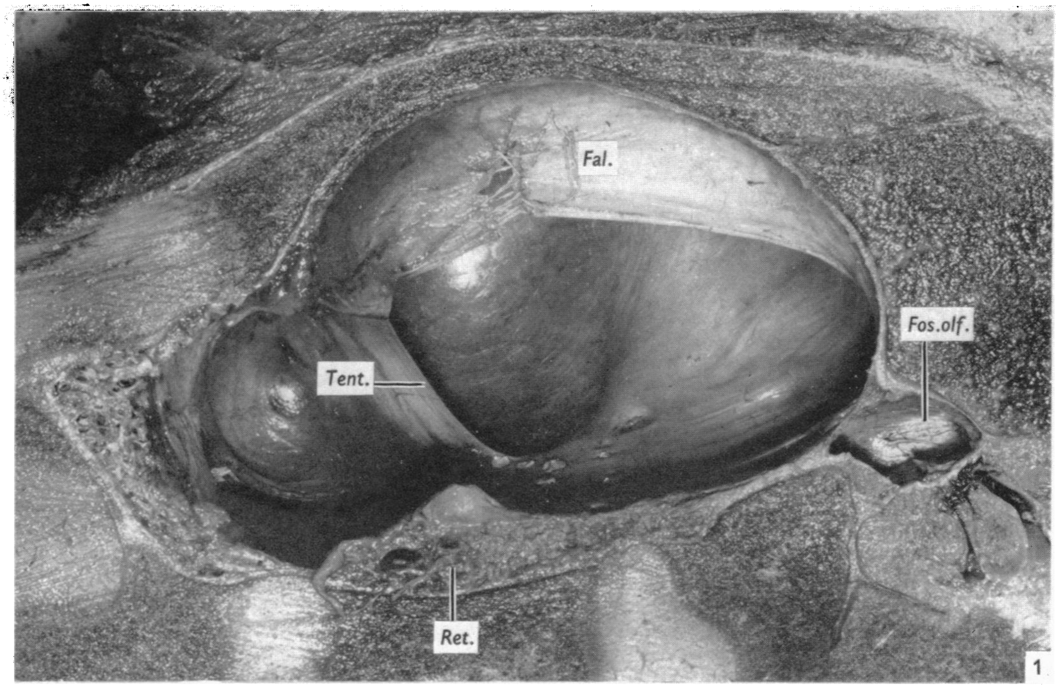
Wilson, R. B. (1933). The anatomy of the brain of the whale (*Balaenoptera sulfurea*). *J. comp. Neurol.* **58**, 419–480.

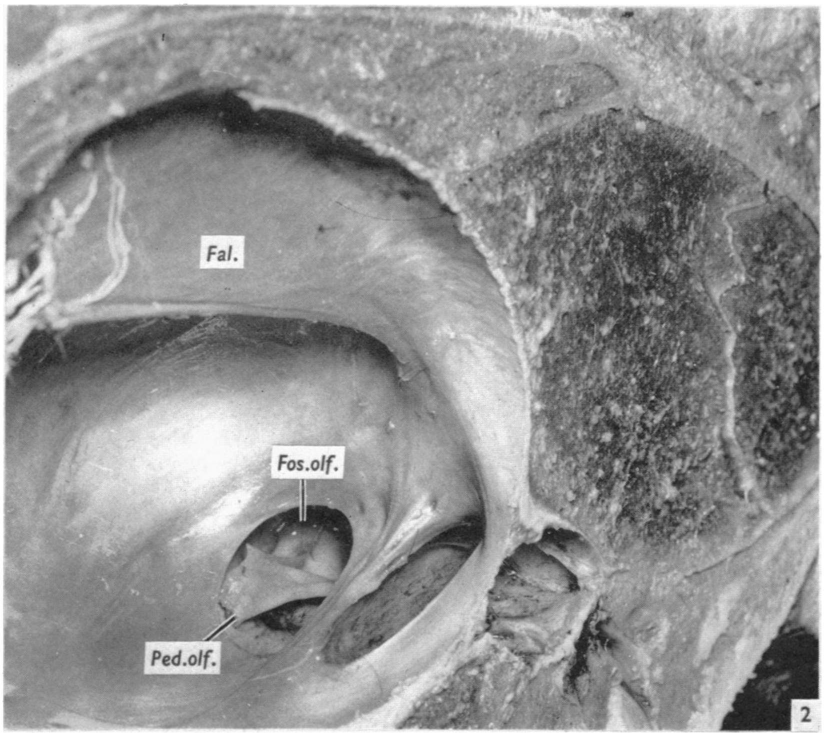
EXPLANATION OF PLATE

Abbreviations: *Fal.*, falx cerebri; *Fos.olf.*, olfactory fossa; *Ped.olf.*, olfactory peduncle; *Ret.*, rete mirabile; *Tent.*, tentorium cerebelli.

Fig. 1. Parasagittal section of skull of foetal fin-whale (*Balaenoptera physalus*) to show relation of olfactory fossa to main endodural space. ×, about 0·6.

Fig. 2. Anterior portion of endodural space of the same specimen viewed from above and behind. There is considerable disproportion between the size of the olfactory peduncle (enveloped in membranes) and that of the olfactory fossa. About natural size.





BREATHNACH—OBSERVATIONS ON ENDOCRANIAL CASTS OF RECENT AND FOSSIL CETACEANS

(*Facing p.* 546)