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NATURAL BRAIN CASTS OF MERYCOIDODONTS.

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Endocranial casts of some genera of the merycoidodonts (oreodonts) are occasionally found in an excellent state of preservation. Since the brain is one of the most conservative elements of any organism, it is therefore of great value in affording clues to relationships and to the evolutionary history of the various groups of fossil forms.

Among the merycoidodonts, some of the brain forms already figured and described are of *Merycoidodon culbertsonii* Leidy, chiefly by Leidy,[7] Black,[1,2] and Moodie[10]; *M. gracilis* Leidy, by Bruce,[3] Gervais,[5] Gratiolet,[6] and Moodie;[10] and *Merycochoerus* by Moodie;[9,10] while an excellent, although somewhat brief, summary of the present knowledge of fossil brain casts has recently been published by Edinger.[4]

In the Marsh Collection of the Yale Peabody Museum there are about twelve endocranial casts of *Merycoidodon*, nearly all exceptionally well preserved. However, they do not add to our knowledge of this group.

In the present paper there is added a description of the endocranial cast of the brain of *Eporeodon socialis* Marsh and of *Promerycochoerus superbus* (Leidy), of Upper Oligocene, or possibly, in the case of the latter, of Lower Miocene age.

Professor Marsh[8] in 1886 (page 64, figure 73) reproduced a dorsal view of the natural brain cast of *Eporeodon socialis* Marsh, shown in position with the skull outlined around it. No description was given either then or subsequently. This figure is herewith reproduced as Fig. 1, while a lateral view recently drawn may be seen in Fig. 2. This brain cast, Cat. No. 13118a Y. P. M., was found at Scott's Bluff, Nebraska, in 1874, in strata of Upper Oligocene age, with the cotype skeletons, Cat. Nos. 13118 and 13119 Y. P. M., of *Eporeodon socialis* Marsh.

The size is about that of *Merycoidodon culbertsonii* Leidy, and its closest correspondence, among living forms, is with the brain of the pig (*Sus*). The general relations show that the olfactory bulbs were large and placed well in advance of the cerebrum, so that the anterior (transverse) portion of the anterior sulcus rhinalis is wide and deep. The cerebrum is

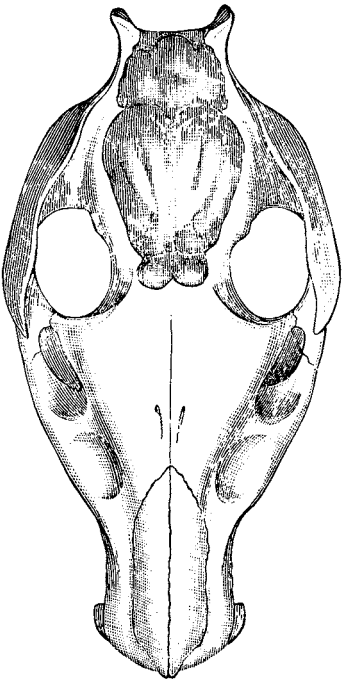

Fig. 1. Dorsal view of endocranial cast of *Eporeodon socialis* Marsh, Cat. No. 13118a Y. P. M. About 2/5 nat. size. After Marsh.

medium-sized and rather low, its crest being just in advance of the transverse fissure. The superior surface slopes gradually forward, not after the abrupt manner of the slope in the horse, but rather more like that of the pig. The maximum transverse and longitudinal measurements of the cerebrum are practically the same, 42 and 43 millimeters respectively. When viewed from above the shape of this portion of the brain is that of an apically truncated pyramid, whose base is near the transverse fissure.

The cerebellum is comparatively large and, with the medulla oblongata, rises slightly higher than the crest of the cerebrum. The medulla oblongata is well preserved for a short distance beyond the posterior edge of the cerebellum.

The rhombencephalon segment of the brain comprises the medulla oblongata, the pons, the cerebellum, the anterior cerebellar peduncles, and the anterior medullary velum, or the fourth ventricle. The basilar part of the entire brain is nearly straight, the only important downward departure being the ventral expansion of the pyriform lobe.

The medulla oblongata is dorsally concealed by the cerebellum, and the posterior portion of the vermis is broken away. The restiform bodies are present in part and are very smooth.

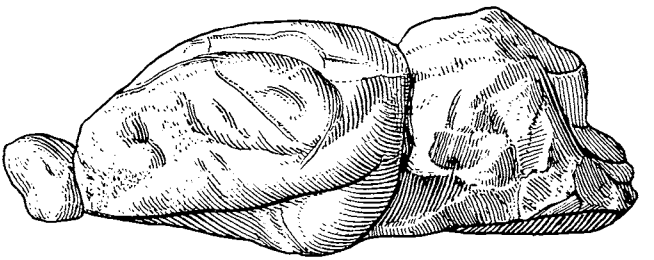

Fig. 2. Lateral view of endocranial cast of *Eporeodon socialis* Marsh. Nat. size. Drawn by R. Weber.

These bodies diverge very close to the cerebellum and form a triangular-shaped, very shallow depression, the posterior part of the rhomboid fossa. The dorso-lateral groove is fairly prominent. A portion of what appears to be the tuberculum cinereum is present. The ventral surface is transversely convex. The fissura mediana ventralis is partially visible, its position being concealed, except for the anterior part where it terminates in a well marked and deep pit, the foramen caecum. The corpus trapezoideum is missing or but very faintly indicated. Its size was evidently quite small. The pyramid is indistinctly visible, as well as the sulcus intermedius ventralis. The pyramidal tracts are small, as in all ungulates. The roots of nerves V, VII, and VIII are plainly marked. The remaining parts of the ventral surface are not sufficiently clear to afford an accurate description. This is also true of the pons. The shape of the medulla oblongata in vertical section is quadrilateral and has nearly the same diameter vertically and trans-

versely, 15 mm. and 18.5 mm. respectively, and it appears to be somewhat compressed downward from above.

The cerebellum is separated from the cerebrum by a deep, wide transverse fissure, which housed the tentorium cerebelli. It overlies the position of the pons, and its superior surface rises somewhat higher than the crest of the cerebrum. Its greater diameter is transverse. The postero-superior part of the postero-median lobule of the vermis cerebelli, or middle segment of the three major divisions of the cerebellum, is broken away, but its crest was probably situated well aft, as in *Merycoidodon.* Instead of being curved in a semicircular form, as in the brains of nearly all recent ungulates, the dorsal outline of the vermis cerebelli in *Eporeodon* is oblong, gently curving anteriorly, and posteriorly probably terminating abruptly vertical. The anterior lobe or lingula does not fill the interval between the cerebellar peduncles as completely as in recent ungulates. The vermis maintains the same diameter, 9.5 mm., throughout its length, thus differing from modern forms in which it usually swells out anteriorly to form nearly all of the anterior part of the cerebellum. The two hemispheres are separated from the vermis by the paramedian fissures. These hemispheres are nearly flat on their dorsal side and in outline, as seen from above, are right triangular, with the sides of the right angle abutting against the vermis and the transverse fissure. The cerebellar peduncles are not well defined.

The mesencephalon or mid-brain consists of the corpora quadrigemina dorsally and the cerebral peduncles ventrally. The former cannot be described from this cast. The cerebral peduncles appear as two large rope-like stalks which lead from the pons through the foramen lacerum anterius with a slight anterior convergence. They represent the maxillary and ophthalmic divisions of the trigeminus or nerve V. The rope- or stalk-like appearance is due to narrow longitudinal grooves in the skull, bearing the internal carotid arteries. The fossa interpeduncularis is plainly visible because the pituitary body, which normally lies close to this fossa, is missing. Since the pituitary gland is connected with this section of the brain by only a hollow tube, the infundibulum, it could hardly be expected that we should find it preserved, except in a most exceptionally perfect natural brain cast. On a basis of the relative proportions of the whole brain and of the position

which, in life, this organ would occupy, its size was probably about that of a small cherry stone.

The prosencephalon or anterior primary segment comprises the optic thalami, hypothalamic tegmenta, pineal body, pituitary body, optic nerves and retinae, cerebral hemispheres, and the olfactory tracts and bulbs, comprising the third and the lateral ventricles. The thalami in this specimen are hidden by the cerebral hemispheres, corpus callosum, and other sections, thus rendering any description of them impossible. The pineal body likewise cannot be described. The pituitary body has been mentioned above. The chiasma opticum is shown as a small downwardly projecting ridge located at the anterior boundary of the interpeduncular fossa. This ridge represents the convergence of the optic nerves.

The cerebral hemispheres form the major part of the brain. As stated above, the shape of the cerebrum from a superior view is that of an apically truncated pyramid, the base of which is immediately anterior to the transverse fissure. Hence the greatest transverse diameter is not just posterior to the middle, as is usual in many recent ungulates, but is nearly at the posterior extremity. The maximum transverse and antero-posterior diameters are nearly the same. The two hemispheres are separated by a thin median ridge, the sagittal sinus, which is forked posteriorly and terminates in the deep and well marked fissura transversa cerebri, separating the cerebrum and cerebellum. The lateral sulcus is deep and prominent, extending longitudinally along the posterior half of the dorsal surface. Its direction is forward and upward, whereas in the pig and horse its direction is backward and upward. The suprasylvian sulcus is deep and convexly curved as seen laterally and bends downward posteriorly toward the posterior rhinal fissure. The ramus lateralis suprasylvii is short and shallow, while the ansate sulcus is short but deeper, and the coronal sulcus is deep and prominent. The ramus descendens suprasylvii is faint but discernible. The praesylvian sulcus is short and shallow. The sulcus rhinalis is deep and prominent, separating the pyriform lobes and other ventral parts of the brain from the rest of the hemispheres. The infero-lateral sinus is shallow and widely open. Ridges formed in the fossae of the middle cerebral arteries may be discerned in advance of the pyriform lobes and below the rhinal fissure. The bulbus olfactorius is oval in outline

and curves upward in advance of the frontal pole of the hemisphere. The bulbs are relatively large and are separated through about one-half of their vertical diameter by the fissura longitudinalis cerebri. On the ventral surface in advance of the optic chiasma lies a deep longitudinal fossa conforming to the basilar part of the skull. Laterally this fossa is bounded by the tuberculi olfactorii and the medial olfactory tracts. The pyriform lobes are relatively large and prominent, as in *Merycoidodon* and in modern edentates, although in the latter this resemblance is wholly of a superficial nature.

MEASUREMENTS OF CAT. NO. 13118a Y. P. M.

	Mm.
Max. length, olfactory bulb to post. part of medulla oblongata, inc.	82.
Max. length of cerebrum	43.
Max. length of cerebellum	25.
Max. width of cerebrum	42.
Max. width of cerebellum	31.5
Max. distance between ventral edges of pyriform lobes	16.
Max. transverse diameter of olfactory bulbs	13.
Max. vertical diameter of cerebrum with pyriform bodies	31.
Max. vertical diameter of medulla oblongata and cerebellum	30.

Eporeodon is considered to have been derived from *Merycoidodon* and is of a later geologic horizon. However, there is very little difference in general size and bodily proportions between the two genera. As we should expect, the skull and brain show a remarkable similarity, the chief difference lying in the possession of auditory bullae in *Eporeodon*. Consequently we see that the evolutionary change has been comparatively slight and is still less reflected in the structure of the brain than in the skeleton.

The gyri of the cerebrum are not especially deep nor numerous. In general terms, the brain cast of *Eporeodon* shows that his reflex centers were well developed, basing this statement on the large relative size of the cerebellum. The large olfactory centers indicate a very acute sense of smell, as in the carnivores. The optic nerves were large, postulating good vision. The cerebrum, all the functions of which are not fully understood, was apparently of no great importance to the animal. In other words, it would seem that the life habits of this genus were based on a complex of reflexes, with very little volitional activity, resulting in creatures mainly of habit and routine.

The cerebrum of the pig (*Sus*) in comparison with that of *Eporeodon* is elongate and oval-shaped, when viewed from

above. The greatest transverse diameter is at the posterior third, thus being similar to, but not exactly like, this area in *Eporeodon.* The cerebellum is much more compressed

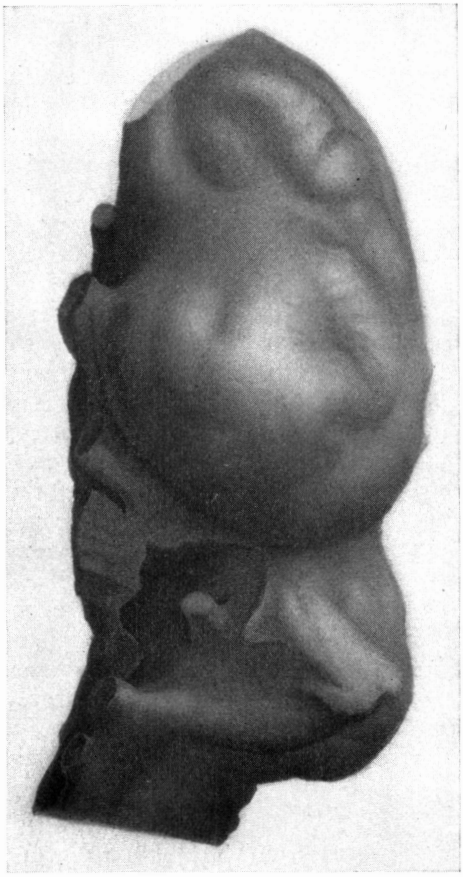

Fig. 3. Lateral view of endocranial cast of *Promerycochoerus superbus* Leidy, Cat. No. 11002 Y. P. M. Nat. size. Drawing made under supervision of Professor Marsh.

in an antero-posterior direction than is that of *Eporeodon,* while the medulla oblongata is similar in both. The vermis cerebelli is relatively large in both genera. The arrangement of the sulci and gyri in *Sus* is more like that of *Eporeodon* and much simpler than that of the brain of the horse or ox.

The olfactory bulbs of *Sus* are also large, and in both genera the tuberculum olfactorium is prominent. The basilar part of the brain of *Eporeodon* is straight, whereas in *Sus* this area is deeply indented from below, in the region of the pituitary body and the roots of the optic nerves, to conform to the configuration of the floor of the skull.

Black[2] has pointed out the ruminant and suilline characters of the skull of *Merycoidodon*, and the same apply to *Eporeodon*.

Our next consideration is that of the natural brain cast of *Promerycochoerus superbus* Leidy, Cat. No. 11002 Y. P. M. This genus and species is from the Upper Oligocene of Oregon and was probably a derivative of the *Eporeodon* stock, although not necessarily a direct descendant.

A major difference lies in the greater size, although the proportions are very similar (Fig. 3). The sulci and gyri are much more shallow on the cerebrum; the transverse fissure is much more open; and the vermis cerebelli is not nearly so prominent as in *Eporeodon*. The medulla oblongata is relatively much larger in *Promerycochoerus*. Its vertical diameter is considerably greater than that of the cerebellum, while in *Eporeodon* the reverse is true. The medulla, as we know, is the continuation into the skull of the spinal cord, and since *Promerycochoerus* is perhaps twice as large as *Eporeodon*, this cord is much larger, but, even taking this into consideration, the medulla of the former is relatively and proportionally much larger. The medulla contains the origin of certain of the spinal nerves and centers largely controlling respiration, circulation, and other important functions, i.e., the somatic and visceral sensory and motor centers are located in this organ.

The ventral surface (Fig. 4) exhibits the nerve endings more clearly than in the endocranial cast of *Eporeodon*. Beginning at the posterior part, the precondylar foramen is well shown, then the foramen lacerum posterius and just above it laterally the internal auditory meatus and the eminence representing the fossa of the petrous bone, next the foramen ovale through which passes the mandibular division of the trigeminus nerve, and then, in advance, the foramen lacerum anterius with the ophthalmic and maxillary divisions of this same nerve (nerve V). The chiasma ridge seems to have been separated

by a thin bony plate which was not apparent in *Eporeodon.* The eminence corresponding to the pituitary fossa is considerably larger than in *Eporeodon,* and the body itself must have been as large as a small cherry. The tuberculi olfactorii are

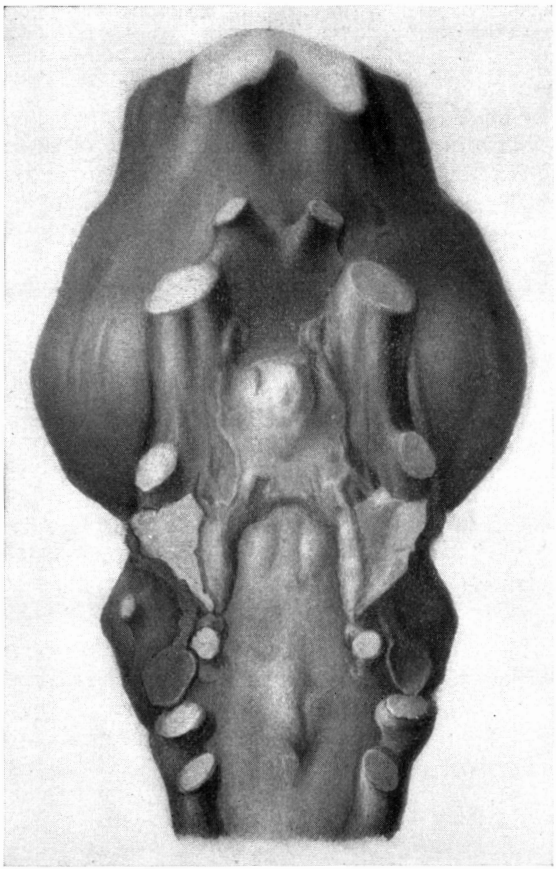

Fig. 4. Ventral view of specimen shown in Fig. 3. Drawing made under supervision of Professor Marsh.

large and separated by a wide shallow fossa, unlike the narrow cleft in *Eporeodon.* Again the depression posterior to the pituitary eminence is shallow, wide and flat, without the deep pit seen in the other genus.

MEASUREMENTS OF CAT. NO. 11002, Y. P. M.

	Mm.
Maximum length, exclusive of olfactory bulb	116.
Maximum length of cerebrum	67.
Maximum length of cerebellum	37.
Maximum width of cerebrum	65.6
Maximum width of cerebellum	47.
Maximum distance between ventral edges of pyriform lobes	33.
Maximum vertical diameter of cerebrum with pyriform bodies	47.5
Maximum vertical diameter of medulla oblongata and cerebellum	44.

In conclusion, it is apparent that the brain of the various groups of oreodonts so far studied did not advance to any appreciable extent, certainly not in the same degree that it did in many of the other contemporaneous groups. This in itself probably was one of the fundamental causes of the extinction of the group. The size of the brain varied, of course, in the different genera, but the proportions remained nearly constant. In *Promerycochoerus* there seems to be an actual retrogression in that the gyri and sulci are much less pronounced than in *Merycoidodon* or in *Eporeodon*. In other words, the cerebrum of *Promerycochoerus* is smoother than in the earlier forms, and yet its actual surface and volume are proportionally no greater. We should expect the opposite to be the case, if the later forms had advanced mentally beyond the ancestral groups.

From Moodie's[10] description of the endocranial cast of *Merycochoerus* it is apparent that the same general proportions prevailed in that genus. It is a more advanced form than any of the preceding, being found in Miocene strata. The gyri, sulci, and other cerebral markings are very similar to those of *Merycoidodon*, according to Moodie, thus affording considerable contrast to the smoother cerebral surfaces of *Promerycochoerus*.

SUMMARY.

From a study of the endocranial casts of these several genera of merycoidodonts, the facts to be emphasized are; first, that the proportions of the various brain elements remained very nearly the same; second, that there was no increase in the cerebrum in the later forms and therefore apparently no great increase in volition or intelligence; third, that *Promerycochoerus* shows actual retrogression in that the cerebral surfaces were relatively smoother and the medulla oblongata larger than in the other forms studied; and, fourth,

that there seems to be conclusive evidence that this group lacked the mentality, especially in the later forms, to discover ways and means of adapting its members to the changing geologic conditions which took place in the Miocene and Pliocene.

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