Cranial Morphology of Some Oligocene Artiodactyla

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By FRANK C. WHITMORE, JR.

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CRANIAL MORPHOLOGY OF SOME OLIGOCENE ARTIODACTYLA

By Frank C. Whitmore, Jr.

ABSTRACT

A study of the cranial morphology of three Oligocene Artiodactyla (*Merycoidodon*, *Poebrotherium*, and *Leptomeryx*), based largely on serial sections, reveals many cranial characteristics found only in the most primitive Recent mammals.

The Oligocene genera had several cranial veins which indicate that these artiodactyls were not far removed from a primitive insectivore-like ancestor. They had a well-developed internal carotid artery in contrast to the Recent Artiodactyla, very few of which retain this structure. The cranial circulation pattern of the Oligocene forms shows an evolutionary tendency in the Artiodactyla to abandon endocranial for extra-cranial paths.

Other primitive characteristics are the lateral partitions of the pituitary fossa (representing the primitive side wall of the skull) and large temporal venous sinus in *Merycoidodon*, and the simple pneumatic sinus system in all three genera.

The selenodont Artiodactyla exhibit an evolutionary trend toward the amastoid skull pattern now found only in bunodont families.

The subarcuate fossa of the pars petrosa of the periotic bone in the Tylopoda has a peculiar shape, constant in the suborder and differing from the condition in other selenodont Artiodactyla. This is added evidence that the Tylopoda must have separated from other artiodactyl lines of evolution no later than the middle Eocene. The simpler subarcuate fossa of *Merycoidodon* and *Leptomeryx* indicates their alliance with the suborder Pecora.

On the basis of cranial structure, the family Hypertragulidae is divided into the subfamilies Hypertragulinae and Leptomerycinae, both of which existed from the early Oligocene through the early Miocene.

INTRODUCTION

The Artiodactyla, or "even-toed ungulates", form one of the largest and most varied of the orders of mammals. They are today near the acme of their development; their distribution is world-wide and they include in their numbers the pigs, peccaries, hippopotami, camels, deer, giraffes, cattle, sheep, goats, antelope and the tiny chevrotains of Asia and Africa.

An examination of the Artiodactyla reveals several characteristics in common: hoofs, a more or less herbivorous diet, and a tendency toward a foot structure in which the weight rests mainly upon two toes of each foot. This mesaxonic type of foot, whose axis runs between the third and fourth toes, has given rise to the name of the order. Two other morphological peculiarities possessed by all the Artiodactyla are not externally visible but are very important. The first of these is the absence of the third trochanter of the femur, an eminence on the posterior side of the bone which serves as a muscle attachment in some mammals. The second and even more useful criterion is the presence upon the astragalus of a distal roller surface (for articulation with the navicular and cuboid bones) in addition to the proximal roller surface present in other mammals.

Many years of study by zoologists have clarified the relationships among the many living artiodactyl groups, diverse as they are; but paleontology has revealed a tangle of problems in the many extinct artiodactyl genera. The relationships of the extinct genera with each other and with modern types are often only a matter of conjecture; their ancestry is unknown. Therefore many uncertainties exist concerning the stratigraphic and paleoecologic significance of many extinct genera and species. Their morphology is, of course, less well known than that of the modern Artiodactyla. It is the purpose of this study to examine in detail the cranial anatomy of some of these extinct genera, because endocranial characteristics are probably nonadaptive, that is, unlikely to be influenced by the environment, and therefore useful in determining the taxonomic position of groups of animals.

These studies were made with the aid of serial sections, a technique used by several workers in the study of fossil skulls (Darrah, 1936; Dunkle, 1940; Graham, 1933; Romer, 1937; Simpson, 1933, 1936; Sollas, 1916, 1920; Sollas and Sollas, 1914; Walton, 1928). The skull can be oriented in relation to the grinding surface to produce sections in any desired direction; the most common types of sections used are the sagittal (parallel to the plane of bilateral symmetry of the skull) and the frontal (at right angles to this plane). The studies presented here are based upon frontal sections. The sectioning technique used has been described in a previous paper (Olsen and Whitmore, 1944).

Simpson, and Dr. E. H. Colbert of the American Museum of Natural History; Dr. E. C. Olson of the University of Chicago; Dr. Glenn L. Jepsen of Princeton University, and Mr. J. Leroy Kay of the Carnegie Museum, for the loan of specimens for comparison.

Mr. F. Russell Olsen, of the Museum of Comparative Zoology, Harvard University, has by his skill made possible the construction of the apparatus used in this work.

Apparatus used in preparing some of the specimens for study was purchased by a grant from the Elizabeth Thompson Science Fund of Harvard University.

CRANIAL MORPHOLOGY OF SOME OLIGOCENE ARTIODACTYLA

Because the serial-section method destroys the specimens used, it was decided to investigate genera of which there are abundant specimens in paleontologic collections. The White River group of Oligocene age has yielded rich collections of mammals for many years, and it was found possible to obtain adequate specimens on which to base a study of the cranial anatomy of the artiodactyls, using three genera representing three different families.

The first of the genera, and that studied in greatest detail, is *Merycoidodon*, a member of the extinct family Merycoidodontidae (Oreodontidae), the "ruminating hogs" of Joseph Leidy. *Merycoidodon* is the most abundant mammalian genus in Tertiary deposits. The second genus studied is *Poebrotherium* (of the Camelidae) an ancestor of the modern camels; and the third is *Leptomeryx*, of the family Hypertragulidae, which are diminutive, hornless, deerlike animals.

These three families comprised most of the selenodont population of the Oligocene epoch of North America; besides it was felt that they would reveal the stage of cranial evolution reached by the selenodont Artiodactyla in Oligocene time.

CRANIAL MORPHOLOGY OF *MERYCOIDODON*

This study is based primarily upon serial frontal sections of a skull of *Merycoidodon culbertsonii* (Leidy), M. C. Z. 6450, from the White River group (Oligocene) of northeastern Wyoming (figs. 14, 15).

Sections were made at 2mm intervals through most of the skull. Posterior to the foramen ovale (fig. 15), an interval of 0.5mm was used because of the complexity of the structures in this region.

In the following description, special attention is paid to those parts of the cranial bones which do not appear upon the surface of the skull, to the relations among those bones, and to the impressions left upon them by blood vessels and nerves. The external characteristics of the skull, as shown in figures 14 and 15, furnish points of reference in locating the features of the internal anatomy.

The brains of *Merycoidodon*, and also those of *Poebrotherium* and *Leptomeryx*, have already been described in the basis of natural casts (Black, 1921; Tilney, 1931; Moodie, 1922; Bruce, 1883), and are not discussed in the present study.

BONES OF THE SKULL
OCCIPITAL

The occipital bone contains, or is bounded by, several foramina for the passage of blood vessels and
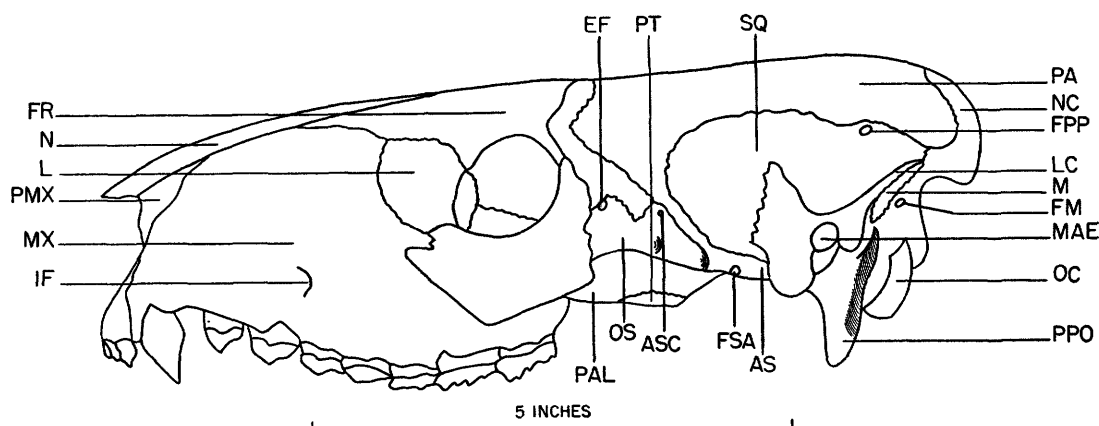
FIGURE 14.—*Merycoidodon culbertsonii* (Leidy). Lateral view, about × ½. Modified after W. B. Scott. Part of zygomatic arch removed.

AS, alisphenoid bone.
ASC, anterior opening of sinus canal.
EF, ethmoidal foramen.
FLA, foramen lacerum anterius.
FM, mastoid foramen.
FPP, postparietal foramen.
FR, frontal bone.
FSA, anterior subsphenoid foramen.

IF, infraorbital foramen.
L, lacrimal bone.
LC, lambdoid crest.
MAE, external auditory meatus.
MX, maxilla.
N, nasal bone.
NC, nuchal crest.
OC, occipital bone.

OS, orbitosphenoid bone.
PA, parietal bone.
PAL, palatine bone.
PMX, premaxilla.
PPO, paroccipital process.
PT, pterygoid bone.
SQ, squamosal bone.

nerves. The mastoid foramen (fig. 14, *FM*) is the exit of a canal which, passing posteriorly through the occipital bone, carries the mastoid emissary vein. This vessel is one of several draining blood from the great system of sinuses of the squamosal bone and the neighboring surface of the dura mater of the brain; it drains blood from the transverse venous sinus of the dura mater to the occipital vein.

Another vessel draining venous blood from the cranium, in this instance from the base of the brain,

ran in the petro-basilar canal (figs. 15, 21, *PBC*). This vessel was a large one, the inferior petrosal sinus. The venous blood flowed posteriorly into it from the cavernous sinus of the base of the brain. The sinus left the petro-basilar canal and extended posteriorly in a groove near the lateral edge of the basioccipital. Before leaving the petro-basilar canal, however, the inferior petrosal sinus gave off a branch, the condyloid vein, which extended posteriorly in a groove on the endocranial side of the basioccipital. It left the skull through the
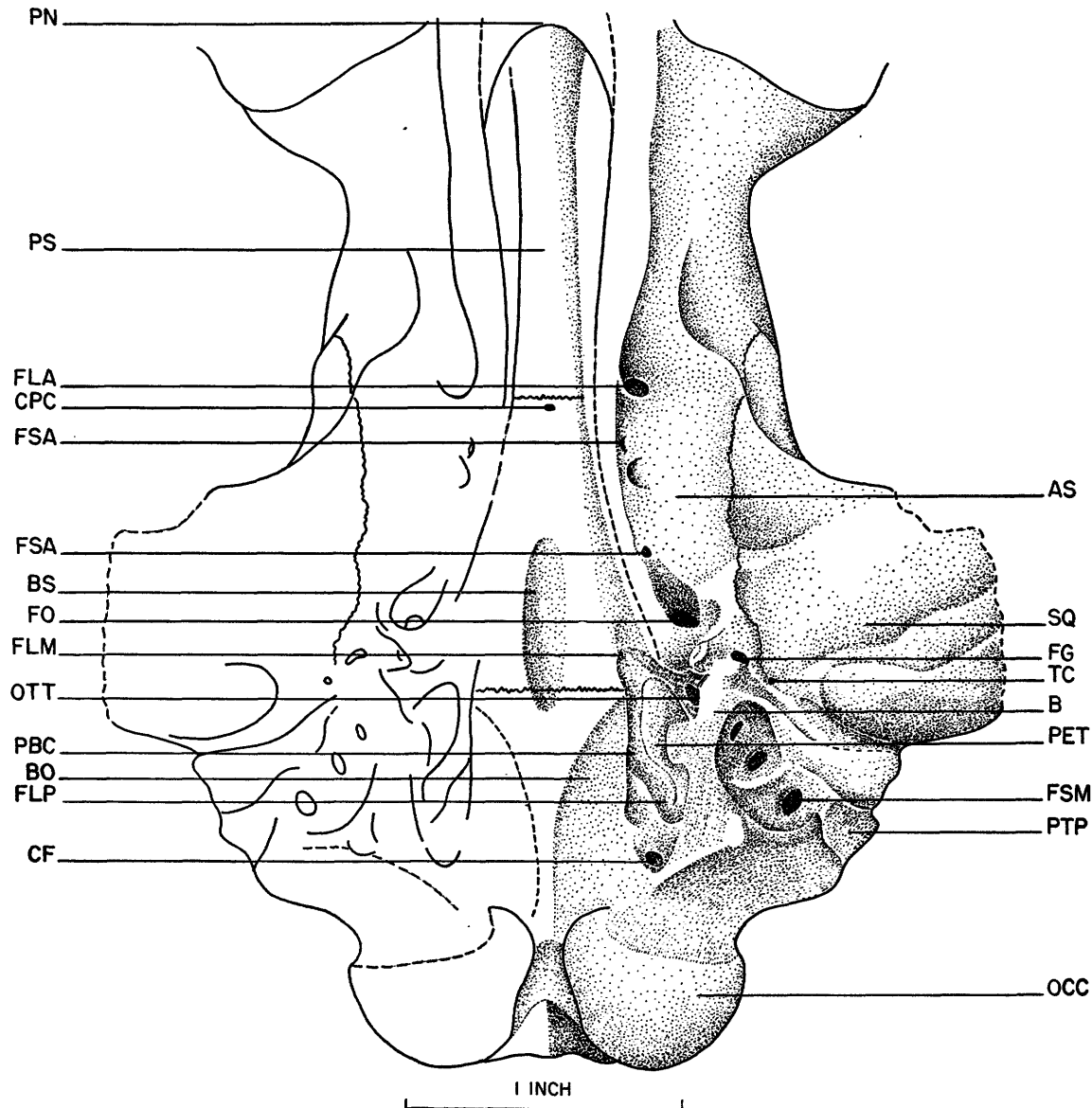
FIGURE 15.—*Merycoidodon culbertsonii* (Leidy), M. C. Z. 5808. Ventral view of basis cranii. Zygomatic arch missing.

AS, alisphenoid bone.
B, tympanic bulla.
BO, basioccipital bone.
BS, basisphenoid bone.
CF, condylar foramen.
CPC, opening of craniopharyngeal canal.
FLA, foramen lacerum anterius.
FLM, foramen lacerum medius.

FLP, foramen lacerum posterius.
FO, foramen ovale.
FSA, anterior subsphenoid foramina.
FSM, stylomastoid foramen.
FG, fissura glaseri.
OCO, occipital condyles.
OTT, ostium tympanicum tubae.
PBC, petrobasilar canal.
PET, pars petrosa of periotic bone.

PN, palatonarial border.
PS, presphenoid bone.
PTP, posttympanic process of squamosal bone.
SQ, squamosal bone (zygomatic arch broken).
TC, opening of temporal canal.
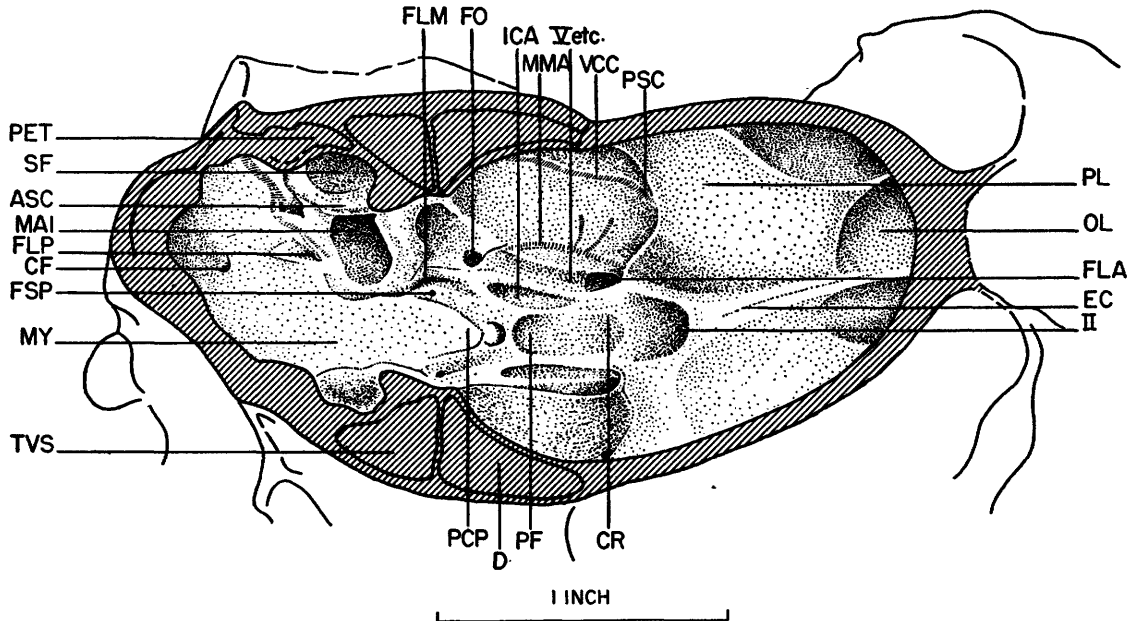
FIGURE 16.—*Merycoidodon culbertsonii* (Leidy), M. C. Z. 6447. Internal view of basis cranii, viewed from above, posteriorly and to the right.

ASC, ridge containing anterior semi-circular canal.
CF, condylar foramen.
CR, chiasma ridge.
D, diplöe in squamosal bone.
EC, ethmoidal crest.
FLA, foramen lacerum anterius.
FLM, foramen lacerum medius.
FLP, foramen lacerum posterius.
FO, foramen ovale.

FSP, posterior subsphenoid foramen.
ICA, groove for internal carotid artery.
MAI, internal auditory meatus.
MMA, middle meningeal artery.
MY, myelencephalic base.
OL, olfactory lobe.
PCP, posterior clinoid processes (broken).
PET, pars petrosa of periotic.
PF, pituitary fossa.

PL, floor of pyriform lobe.
PSC, posterior opening of sinus canal.
SF, subarcuate fossa.
TVS, temporal venous sinus.
VCC, groove for vena collateralis cerebri.
II, opening of canal for optic nerve.
V etc., groove for nerves III, IV, (1, 2) and VI.

condylar foramen (figs. 15, 16, *CF*) and extended posteriorly as the occipital vein. The twelfth cranial nerve also found its exit through the condylar foramen.

A few millimeters antero-lateral to the condylar foramen is the foramen lacerum posterius (fig. 15, *FLP*), from which emerged the inferior cerebral vein, one of the posterior branches of the inferior petrosal sinus, and a tributary of the internal jugular vein (fig. 17).

The ninth, tenth and eleventh cranial nerves also passed through the foramen lacerum posterius.

BASISPHENOID

The basisphenoid bone is much thicker dorso-ventrally than is the basioccipital. The result of this is that, while the basicranial axis is horizontal when viewed from below, the brain itself shows a sharp ventral bend at the level of the posterior clinoid processes (fig. 16, *PCP*), which arise from the posterior end of the pituitary fossa. Thus the bases of the pyriform lobes of the brain and of the pituitary fossa (fig. 16, *PL*, *PF*) are in essentially the same plane, while the myelencephalic base dips posteriorly at an angle of about 20° from the plane of the base of the cerebral hemispheres. This is a marked difference from any modern ungulates, in which the base of the brain slants

gently backward in essentially one plane from the optic nerves to the foramen magnum.

The foramen lacerum medius, whose anterior border is formed by the basisphenoid, transmitted blood both to and from the cranial cavity. The internal carotid artery, the chief blood vessel nourishing the brain, entered the cranium here after having passed through the auditory bulla on its way from the common carotid artery. Inside the skull, this artery traveled anteriorly in a groove in the basisphenoid bone, immediately lateral to the pituitary fossa (fig. 22, *ICA*). At the anterior end of the basisphenoid, at the level of the chiasma ridge (fig. 16, *CR*), the artery branched into smaller arteries that traversed the surface of the cerebral hemispheres. The grooves for these arteries were observed in the dissected braincase shown in figure 16, but not in the sections, because they lie about in the plane of sectioning. Posterior to the pituitary fossa is a groove in which ran the posterior communicating artery, which connected the internal carotid arteries of both sides.

In the same groove as the internal carotid artery (fig. 16, *ICA*) ran the cavernous sinus, a venous vessel. The cavernous sinus received venous blood from the region of the face via the orbital venous plexus. This blood entered the cranium through the foramen lacerum
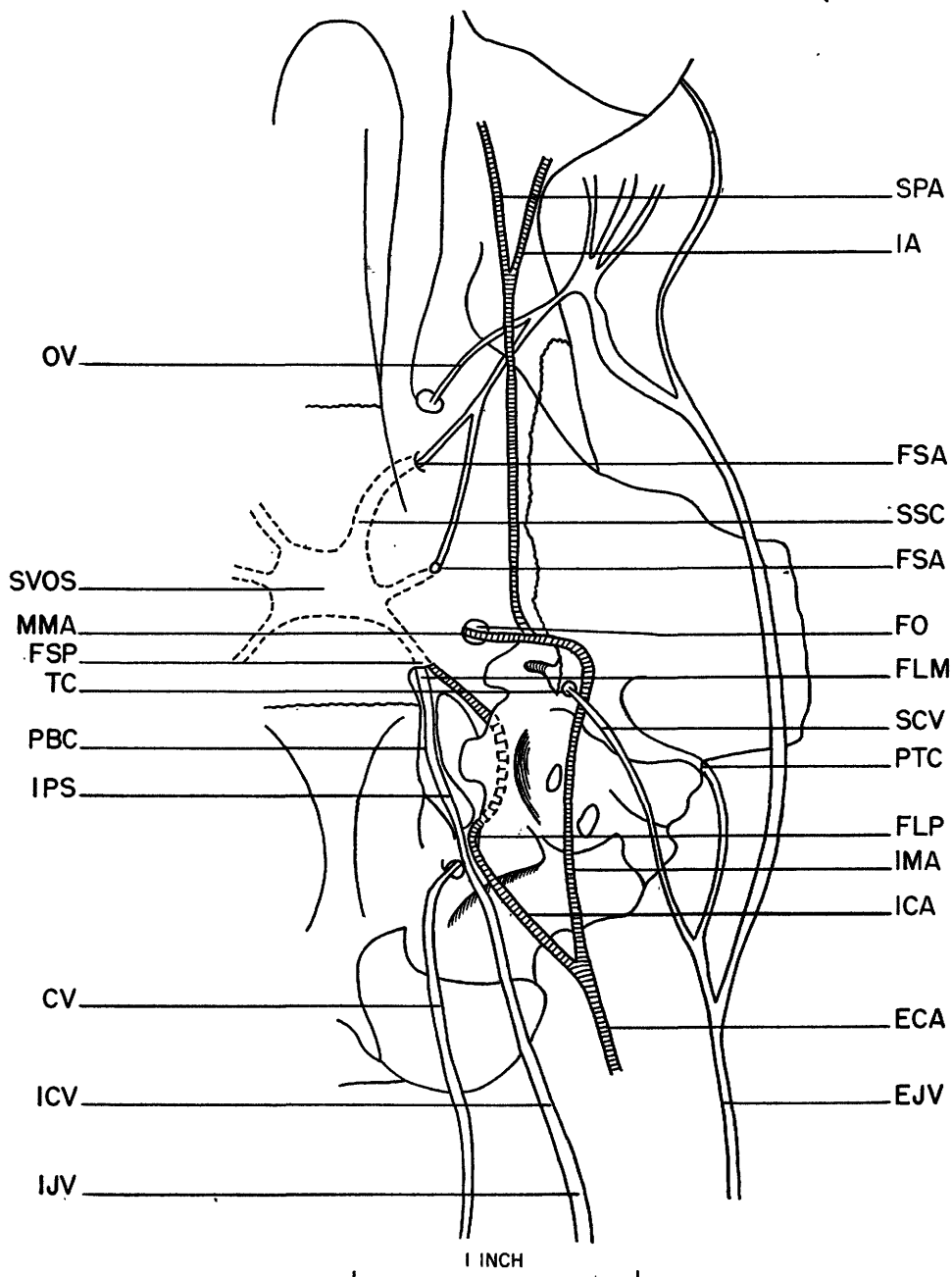
FIGURE 17.—*Merycoidodon culbertsonii* (Leidy), M. C. Z. 5808. Ventral view of basis cranii, with restoration of blood vessels.

CV, condyloid vein.	*IA*, infraorbital artery.	*PBC*, petrobasilar canal.
ECA, external carotid artery.	*ICA*, internal carotid artery.	*PTC*, opening of posterior branch of temporal canal.
EJV, external jugular vein.	*ICV*, inferior cerebral vein.	
FLM, foramen lacerum medius.	*IJV*, internal jugular vein.	*SCV*, superior cerebral vein.
FLP, foramen lacerum posterius.	*IMA*, internal maxillary artery.	*SPA*, sphenopalatine artery.
FO, foramen ovale.	*IPS*, inferior petrosal sinus.	*SSC*, subsphenoid canal.
FSA, anterior subsphenoid foramen.	*MMA*, middle meningeal artery.	*SVOS*, sinus venosus ossis sphenoidalis.
FSP, posterior subsphenoid foramen.	*OV*, ophthalmic vein.	*TC*, foramen jugulare spurium.

anterius (figs. 15, 16, *FLA*). After making its exit through the foramen lacerum medius, it passed posteriorly into the inferior petrosal sinus (see above). Posterior to the pituitary fossa, the cavernous sinuses of the two sides were connected by the intercavernous sinus, running in the same groove as the intercarotid artery.

The pituitary fossa (sella turcica), which is surrounded on three sides by grooves for blood vessels, is an extremely shallow depression in the cranial surface of the basisphenoid bone (fig. 16, *PF*). It thus resembles that of the modern Tylopoda and differs from that of the Bovidae, which is very deep. This lack of excavation of the basisphenoid bone is compensated,

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however, by the presence of a vertical lamina of bone upon either side of the sella turcica. These laminae are of delicate construction and cannot be found in fragmentary skulls or natural brain-casts. They are well shown, however, by serial sections (fig. 22, *LCP*). At their highest point they are 4 mm. high. Their antero-posterior length is about 10 mm. Posteriorly they decrease gradually in height until the level of the braincase floor is reached; anteriorly they are continuous with the posterior root of the orbitosphenoid bone (fig. 22, *POS*). No structures of this sort are found in living Artiodactyla; the nearest parallel to them occurs in the embryonic stages in *Lepus*, in which the posterior clinoid processes extend along the sides of the sella turcica in the same way (Voit, 1909, p. 549). Voit agrees with Gaupp (1902, 1906) that these lateral laminae represent the taenia interclinoidalis of the chondrocranium, and thus are a remnant of the primitive lateral wall of the braincase. This thesis is supported by de Beer (1937, p. 388).

In many recent mammals (*Canis*, among others) the taenia interclinoidalis is represented by the anterior and posterior clinoid processes. The condition observed in *Merycoidodon*, in which these two vestigial processes are joined, is an earlier stage in the reduction of the primitive lateral wall of the skull.

Just lateral to the groove for the internal carotid artery and the cavernous sinus is a deeper groove, which runs from the region of the foramen ovale to the foramen lacerum anterius. It served as a course for the forward passage of the oculomotor (III), trochlear (IV), abducens (VI), ophthalmic (V_1), and maxillary (V_2) nerves, which originate on the base of the brain posterior to the pituitary fossa. The third branch of the trigeminal nerve passed out of the skull through the foramen ovale (fig. 15, *FO*).

Within the foramen lacerum medius, and perforating its anterior (basisphenoid) wall, careful examination reveals a small foramen, which we shall term the posterior subsphenoid foramen (fig. 16, *FSP*). The serial sections (fig. 22) show that these foramina open into canals (*SSC*) that extend forward and medially in the body of the basisphenoid bone about 6 mm. medial to the foramen ovale (fig. 17, *SSC*). Below and behind the pituitary fossa (directly ventral to the posterior clinoid processes) and about 6 mm. from the foramen lacerum medius the two canals meet in the midline to form a cavity in the thickest part of the body of the basisphenoid (fig. 17, *SVOS*). This cavity is approximately 6 mm. long, 8 mm. wide, and 3 mm. deep in its deepest part.

From its anterior corners spring two canals which diverge sharply and, about 6 mm from the cavity,

emerge into the infratemporal fossa, one on either side of the basisphenoid bone, through a foramen situated from 2 to 5 mm posterior to the foramen lacerum anterius. In some specimens one of the canals divides again just before its emergence into the infratemporal fossa, with the result that two foramina are present between the foramen lacerum anterius and the foramen ovale.

These canals have never before been observed in any Artiodactyla, and they are beyond doubt absent in all living members of the order. A large cavity was noted in the basisphenoid bone of one sagittally sectioned skull of *Sus scrofa*, but it was in no way connected with the exterior. The canals were first observed in serial sections of the skull of *Merycoidodon culbertsonii;* then the basisphenoid bones of three other specimens were dissected, and the canals were found in all (fig. 17 *SSC*). Skulls of *Merycoidodon gracilis*, the smallest species of the genus, were too rare in the Museum of Comparative Zoology collections to be dissected; examination of all available specimens, however, showed the presence of foramina which are undoubtedly the anterior openings of these canals. External examination of other skulls of Merycoidodontidae in the Museum collections revealed the presence of the anterior foramina in *Protoreodon* (late Eocene), their doubtful presence in one of five specimens examined of *Cyclopidius* (Miocene) and their undoubted absence in *Merycoides* (early and middle Miocene), *Promerycochoerus* (late Oligocene and early Miocene), *Mesoreodon* (early Miocene) and *Eporeodon* (middle Oligocene to early Miocene). Conclusions reached on the basis of such superficial examination are, of course, questionable. The evidence in this case, however, suggests that such canals are present in the basisphenoid bone only in the more primitive Merycoidodontidae.

Because of the absence of such structures in modern artiodactyls and the lack of knowledge of such details in fossil forms, it was necessary to seek their explanation in the cranial anatomy of other modern mammals. It was then found that similar canals in the body of the basisphenoid bone occur in *Lepus* (Arai, 1907), in some Rodentia (Bovero, 1905) and in Marsupialia and Insectivora (Gregory, 1910). The close correspondence between the bony canals in these groups and those observed in *Merycoidodon* makes it apparent that they are for the transmission of veins.

The anterior foramen (Arai called it "foramen venosum", but anterior subsphenoid foramen seems a more specific term) receives a vein from the orbital venous plexus. The blood travels posteriorly in the subsphenoid canals (a term used by both Arai and Bovero) until it reaches the sinus venosus ossis sphenoidalis (again a term introduced by Arai), which

occupies the above-mentioned cavity in the body of the basisphenoid. Posterior to this the subsphenoid canals resume their course postero-laterally, debouching through the posterior subsphenoid foramen (fig. 17, *FSP*). They empty their venous blood into the posterior end of the cavernous sinus, whence it flows posteriorly into the inferior petrosal sinus.

The subsphenoid canals will be further discussed below, in connection with the venous circulation in *Merycoidodon*.

The foramen rotundum is absent in *Merycoidodon*. As mentioned above, the maxillary nerve undoubtedly found its exit through the foramen lacerum anterius, its usual course in the absence of the foramen rotundum.

Thorpe (1931), in discussing the osteology of *Eporeodon*, states that the foramen rotundum is always present in *Merycoidodon*; this he points out as an expression of the more primitive skull structure of the latter genus. Thorpe's foramen rotundum of *Merycoidodon* is actually the anterior subsphenoid foramen, mentioned above. Identification of the foramen rotundum as a primitive feature is probably unwise in view of Gregory's observations (1910), which seem to indicate that such a foramen is easily formed secondarily by the formation of a cartilage bar separating the maxillary nerve from the other nerves that leave the cranium through the foramen lacerum anterius. This fact does not, however, invalidate the general rule that the presence of many separate foramina in the basicranial region is a primitive condition.

ALISPHENOID

The alisphenoid bone in *Merycoidodon* has its usual mammalian form: it is a plate of bone projecting dorso-laterally from the basisphenoid and forming the median wall of the inferotemporal fossa (fig. 14, *AS*). It ossifies from a center distinct from the basisphenoid, but in *Merycoidodon* it is usually partly, sometimes entirely, fused with it.

The anterior end of the auditory bulla marks the posterior termination of the surface exposure of the alisphenoid bone. The serial sections, however, show that a slim, dorso-ventrally flattened process of the alisphenoid projects posteriorly between the squamosal and petrosal bones (fig. 21, *AS*). It is suturally attached laterally to the squamosal. At the beginning of its posterior course it serves as a roof for the eustachian tube; farther backward it lies dorsal to the anterior portion of the bulla and forms a small part of its roof, separating it from the petrosal.

This backward-projecting process of the alisphenoid is the pars ossea tubae (van Kampen 1905, p. 370). Joined with it and forming the lateral bony wall of the tube is the styliform process of the tympanic bone.

The anterior terminus of the pars ossea tubae is at the point of entry of the eustachian tube into the pharynx; its posterior end is marked by the ostium tympanicum tubae, the gap in the anteromedial wall of the tympanic cavity whereby the eustachian tube enters the middle ear.

The presence of the pars ossea tubae is typical of the ungulates (van Kampen 1905, p. 370). *Merycoidodon* differs from modern Artiodactyla in that the pars ossea does not form a complete bony tube around the eustachian tube. Examination of any modern artiodactyl, such as *Ovis*, explains this difference: in modern Artiodactyla the ventral wall of the bony tube is formed by the expanded medial wall of the tympanic bulla, which has come into contact with the basisphenoid bone. This is also true of most merycoidodont genera in and after the late Oligocene. *Merycoidodon*, in which the bullae are not as yet greatly inflated, may be regarded as primitive in this respect.

Within the pars ossea tubae of the alisphenoid, near its medial border and extending antero-posteriorly, the serial sections (fig. 21, *VCL*) revealed a tiny canal, extending from the foramen lacerum medius to the tympanic cavity. This probably carried a vestigial vein, no longer of any importance in drainage of the blood from the cranium. It will be further discussed in connection with the venous circulation.

Extending antero-posteriorly in a gently curved course along the ventro-lateral side of the pyriform lobes (fig. 16, *VCC*) is a shallow groove in the endocranial surface of the alisphenoid bone, which ends anteriorly in a small foramen (fig. 16, *PSC*) at the transverse ridge separating the pyriform lobe from the tuberculum olfactorium. The serial sections (fig. 22) show that this foramen is the posterior opening of a canal (*SC*) running posteriorly between the alisphenoid and orbitosphenoid from a foramen on the anterior border of the surface exposure of the alisphenoid bone (fig. 14, *ASC*). This canal and the groove which is its continuation are clearly homologous with the sinus canal found by W. K. Parker in the Insectivora (1886). It carries a posterior branch from the orbital venous sinus to join the vena collateralis cerebri. The latter travels around the pyriform lobe and enters the temporal venous sinus system, which drains blood to the external jugular vein. These veins will be further considered below.

PRESPHENOID

The presphenoid bone (fig. 15, *PS*) contains a large cavity, the posterior end of the spheno-palatine sinus, an air cavity which is in direct connection with the nasal passage. This sinus extends posteriorly beneath

the olfactory lobes, reaching as far back as the chiasma ridge (fig. 16, CR).

ORBITOSPHENOID

Within the skull, the anterior portions of the orbitosphenoid bones possess horizontal, flat, medially projecting processes, which meet ventrally at the midline to form the floor of the olfactory fossa of the braincase (fig. 22, OL). Anteriorly these plates are separated, and the ethmoidal crest of the mesethmoid bone (fig. 22, EC) rises between them in the midline. This crest serves as a septum that partly separates the olfactory lobes. Anteriorly, the orbitosphenoid walls of the olfactory fossa are bounded by the cribriform plate of the mesethmoid bone.

ETHMOID AND TURBINALS

The two chief parts of the ethmoid bone, the cribriform plate and the mesethmoid bone, can be observed in serial sections. There also can be seen traces of the three turbinal bones, the ethmoturbinals, nasoturbinals, and maxilloturbinals.

Posteriorly the mesethmoid projects backward into the sphenopalatine sinus below the olfactory lobes. Such a backward extension appears to be common (see Paulli, 1900) in all but the smallest mammals.

In the posterior part of the nasal cavity proper (fig. 23), the mesethmoid forms a complete vertical septum about 1 mm thick. Dorsally it is fused to the frontal bone; ventrally it rests upon the vomer, a very small bone in this part of the nasal cavity.

About 8 mm anterior to the plane of section in (fig. 23), the mesethmoid divides in about its ventral third. From the point of division a thin plate descends laterally on either side, joining the horizontal plate of the maxilla at an angle of approximately 45 degrees. The passage, triangular in cross section, is termed by Paulli (1900, p. 199) the "pneumatic part of the nasal septum." It leads posteriorly directly to the posterior nares, and is the most direct route by which inspired air can travel from the nostrils to the pharynx. A homologous formation can be found in some living mammals, but in many individuals it is hard to detect because of the extremely intricate infolding which has taken place in the mesethmoid walls of the passage, rendering it difficult to distinguish in cross section from other parts of the nasal cavity.

In living Mammalia, the Dicotylidae (peccaries) show the nearest approach to the structure of the pneumatic part of the nasal septum as observed in Merycoidodon (fig. 18). As figure 18 shows, however, even the Dicotylidae exhibit a considerably more complex structure in this region than Merycoidodon. Dicotyles possesses a maxillary extension (I') of the frontal sinus.

A

B

1 INCH
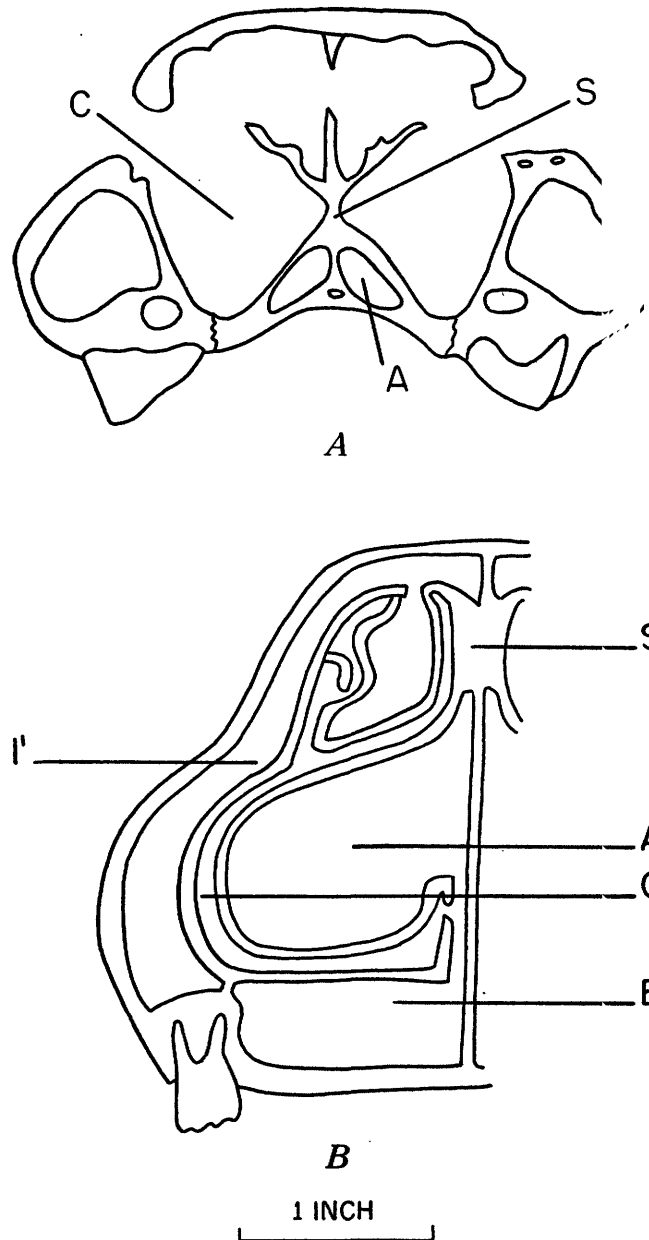
FIGURE 18.—Frontal sections, at the level of the first molar, of the skulls of *Merycoidodon culbertsonii* (Leidy) (M. C. Z. 5450) and *Dicotyles labiatus* (after Paulli, 1900).

A, pneumatic part of nasal septum.
B, sinus in horizontal plate of maxilla.
C, lateral nasal cavity.
I', maxillary extension of frontal sinus.
S, bony nasal septum.

This is typical of the living Non-Ruminantia, and is lacking in *Merycoidodon*.

The two cavities of the nasal passage proper are found both in *Merycoidodon* and in *Dicotyles*, and are labelled *A* and *C* in figure 18. The cavity contained in the pneumatic part of the nasal septum (A) is in *Dicotyles*, in cross-section, about three times the size of that in *Merycoidodon*, due partly to the lateral expansion of its lateral wall, partly to the fact that this

wall springs from a higher point on the nasal septum, or mesethmoid (*S*). This expansion of the pneumatic part of the septum in *Dicotyles* takes place at the expense of the lateral nasal cavity (*C*), which contains the maxilloturbinals, the nasoturbinals and, posterior to the section shown in figure 18, the ethmoturbinals.

The pneumatic part of the nasal septum in *Merycoidodon* may, from its comparative simplicity, be regarded as a primitive stage in the inflation of this septum.

Anteriorly, the walls of the pneumatic portion of the nasal septum diverge and are continuous with the maxilloturbinals.

Still farther anteriorly the mesethmoid is extremely heavily ossified, especially in the area midway between the palate and the roof of the nasal cavity.

In *Merycoidodon culbertsonii*, the mesethmoid forms a complete, strong bony nasal septum as far forward as the level of the first premolar, and continues for about 6 mm. anterior to this as a partial bony septum attached dorsally to the nasal bones. Thus it forms a vertical median septum in the nasal cavity for a distance of 72 mm. in a skull whose anteroposterior length is 190 mm. Comparison with modern osteological material and a search of the literature reveal that very few mammals have a comparable degree of ossification of the mesethmoid. Such ossification was present in the extinct Rhinocerotidae, but has been greatly reduced in their living descendants. The order Pinnipedia also shows as much mesethmoid ossification (Flower, 1885). *Dicotyles* possesses a more completely ossified nasal septum even than *Merycoidodon*. Of 25 peccary skulls examined, all the adult specimens possessed a bony nasal septum reaching at least as far forward as the canine teeth, that is, within 25 mm. of the end of the snout. In *Sus*, the bony nasal septum also terminates anteriorly at the level of the canine tooth; however, the snout extends much farther in advance of the canines than it does in *Dicotyles*.

The conclusion forcibly suggested by these observations is that *Merycoidodon* was, like *Dicotyles*, an animal of rooting habits. This theory is borne out by the fact that the strong nuchal crest of *Merycoidodon* indicates such powerful cervical musculature as is possessed by *Dicotyles* and by *Sus*. The vegetation of the Oligocene epoch seems also to have been such as would allow this mode of life, for it is well known that the early Tertiary flora was primarily lush, and that the increasingly dry climate of the West in Miocene and Pliocene time increased the area occupied by grasslands (Scott, 1937; Chaney and Elias, 1938).

After the Miocene epoch, it is probable that the Merycoidodontidae abandoned their rooting habits, for the nasals are greatly reduced in many genera, eliminating an important snout support. Also, the general snout structure in many later Merycoidodontidae is much weaker than in *Merycoidodon* itself.

The ethmoturbinal bones are extremely delicate, and it is surprising that in the *Merycoidodon* skull sectioned for this study they should have been preserved at all. They are attached not only to the orbital wall of the frontal bone, but also to the frontal where it forms the walls of the supraorbital extension of the nasal cavity (the anterior continuation of the frontal pneumatic sinus). This dorsal extension of the turbinals occurs in all mammals possessing large hollow supraorbital processes of the frontal bone.

Examination of the serial sections reveals that *Merycoidodon* has five ethmoturbinals. Their broken condition makes it impossible to determine whether they are ectoturbinals or endoturbinals except in one of the sections, which shows a strong scroll with a heavy base, easily identifiable as an endoturbinal. This is situated at the base of the orbital wing of the frontal bone, the farthest ventral position which can be occupied by an ethmorturbinal.

The number of ethmoturbinals (five) possessed by *Merycoidodon* is typical of the Ruminantia (Paulli, 1900) as opposed to the Non-Ruminantia, which have six to eight. A striking difference from the modern Ruminantia is, however, the fact that in *Merycoidodon* the strongest ethmoturbinal is the fifth, or basal one, whereas in all modern ruminants the second ethmoturbinal is far stronger.

The only modern mammals showing a strong development of the farthest ventral ethmoturbinal are the Carnivora, which, however, have only four ethmoturbinals.

The serial sections show almost no trace of the nasoturbinal bone, a scroll derived from the ethmoid cartilage and, in most mammals, fused to the frontal and nasal bones along the whole length of the roof of the nasal cavity. The only evidence of the presence of this bone is in two successive serial sections (fig. 18), in which the roots of the nasoturbinals are seen springing dorsally between the dorsal maxilloturbinals and the median nasal septum. Probably the nasoturbinal scroll itself was too delicate to be preserved.

The maxilloturbinal bones are by far the best developed of the turbinals in *Merycoidodon*. They are attached not only to the maxillae but also to the frontal bones, and extend from the level of the lacrimal fossa to the anterior nasal opening, a distance of 60 mm. (fig. 23). They lie anterior to the ethmoturbinals and below the nasoturbinals. The maxilloturbinals are not equally well developed throughout their extent, but

reach their maximum size in the region of the lacrimal fossa and at the anterior end of the nasal cavity.

The maxilloturbinals may be subdivided into several parts. Beginning posteriorly, the first of these to appear are the dorsal maxilloturbinals which, at the level of the lacrimal fossa (fig. 23), spring from the nasal septum. Four millimeters farther forward the dorsal maxilloturbinals are fused to the frontal bones. Thus, for a short distance (and probably for a longer space in life, when the partitions were extended by cartilage) the nasal passage is divided into four passages. Of these, the ventral one (pneumatic part of the nasal septum) was the most direct air passage. The dorsal pasage was most closely concerned with the sense of smell (an important function in *Merycoidodon*, which was macrosmatic; see Black, 1920). The lateral passages, one on either side, were connected through large apertures with the pneumatic sinuses of the maxillary bones, whose mucous membrane lining, together with that of the maxilloturbinals, probably played some part in warming the inhaled air.

Anterior to the region just described, at the level of the anterior part of the lacrimal fossa, appear the ventral maxilloturbinals, which are attached at their lower ends to the horizontal plate of the maxilla, directly above the palatine canal. They form, on either side, a scroll that is rolled in a lateral direction and is not attached to the mesethmoid bone.

Anteriorly these scrolls divide to form a small dorsal scroll in addition to the large lateral one. The bodies of the ventral maxilloturbinals are strong laminae, as much as 2 mm. thick. The scrolls, on the other hand, are delicate, and do not extend as far forward as the stronger laminae which support them.

The bones which we shall term here anterior maxilloturbinals are, in most living mammals, the only maxilloturbinals present. They are the scroll-shaped bones visible in the dried skull as one looks into the anterior nares.

The above observations on the turbinal bones make it plain that, in *Merycoidodon*, they are far more strongly ossified than in any living mammals except, perhaps, *Dicotyles*. This exceptional degree of ossification is undoubtedly a result of the heavy ossification of the mesethmoid cartilage which, in turn, is correlated with the probable rooting functions of the animal.

VOMER

The vomer is a long, slim, trough-shaped bone, which runs antero-posteriorly along the mid-line of the floor of the nasal cavity. Its concave side is dorsal, and in it rests the base of the vertical nasal septum.

In the anterior portion of the nasal cavity, the nasal septum rests between two upturned flanges, one spring-

ing from the medial border of each of the palatine processes of the maxillae. These flanges are in contact along the floor of the nasal cavity, and diverge upward, forming a V-shaped trough like that of the vomer.

This condition is not found in living Artiodetyla, but occurs in the Carnivora.

PREINTERPARIETAL AND INTERPARIETAL

A preinterparietal bone is present in *Merycoidodon*. It is very small and does not appear on the surface of the skull, being covered by the parietal. In the specimen sectioned it occupies the dorsal wall of the braincase for 6 mm. on either side of the midline, just posterior to the fronto-parietal suture. This bone is not found in adult Artiodactyla, but Wilhelm (1924) notes its presence in the young of *Bos*, and it probably occurs in youth in many other genera. In spite of its possession of the preinterparietal, the skull of *Merycoidodon* examined here is an adult, as is shown by the molar teeth.

The interparietal bone, which also appears in the young of modern Artiodactyla, is absent as a separate ossification in the skull here studied.

Not much importance can be attached to the presence or absence of the preinterpartietal and interparietal bones. Their independent existence is characteristic of an early ontogenetic stage in the ossification of the dermal bones of the skull roof, and it is natural that the time of their fusion with the neighboring parietal should be subject to individual variation.

PARIETAL

The parietal bone (fig. 14, *PA*) forms most of the roof of the braincase.

The parietal walls of the braincase are very thick and filled with diploë.

Toward the posterior end of the parietal, between the cerebrum and the cerebellum, the diploë reaches its maximum thickness of about 14 mm. Into this diploë there extends, on either side of the skull, a cavity that is the dorsal extension of the temporal venous sinus (fig. 21, *SVT*), a large blood vessel which is further discussed below.

Within the cranial cavity, the parietal surface directly below the sagittal crest is excavated by an antero-posterior groove that contained the sagittal venous sinus, one of the vessels draining blood posteriorily from the brain and from the face (fig. 22, *SS*).

FRONTAL

The frontal bones (fig. 14, *FR*), by reason of their heavy supraorbital extensions and their postorbital processes, are strongly developed in *Merycoidodon* as in most members of the family Merycoidodontidae.

Anterior to the temporal ridges, the frontals form an almost flat surface between the orbits. On this surface, only a few millimeters on either side of the sagittal suture, are the supraorbital foramina. These are the dorsal openings of the supraorbital canals, which open into the dorsal side of the frontal pneumatic sinus. A continuation of the same canal leads from the ventral side of the supraorbital extension of the frontal sinus, through the lower wall of the supraorbital process, and into the orbit through a foramen in its roof.

As in modern Artiodactyla, the supraorbital canal carried the frontal vein from the orbital plexus (or orbital venous sinus) upward through the frontal pneumatic sinus and out through the supraorbital foramen.

On the suture between the orbital wing of the frontal and the orbitosphenoid bone is situated the ethmoidal foramen (fig. 14, EF). This leads into a canal that runs posteriorly in the orbital wing as far as the cribriform plate. It carries the ethmoidal artery, a branch of the ophthalmic artery.

The ethmoidal foramen and canal are present in all modern Artiodactyla.

Anterior to the postorbital constriction are the farthest posterior extensions of the frontal pneumatic sinus. In cross section, these extensions appear as two small cavities, about 3 mm in maximum diameter, one situated at either lateral limit of the diploic portion of the bone.

In a section just anterior to the posterior nares, the frontal sinuses are considerably larger. Here each is incompletely divided into two parts: a medial cavity, still situated at the lateral edge of the diploë, and a lateral one occupying the supraorbital process. Both these cavities were separated from the olfactory lobes only by a very thin wall of bone, which in this section has been broken through. That the two were originally separated by bone was determined by cleaning the matrix from the inside of the braincase of the skull from which figure 16 was made.

A cross-section of the posterior part of the nasal cavity shows the right frontal sinus, which here occupies the supraorbital process, widely open into the nasal cavity proper.

A narrow extension of the frontal sinus reaches into the anterior processes of the frontals that thrust forward between the nasal and the lacrimal bones. In most sections this is a mere excavation of the frontal wall of the nasal cavity; in one section, however, it is separated from the nasal cavity by a thin wall. This suggests that the part of the frontal sinus immediately posterior to this section may also have been so separated.

SQUAMOSAL

The squamosal bones (fig. 14, SQ) form a large portion of the lateral walls of the braincase; they are thick and heavy, and their relations to the neighboring skull elements are in places rather complex.

The posttympanic process of the squamosal forms the entire posterior wall of the bony external auditory meatus (fig. 15, PTP). In this region the squamosal extends medially a distance equivalent to the length of the external auditory meatus (fig. 19). Its medial surface is the continuation of the inner squamosal surface which, farther dorsally, forms part of the braincase wall. Medial to the posttympanic process, however, this surface is in close contact with the lateral wall of the pars petrosa of the periotic bone (figs. 15, 16, PET).

An anterior extension of the posttympanic process forms the medial part of the ventral wall of the external auditory meatus. The lateral end of this wall (the only part readily visible from the exterior of the skull) is formed by the tympanic portion of the meatus.

In the modern Giraffidae and Cervidae, the posttympanic process forms a part of the posterior wall of the external auditory meatus; but in no modern artiodactyl does it participate in the formation of the ventral wall, as in Merycoidodon. This participation of the squamosal in the ventral wall of the meatus must not be confused with the meatus auditorious spurius, present in some modern and a few fossil Artiodactyla, in which the posttympanic and postglenoid processes meet and fuse below the external auditory meatus of the tympanic bone. The meatus spurius simply covers the wall of the true auditory meatus; it is not a part of it. It is present in the Suidae and some Bovidae, and is very nearly complete in the Hippopotamidae.

The serial sections show the squamosal bone to be thick and filled with diploic tissue, especially in the lower part of its cranial portion (fig. 22) and, to a lesser extent, in the zygomatic process.

In the diploic bone of the cranial wall of the squamosal, dorso-medial to the postglenoid process, lies a cavity, 6 mm long, 6 mm wide, and 15 mm high (fig. 21, SVT). It tapers anteriorly to a blind end, and is surrounded on all but one side by the squamosal. The only other bone abutting upon it is the pars petrosa of the periotic, part of whose lateral side covers a large gap in the medial wall of the cavity.

This cavity has two openings, one into the cranium and another to the exterior of the skull. The former is a gap between the squamosal and the apex of the pars petrosa of the periotic (fig. 20, FJSP). The latter is in the form of a canal that leaves the base of the cavity near its anterior end and extends posteroventrally through the squamosal bone, just medial to the
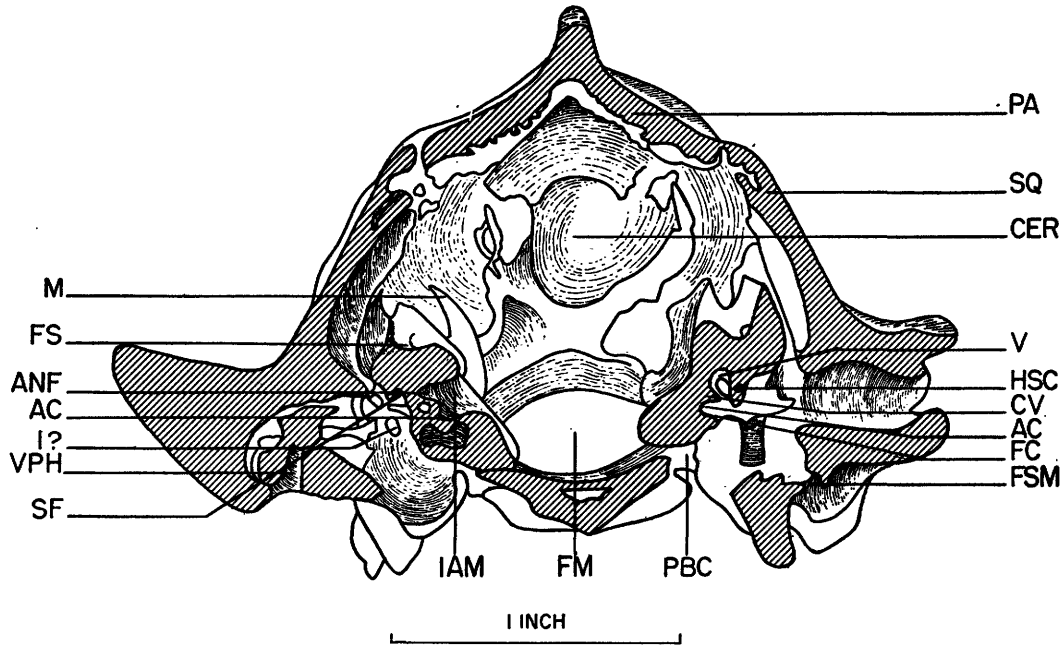
FIGURE 19.—*Merycoidodon culbertsonii* (Leidy). × 1½. Thick section of skull constructed from section M9–31, looking posteriorly into cerebellar fossa from level of auditory bulla.
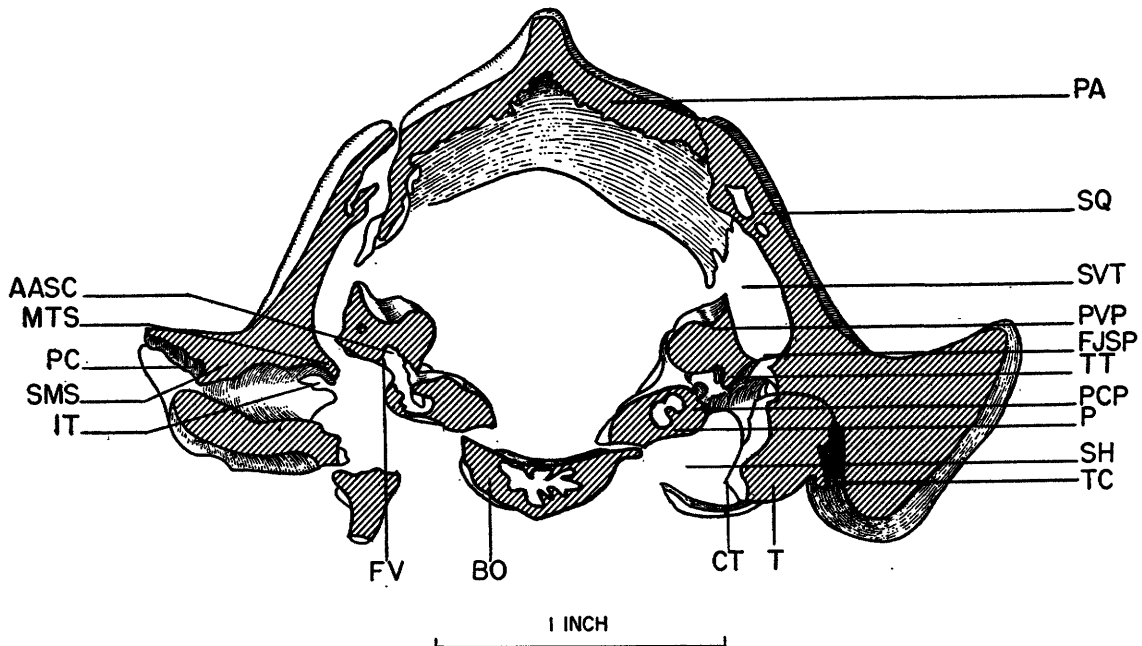
FIGURE 20.—*Merycoidodon culbertsonii* (Leidy). × 1½. Thick section of skull from sections M33–38, in region of auditory bulla, looking anteriorly.

Symbols used in figures 19–23

AASC, ampulla of anterior semicircular canal.
AC, area cochleae.
ANF, area nervus facialis.
AS, alisphenoid.
BO, basioccipital.
BS, basisphenoid.
CER, cerebellum.
CT, crista tympanica.
CV, crista vestibuli.
DMT, dorsal maxilloturbinal.
DP, diploe of parietal bone.

DPS, groove for dorsal petrosal sinus.
DS, diploe of squamosal bone.
EC, ethmoidal crest.
ENT, endoturbinal.
ET, endotympanic.
FC, fenestra cochleae.
FCA, anterior carotid foramen.
FG, fissura glaseri.
FJSP, foramen jugulare spurium primitivum.
FLA, foramen lacerum auterius.
FM, foramen magnum.

FR, frontal.
FS, facial sulcus.
FSM, stylomastoid foramen.
FV, fenestra vestibuli.
HCF, hiatus canalis facialis.
HSC, horizontal semicircular canal.
I?, incus?
IAM, internal auditory meatus.
ICA, groove for internal carotid artery.
IT, incisura tympanica.
LCP, lateral clinoid processus.
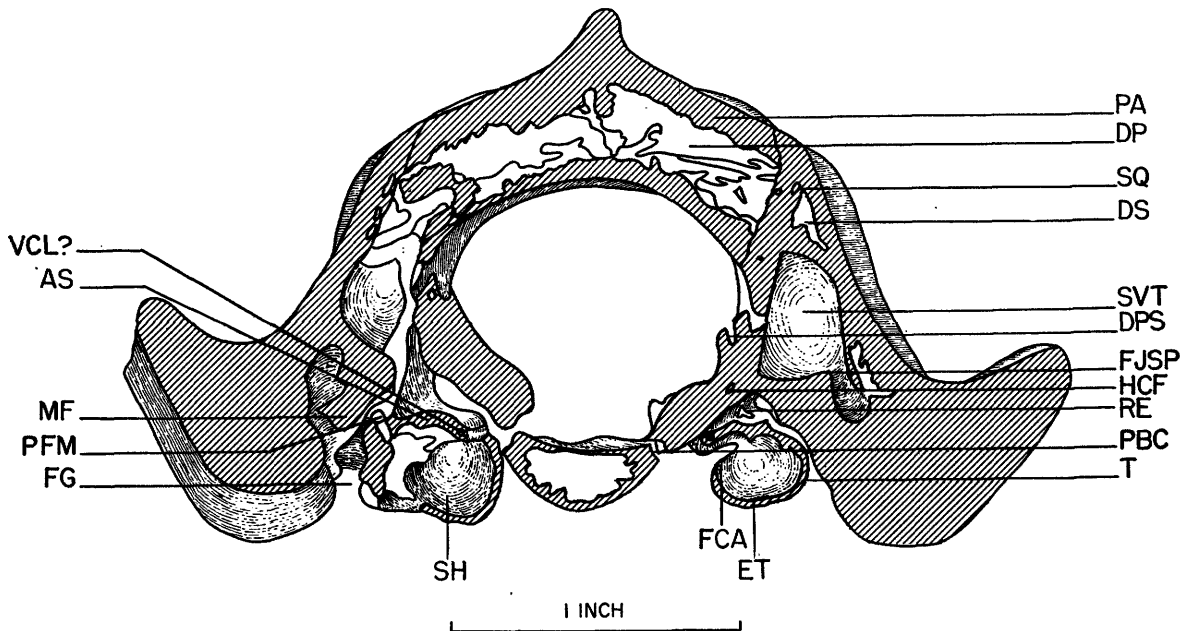
FIGURE 21.—*Merycoidodon culbertsonii* (Leidy). × 1½. Thick section of skull from sections M42–54, at level of post-glenoid processes. Looking anteriorly.
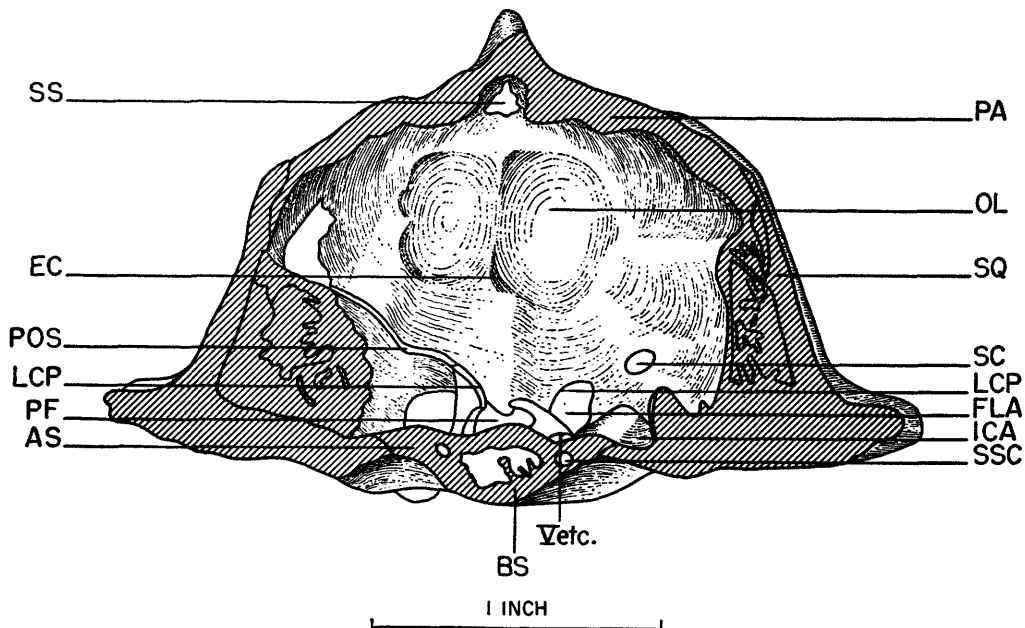
FIGURE 22.—*Merycoidodon culbertsonii* (Leidy). × 1½. Thick section of skull from sections M57–77, looking anteriorly into olfactory lobes.

Symbols used in figures 19–23—Continued

M, pars mastoidea.
M2, second molar.
ME, mesethmoid.
MF, margo fissurae of squamosal.
MTS, margo tympanici of squamosal.
MX, maxilla.
NC, nasal cavity.
O, orbit.
OL, olfactory lobes.
P, promontorium.
PA, parietal.
PAL, palatine.
PBC, petrobasilar canal.

PC, pars cochlearis of pars petrosa.
PCP, posterior clinoid process.
PET, pars petrosa.
PF, pituitary fossa.
PFM, processus folii of malleus.
PME, pneumatic part of mesethmoid.
POS, posterior root of orbitosphenoid.
PVP, pars vestibularis of pars petrosa.
RE, recessus epitympanicus.
SC, sinus canal.
SF, subarcuate fossa.
SH, hypotympanic sinus.

SMS, superficies meatus of squamosal.
SQ, squamosal.
SS, sagittal sinus.
SSC, subsphenoid canal.
SVT, sinus venosus temporalis.
T, ectotympanic.
TC, temporal canal.
TT, tegmen tympani.
V, vomer.
VCL, vena capitis lateralis.
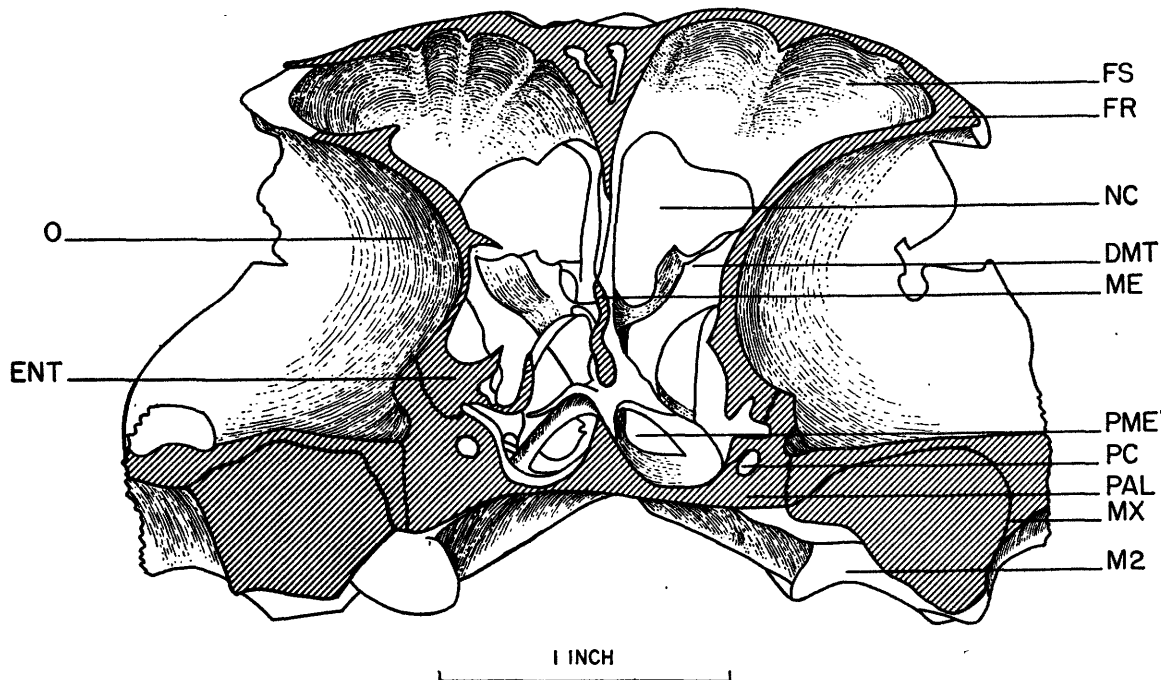VPH, vagina processus hyoidei.
V etc., groove for cranial nerves.

FIGURE 23.—*Merycoidodon culbertsonii* (Leidy).   × 1½.   Thick section of skull from sections M86–120, looking anteriorly through nasal cavity.

postglenoid process (fig. 20, *TC*). The external opening of this canal is through the foramen jugulare spurium (*TC*, fig. 15) between the tympanic bulla and the postglenoid process.

The positions of the outlets of this cavity lead to the conclusion that it must play a part in the venous circulation of the skull, in close connection with the large venous sinuses of the posterior portion of the brain. The canal linking it with the exterior is, from its course and the position of its exit, the temporal canal. This canal, to some degree present in all mammals, carries the superior cerebral vein to its junction with the external jugular vein. The above-mentioned cavity in the squamosal is simply an enlargement of the temporal canal to form a venous sinus similar to those lining the cranial cavity, but surrounded by bone. The term sinus venosus temporalis is here applied to it. Its opening into the cranial cavity is therefore the foramen jugulare spurium primitivum (van Kampen, 1905, p. 382). This corresponds to the foramen through which, in the embryological stages, the superior cerebral vein left the chondrocranium.

The sinus venosus temporalis is found in no living mammals, to the best of the author's knowledge. The only mention of its presence in fossil skulls is by Simpson (1936) who reports the presence of an identical cavity in the squamosal bone of *Oldfieldthomasia*, a primitive notoungulate from the Eocene of Argentina. *Merycoidodon* and *Oldfieldthomasia* are both primitive mammals, with small brains relative to the size

of the skulls and to the area of insertion necessary for their temporal muscles. It is therefore possible that the presence of the sinus venosus temporalis indicates that the small size of the brain and concomitant thickness of the diploic portion of the squamosal bone allowed the superior cerebral vein to attain a large size. Since the exit of the temporal canal (fig. 15, *TC*) is small, the sinus venosus temporalis must have served as a reservoir for venous blood, rather than as a main drainage vessel. Blood probably flowed both into and out of it through the diploic veins. In modern mammals, with their large brains, the dorsal cerebral vein and the temporal canal are of relatively minor importance. The lateral growth of the brain prevents any large veins from taking a dorso-ventral course around it; therefore all venous drainage of the braincase is along its roof (as the mastoid emissary vein) or along its base (as the inferior petrosal sinus).

Another ramification of the cranial venous system is indicated by the presence of a canal running posterolaterally from the temporal canal, between the squamosal and tympanic bones. It has its exit just anterior to the external auditory meatus, through the postsquamosal foramen of Cope (1880). This foramen was not observed by Cope in *Merycoidodon;* it is very small in this genus and absent in some specimens.

The postsquamosal foramen is reported by Cope to occur in the Hippopotamidae, Giraffidae, Cervidae, Antilopidae and Capridae among the Artiodoctyla.

Still another canal of the cranial venous system ex-

tends backward along the suture between the parietal and squamosal bones from the frontal plane of the external auditory meatus to the plane of the condylar foramen), where it emerges upon the surface of the skull through the postparietal foramen of Cope (1880), (fig. 14, *FPP*). These foramina (there may be two or three on either side of the skull) are present in all the Merycoidodontidae but in few living Artiodactyla (the Antilocapridae, Cervidae, Antilopinae and Caprinae).

Other aspects of the squamosal bone will be considered in the discussion of the tympanic region.

TYMPANIC REGION

For purposes of discussion, this complex region will be divided into four parts: (a) the pars petrosa of the periotic bone; (b) the middle ear and surrounding structures, including the auditory bulla; (c) the external auditory meatus; and (d) the pars mastoidea of the periotic bone.

PARS PETROSA OF THE PERIOTIC BONE

This bone, contained entirely within the cranial cavity (fig. 16, *PET*), is composed of two parts. The dorso-lateral portion is the pars vestibularis (fig. 20, *PVP*). It contains the semi-circular canals, and is situated mainly posterior, as well as dorsal to the pars cochlearis (fig. 20, *PCP*).

As has been pointed out, the pars petrosa is in contact laterally with the inner face of the ventral plate of the squamosal, and ventro-medially with the lateral border of the basioccipital. It reaches its greatest size posteriorly; anteriorly its dorsal surface slopes to its termination at a point lateral to the foramen lacerum medius. Just posterior to this point, the pars petrosa gives off a slim process which mounts dorso-laterally along the cranial wall of the squamosal. This is the processus perioticus superior. Its position in *Merycoidodon* is nearer that of modern mammals than that of the Eocene *Oldfieldthomasia* (Simpson, 1936) in which the process projects laterally along the floor of the temporal venous sinus. In *Merycoidodon*, this process is separated from the sinus by about 5 mm. of diploic bone.

Posterior to the processus perioticus superior a groove extends backward along the dorsal crest of the pars petrosa (fig. 21, *DPS*). It is about 3 mm. long, and in life carried the dorsal petrosal sinus, which joined the transverse venous sinus at the foramen jugulare spurium primitivum, thus emptying blood from the midbrain region into the temporal sinus and canal.

Posterior to the above-mentioned groove (figs. 16, 19, *SF*), is a depression, the subarcuate fossa, in the dorsal surface of the pars petrosa. In its center is a small, deep depression.

The subarcuate fossa must have lodged the lobulus petrosus of the flocculus of the cerebellum, and small blood vessels probably passed ventrally from the flocculus into the pars petrosa. Davidson Black (1920, p. 309) notes the similarity of the deep subarcuate fossa of the Merycoidodontidae to that of the Carnivora (such a fossa is also present in Rodentia and many Primates; Bolk et al., 1936, vol. 2, p. 89). Black contrasts this condition with that of the living Artiodactyla, in which, he says, the subarcuate fossa is shallow or absent because of the absence of the lobulus petrosus of the cerebellum. This is true, so far as can be determined by examination of the literature and of dried skulls of recent Artiodactyla, except in the suborder Tylopoda, which have a very large lobulus petrosus. This condition will be discussed further in the section on *Poebrotherium*.

The subarcuate fossa of *Merycoidodon* is smaller and much simpler than that of the living Tylopoda or of the contemporary *Poebrotherium*, and resembles very closely the fossa of the Carnivora. The presence of this fossa seems to indicate that *Merycoidodon*, like the Carnivora, Rodentia, and some Primates, possessed a motor reflex center that is present only in the Tylopoda among modern Artiodactyla.

On the medial side of the parts petrosa is a large opening, the internal auditory meatus (fig. 16, *MAI*). Its course is directly lateral through about two-thirds the thickness of the pars petrosa. At its fundus, the internal auditory meatus divides into two parts (fig. 19). The dorsal branch is the area nervus facialis (ANF), into which passes the seventh cranial nerve on its way to the facial canal. The more ventral of the two branches is the area cochleae (*AC*), through which the duct of the auditory nerve passes to the cochlea.

Backward for a short distance from the internal auditory meatus, the facial canal lies in the pars petrosa. It then passes out of the pars petrosa, through the apertura tympanica canalis facialis, into the cavity of the middle ear, along whose roof it travels as the facial sulcus (fig. 19, *SF*).

From the fundus of the internal auditory meatus extends anteriorly a very narrow canal, the hiatus canalis facialis (fig. 21, *HCF*). It issues into the cranial cavity through a foramen on the anterior slope of the pars petrosa. It carries the nervus facialis superficialis major, an anterior branch of the facial nerve, which extends anteriorly as the nerve of the pterygoid canal to the sphenopalatine plexus and ganglia. It is the equivalent of the palatine nerve of lower vertebrates.

The facial sulcus, a groove on the ventro-lateral side

of the pars petrosa (fig. 19, *SF*), is the posterior continuation of the facial canal. It extends posteriorly about 4 mm., attaining such a depth (about 3 mm.) that it might be called a recessus epitympanicus. Regardless of the terminology employed, however, this sulcus almost certainly carried the facial nerve, as it ends posteriorly directly above the stylomastoid foramen, the exit of the facial from the tympanic cavity (fig. 19, *FSM*).

The central cavity of the pars vestibularis of the pars petrosa (fig. 20, *PVP*) is the vestibule (fig. 19, *V*). This cavity has in its ventro-lateral wall an opening, the fenestra vestibuli or fenestra ovalis, through which it communicates with the cavity of the middle ear.

In the anteroventral wall of the vestibule is a small circular depression, the recessus sphericus. This, in life, contained the saccule of the inner ear.

The posterior end of the vestibule is just anterior to the level of the stylomastoid foramen (fig. 15, *FSM*). Ventrally, a horizontal crest projecting laterally from the body of the pars petrosa separates the vestibule from the fenestra cochleae, which lies below it. This crest is the crista vestibuli (fig. 19, *CV*).

Within the vestibule are several openings, leading to other parts of the cavity of the internal ear. One of these, near the posterior termination of the vestibule and on its medial side, is the opening of the aquae-ductus vestibuli, a bony canal running postero-laterally and opening upon the medial surface of the pars petrosa. This canal transmits the endolymphatic duct, which ends, in modern mammals, in a cul-de-sac between the layers of the dura mater.

Nothing need be said here concerning the semicircular canals. As is shown by the work of Turkewitsch (1933), the only differences that they exhibit within a mammalian order are those of dimensions, and such measurements must be based upon a large suite of specimens.

The lateral side of the pars vestibularis of the pars petrosa is an eminence, the prominentia canalis lateralis, which is closely applied to the squamosal bone. Its lower edge forms the tegmen tympani (fig. 20, *TT'*).

The tegmen tympani, as the serial sections show, is simply a projection of the pars vestibularis over the tympanic cavity. In *Merycoidodon* this projection is far greater than in living Artiodactyla, with the result that the tegmen forms almost the entire roof of the tympanic cavity, whereas in modern artiodactyls it rarely forms more than half.

When the pars petrosa of *Merycoidodon* is compared with that of *Ovis*, which is typical of modern Ruminantia, it becomes apparent that the tegmen tympani of the former is borne relatively much lower on the lateral side of the bone. This is a reflection of the fact that, in *Merycoidodon*, the pars vestibularis of the pars petrosa is a more important element in the side wall of the braincase than in modern Ruminantia. The same comparison seems to hold with the Non-Ruminantia.

The total antero-posterior length of the tegmen tympani is approximately six millimeters; it extends posteriorly from the level of the foramen jugulare spurium (figs. 15, 20, *TC*) to that of the stylomastoid foramen (fig. 15, *FSM*). The tegmen tympani is absent in the anterior half of the roof of the tympanic cavity, which is formed by the squamosal (fig. 21). This is a rare condition in modern mammals, being found, according to van Kampen (1905, p. 345) only in the Marsupialia and Chiroptera.

Medial to the tegmen tympani, directly anterior to the facial sulcus, and below the hiatus canalis facialis, lies a short, deep groove in the pars petrosa (fig. 20). This is the sulcus in which is inserted the tensor tympani muscle.

From the posterior side of the fenestra cochleae (fig. 19, *FC*) a small canal runs posteromedially through the bone. This is the aquae-ductus cochleae which, like the aquae-ductus vestibuli, formed a path for interflow of lymph between the inner ear and the subarachnoid space between the arachnoidea and the pia mater of the brain.

The lower part of the lateral wall of the pars petrosa, which forms most of the medial wall of the middle ear cavity, bulges somewhat into that cavity. The bulge, which is caused by the first coil of the cochlea, is known as the promontorium (fig. 20, *P*). The promontorium in *Merycoidodon* is conspicuous, but not so much so as in *Oldfieldthomasia* (Simpson, 1936). No data are available as to the relative degrees of prominence of the structure in modern mammals.

The cochlea, as revealed in frontal section, appears to possess 2½ spiral turns, the same number as in modern ungulates.

MIDDLE EAR AND SURROUNDING STRUCTURES

Of the various cavities (usually termed "sinuses" and "recesses") of the middle ear, the one underlying the auditory ossicles is the largest in *Merycoidodon*. This cavity occupies the hollow auditory bulla (fig. 15, *B*), and is thus surrounded on all but the dorsal side by the inflated tympanic bone. It is known as the hypotympanic sinus (fig. 20, *SH*). The upper boundary of the main part of the hypotympanic sinus lies at the level of the chain of auditory ossicles. Anteriorly, the sinus extends about 4 mm beyond the ossicles (fig. 21, *SH*), and for a short distance is entirely surrounded by the tympanic bone; behind this point the tympanic is incomplete dorsally and the horizontal

part of the squamosal forms the roof of the sinus. The dorsal gap in the tympanic bulla is the "tympanicum-defekt" (Bondy, 1907). It is larger in *Merycoidodon* than in modern Artiodactyla.

In spite of the fact that *Merycoidodon* has extremely small auditory bullae, the hypotympanic sinus is rather large. This is, of course, because the bulla is entirely hollow, with no filling of cancellous bony tissue such as occurs in many Artiodactyla, including the later merycoidodonts. The sinus is shown at its maximum size in figure 21 (*SH*).

In the Mammalia, the middle ear cavity may extend into two cavities dorsal to the auditory ossicles, known as the epitympanic recess and the epitympanic sinus.

The epitympanic recess is the cavity lying immediately dorsal to the auditory ossicles. It is enclosed in the ventral wall of the skull (usually between the pars petrosa and squamosal) and composes the dorsal portion of the tympanic cavity proper.

The epitympanic sinus, on the other hand, is an accessory cavity of the tympanic cavity. Where present it lies in the squamosal or the pars mastoidea, and opens into the epitympanic recess.

The epitympanic recess in *Merycoidodon* is a cavity about 2 mm. deep and 3 mm. long, situated dorsal to the deepest portion of the hypotympanic sinus (fig. 21, *RE*). Its roof consists of three elements. The middle element is the slanting lateral surface of the pars petrosa of the periotic, and the lateral element is the facies epitympanica of the squamosal bone. This portion of the squamosal lies medial to the postglenoid process and forms the floor of the temporal venous sinus.

The facies epitympanica is in contact with the pars petrosa; between them lies a small bone whose identity is in doubt, but which is probably a piece broken from the tegmen tympani of the pars petrosa. This is the third element of the roof of the epitympanic recess.

The living Artiodactyla in which the epitympanic recess most closely resembles that of *Merycoidodon* are the Cervidae and Camelidae. In both these families the recess is small, and roofed over as much by the pars petrosa as by the squamosal, but in the Suidae and Bovidae it is roofed mainly by the squamosal. The recess in the Tragulidae resembles that of *Merycoidodon* except that the tympanic bone, in addition to the squamosal, forms its lateral boundary. This is because the "tympanicumdefekt" in the Tragulidae is smaller.

The epitympanic sinus has less functional importance than the recess, and is correspondingly more varied. In many mammals it is absent, but in others, such as the Notoungulata (Simpson, 1936) it attains enormous size.

In *Merycoidodon*, the epitympanic sinus is absent, the part of the squamosal above the epitympanic recess being a solid plate containing no cavities. This is also true, so far as could be determined, of all the living Artiodactyla.

In addition to the large cavities of the middle ear, there is in *Merycoidodon* a very small cavity, the incisura tympanica (fig. 20, *IT*), which lies just dorsal to the tympanic membrane. Its lateral wall is formed by the facies epitympanica of the squamosal, and its roof by an overhanging process from that bone. Ventrally it is bounded by the tympanic bone. In the fossil it is open medially into the epitymanic recess, but in life this opening was covered by a membrane (the membrana shrapnelli or pars flaccida), a non-functional part of the tympanic membrane. Its lower border is the dorsal part of the sulcus tympanicus, the part of the tympanic ring in which the tympanic membrane was held and stretched taut.

The position of the incisura tympanica in *Merycoidodon* is the same as that in the Suidae. Data concerning its condition in the Ruminantia are incomplete, but it is known to be large in the Cervidae, and absent in the Camelidae and Tragulidae.

The most striking external feature of the ear region (although smaller in *Merycoidodon* than in most mammals) is the auditory bulla (fig. 15, *B*). The most anterior part of the bulla is, as in all other animals with small or medium-sized bullae, the styliform process. This slim anteriorly projecting extension is applied closely to the lower surface of the squamosal and, in *Merycoidodon*, branches at its anterior end into a medial and a lateral arm, each about 1 mm. long. It formed the lateral wall of the ostium tympanicum tubae (see above), and probably, as in living Artiodactyla, provided the origin for the levator veli muscle.

In the living Cervidae and Bovidae the styliform process is present and probably performs the same functions as in *Merycoidodon*. In the living Camelidae the anterior wall of the bulla forms the lateral covering of the ostium tympanicum tubae, and there is only a suggestion of a styliform process. No process at all is present in *Tragulus* or the Suidae.

Just posterior to the styliform process, the bulla of *Merycoidodon* is slightly notched for the reception of the eustachian tube, which passes medial to it.

The bulla in *Merycoidodon* is a low inflated hemisphere of bone situated between the postglenoid process and the basioccipital. Its longest dimension is the antero-posterior one, and it does not project so far ventrally as does the postglenoid process. Laterally it overlaps ventrally the facies epitympanica of the squamosal; medially it is separated from the basioccipital

by a broad groove that in life held the inferior petrosal venous sinus (fig. 15, *PBC*). Posteriorly, the bulla narrows to a ridge, which is suturally attached to the antero-lateral side of the paroccipital process of the occipital bone (fig. 14). Here it forms a part of the medial wall of the articulation for the tympanohyal bone. In contrast with some modern Artiodactyla, the bulla is not fused to the pars petrosa of the periotic, and there is a gap between the two through which the internal carotid artery probably passed (fig. 21, *FCA*).

The bulla of *Merycoidodon* is smaller in proportion to skull size than that of any modern artiodactyl, although the Cervidae and Giraffidae have a small bulla. In most of the living genera there is a tendency to develop a large bulla, that is laterally compressed and reaches ventrally well below the postglenoid process.

The presence of a gap between bulla and basioccipital is correlated with the size of the bulla, and occurs among modern Artiodactyla only in the Cervidae and Giraffidae. No such direct explanation can be found, however, for the presence or absence of fusion of the bulla to the pars petrosa of the periotic. The two are independent of each other, as in *Merycoidodon*, in the Suidae, Hippopotamidae, Camelidae, and Caprinae. In the Suidae alone of these the two bones are in contact. They are fused together in the Bovidae and in some Cervidae. The most obvious explanation of these various conditions in living Artiodactyla is the degree of development of the internal carotid artery. In living Artiodactyla this is present in the late embryological stages but degenerates and becomes small or disappears entirely in the adult. Thus the presence of a gap between bulla and pars petrosa and its size, if present, may depend upon the ontogenetic stage at which the internal carotid disappeared or ceased to function. This is borne out by the fact that in Suidae, where a gap is present, the artery is functional, though greatly reduced. This is also true in *Camelus*.

One of the chief problems concerning the auditory bulla has been that of its composition. It was first thought to be formed by one bone, the tympanic (more properly ectotympanic). Later it was discovered that another bone, the entotympanic, sometimes participates in the formation of the bulla. This is a neomorph in mammals, and ossifies relatively late in ontogeny. As its name indicates, it forms, if present, the medial side of the bulla. More and more instances of the presence of the entotympanic in the wall of the bulla are being brought to light (van Kampen, 1905; van der Klaauw, 1931).

It has been the consensus of opinion that in the Artiodactyla (with the very doubtful exception of the Suidae: Parker, 1886) the bulla is composed entirely of the ectotympanic.

The composition of the bulla remains largely a matter of opinion, as stated above, because any elements forming it are in almost every case completely fused together in the adult stage. In a few, however, a suture is present in the adult, indicating the presence of both ectotympanic and entotympanic. Such a suture was found in the sectioned skull of *Merycoidodon* (fig. 20, *T* and fig. 21, *ET*) and in 1 of 12 other *Merycoidodon* skulls examined. It thus seems possible that this genus is an exception to the previously accepted rule as to the composition of the bulla in the Artiodactyla.

The auditory bulla is bordered by several openings in the skull. Among these is the fissura glaseri (figs. 15 and 21, *FG*), through which the chorda tympani branch of the facial nerve passes from the tympanic cavity on its way to anastomose with the mandibular branch of the trigeminal nerve (see Goodrich, 1930, p. 462). Into the inner end of the fissura glaseri projected the processus folii of the malleus, a remnant of Meckel's cartilage.

The fissura of *Merycoidodon* is completely surrounded by the ectotympanic bone except for a space of about 2 mm on its antero-lateral side where the squamosal participates in its wall. This surface of the squamosal (fig. 21, *MF*) is known as the margo fissurae. This condition differs from that in living mammals in which the entire lateral wall of the fissura glaseri is formed by the margo fissurae of the squamosal.

Between the ventral crest of the external auditory meatus and the posterior crest of the tympanic bone, which is suturally attached to the paroccipital process, lies the vagina processus hyoidei, the pit in which is lodged the cranial end of the tympanohyal bone. It lies posterior to the inflated part of the bulla, and is separated by a low ridge of the occipital bone from the stylomastoid foramen, which lies posterior and slightly lateral to it (fig. 15, *SM;* the vagina processus hyoidei is not labelled in this figure).

The vagina is seen, in section, to be an excavation in the thick portion of the ectotympanic bone that forms a part of the external auditory meatus (fig. 15, *VPH*).

In the modern Artiodactyla, as in *Merycoidodon*, the vagina processus hyoidei is well separated from the stylomastoid foramen. In the living families their swollen bullae grow around the tympanohyal, making the vagina deeper and more conspicuous. In some families this posterior inflation of the bullae is so great that the tympanohyal springs from the side of the bulla instead of behind it (Tragulidae, Bovidae). The inflated bullae may entirely surround the tympanohyal, forming a pit. This is true of the Tragulidae, Giraffidae, Camelidae, and some of the Bovidae.

The stylomastoid foramen (figs. 15 and 19, *FSM*) lies just posterior to the vagina processus hyoidei. It opens into the extreme posterior end of the tympanic cavity, separated from the foramen lacerum posterius by the paroccipital process. *Merycoidodon* thus resembles the living Ruminantia and the early Tertiary bunodonts (presumably Non-Ruminantia) (Colbert, 1938). It differs from the living Non-Ruminantia, in which the stylomastoid foramen is confluent with the foramen lacerum posterius.

The facial nerve leaves the tympanic cavity through the inner opening of the stylomastoid canal. This is the foramen stylomastoideum primitivum. Here the chorda tympani leaves the facial nerve and goes forward into the tympanic cavity.

EXTERNAL AUDITORY MEATUS

This bony tube (fig. 14, *MAE*; fig. 15), which connects the middle ear with the exterior of the skull, has already been discussed in part under the consideration of the squamosal bone, which forms its dorsal, posterior and part of its ventral wall.

The remainder of the meatus is formed by the ectotympanic bone; in other words, it is a direct lateral extension of the auditory bulla. The meatus is much more heavily ossified than the bulla. Its course from the exterior is inward and slightly downward for most of its length. At the medial border of the postglenoid process, it turns slightly anteriorly and enters the bulla.

At its entrance into the bulla, the ectotympanic wall of the meatus projects about 5 mm. into the tympanic cavity (fig. 20, *CT*). This projection is called the crista tympanica of the meatus (Bondy, 1907; Simpson, 1936). The tympanic cavity extends laterally both anterior and posterior to the crista; such an extension is known as a recessus meatus. This is also present in all living Artiodactyla.

The medial termination of the external auditory meatus is an almost complete ring (it is open for a few millimeters dorsally) upon which was stretched the tympanic membrane (fig. 20, *CT*). This semi-ring represents the earliest point of ossification of the ectotympanic. The dorsal gap in the tympanic ring is filled by the margo tympanici of the squamosal, a medially projecting process of the superficies meatus, which forms the dorsal wall of the external auditory meatus (fig. 20, *MTS, SMS*). This is in contrast with most living genera of Ruminantia and also with Hippopotamus (van Kampen, 1905, p. 592). In these genera, the entire external auditory meatus is formed by the tympanic bone. To the margo tympanici was attached the dorsal edge of the tympanic membrane.

The orientation of the external auditory meatus

(pointing backward and slightly upward) agrees with that of the Ruminantia and differs sharply from that of the Non-Ruminantia.

PARS MASTOIDEA OF THE PERIOTIC BONE

This is the posterior part of the ossification of the otic capsule, and is distinguished by its cancellous structure from the pars petrosa, which is rock-like in its density.

The pars mastoidea is exposed on the occipital surface of the skull as a plate of bone (*M*, fig. 14) lateral to the occipital bone and medial to the lambdoid crest. This plate terminates ventrally between the posttympanic and paroccipital processes as the very small mastoid process, quite insignificant as an area of muscle attachment. Medially, this process is in contact with the paroccipital process.

Sections show that the mastoid process is in contact with the posttympanic process not only posteriorly, but also medially. A small flange (*M*, fig. 19) projects anteriorly from the mastoid, between the posttympanic process and the pars petrosa, and forms part of the lateral wall of the stylomastoid foramen.

Because the pars mastoidea is exposed at the surface of the skull, *Merycoidodon* is one of the "mastoid Artiodactyla," one of the two divisions of the order suggested by Helga Pearson (1927). In the other division, the "amastoid Artiodactyla," the pars mastoidea is covered by a flange of the squamosal, which overlaps upon the occipital plate.

Miss Pearson limits her two groups as follows (1927, p. 458):

Choeropotamus, Cebochoerus, Hippopotamus, the Anthracotheriidae, *Mixtotherium, Entelodon,* and the Suidae appear to belong to one group of Artiodactyla, while the Dichobunidae, *Dacrytherium,* the Anoplotheriidae, *Tapirulus, Amphimeryx,* the Cainotheriidae, together with the remaining post-Eocene families, form another. These may conveniently be termed the "amastoid" and the "mastoid" Artiodactyla respectively.

In most living Ruminantia, as in *Merycoidodon,* the pars mastoidea is well exposed upon the occipital surface. However, in the Giraffidae and the Camelidae, the posttympanic process touches the paroccipital process, and covers the ventral surface of the pars mastoidea.

For the purpose of comparison with *Merycoidodon,* the mastoid regions of a series of Merycoidodontidae were examined at the American Museum of Natural History through the courtesy of Dr. C. Bertrand Schultz and Mr. Charles H. Falkenbach. This series of skulls, culminating with the genus *Brachycrus,* of late Miocene and Pliocene time, exhibits a progressive tendency of the external auditory meatus to migrate upward and backward between the squamosal and the
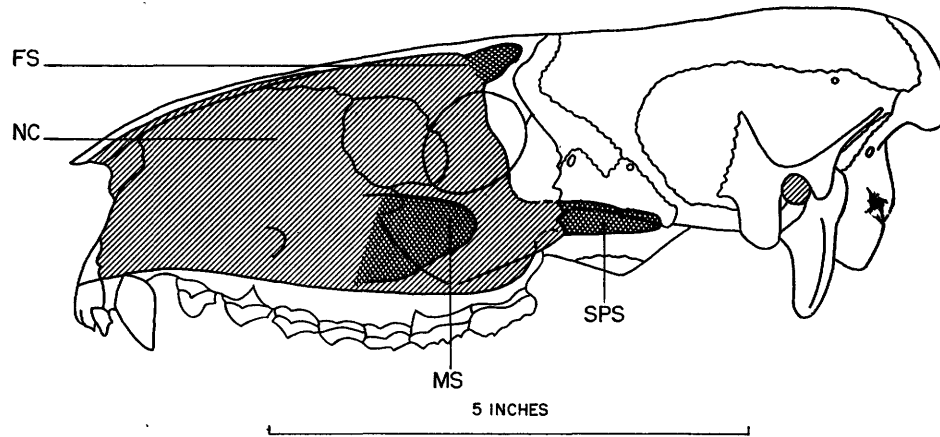
FIGURE 24.—*Merycoidodon culbertsonii*, same as figure 14, but with nasal cavity and pneumatic sinuses outlined. × ½.

Parallel lines slanting to right: nasal cavity.
Parallel lines slanting to left: pneumatic sinuses.
FS, frontal sinus.

MS, maxillary sinus.
NC, nasal cavity.
SPS, sphenopalatine sinus.

exoccipital. These two bones in *Brachycrus* show the beginning of a tendency to grow over the auditory tube; the continuation of this trend, had the Merycoidodontidae survived beyond the Pliocene epoch, would have resulted in the amastoid condition typical of the non-Ruminantia.

Thus we see, within one well-defined family, an almost complete transition from one to the other of Miss Pearson's two artiodactyl types. The possibility of such a transition is suggested by Miss Pearson in her statement (1927, p. 459) that the mastoid Artiodactyla show a tendency toward reduction of the size of the pars mastoidea.

These observations prove that the mastoid condition is a primitive one relative to the amastoid. All Artiodactyla are evolving more or less in the direction of the amastoid condition; the Non-Ruminantia attained it in Eocene time, the Merycoidodontidae approached it in Pliocene time. The Ruminantia, however, show at present only a slight tendency toward it. The chief difference, then, between the mastoid and amastoid Artiodactyla is in the relative speed with which the mastoid region is evolving.

PNEUMATIC SINUSES

These sinuses have been described individually under the discussion of the bones that contain them. Here they will be discussed as a system, and compared with the systems of other Artiodactyla.

The pneumatic sinus system of *Merycoidodon* is shown in figure 24. It consists of three sinuses, each opening directly into the nasal cavity (*NC*).

The sphenopalatine sinus (*SPS*) projects the farthest posteriorly of the three. It is a long, narrow sinus whose posterior end is contained in the presphenoid bone and whose anterior part is surrounded by the pala-

tine and the orbitosphenoid. It extends posteriorly below the anterior part of the cerebrum.

The development of the sphenopalatine sinus as seen here is typical of large mammals. In the smaller ones the development of the orbits and braincase, which are very large in proportion to their skull size, have restricted the growth of the presphenoid bone. Thus the sphenoid portion of the sphenopalatine sinus is reduced or absent.

The frontal sinus (*FS*) terminates posteriorly in the frontal bone. It is the only pneumatic sinus contained in the roofing bones of the skull.

The maxillary sinus is the largest of the three, and is most widely open into the nasal cavity. Its posterior termination is a blind end in the zygomatic process of the maxilla.

The extent of the pneumatic sinus system is to a large degree determined by skull size. The raison d'être of the pneumatic sinuses seems to be to effect an adjustment between the space necessary to house the soft parts within the skull and the external area necessary for muscle attachment, lodgment of the teeth, etc. The larger the skull, the greater is likely to be the disparity between the space thus required within and outside the skull.

Among the Artiodactyla, the sinus system of *Merycoidodon* most closely resembles that of *Ovis*; the skulls of *M. culbertsonii* and of *O. aries* are about the same size. The chief difference is that *Ovis* lacks the sphenopalatine sinus, which is well developed in *Merycoidodon*. Also, the frontal sinus in *Ovis* is larger and, unlike that of *Merycoidodon*, communicates around the orbit with the maxillary sinus.

The small size of the cerebrum in *Merycoidodon* explains the presence and size of the sphenopalatine sinus; except for this, the sinus system of the genus

is less extensive than in most modern Artiodactyla of comparable size. This is the more astonishing when one considers that the small brain is surrounded by a great thickness of parietal and squamosal bone that might be expected to be pneumatized, as it is in the Suidae which have a parietal pneumatic sinus extending ventrally into the squamosal and thence into the zygomatic arch.

The Suidae also possess a well developed sinus in the horizontal plate of the maxilla (see *Dictyles*, fig. 18), which is absent in *Merycoidodon*.

Of the Ruminantia, only the Cervidae, Tragulidae, and Camelidae have a less extensive pneumatic sinus system than *Merycoidodon* (Aubert, 1929). The first two of these families possess only a maxillary sinus; the last, frontal and sphenopalatine sinuses but no maxillary.

The sinus system of *Merycoidodon* is not a highly evolved one; the sinuses connect only with the nasal cavity, and have no connections with each other (compare the extremely complicated systems of the Giraffidae and of most Bovidae; Paulli, 1900).

The sinus pattern of *Merycoidodon* most closely resembles that of the Camelidae among the Artiodactyla, and bears least resemblance of all to that of the living Non-Ruminantia. However, the skulls of the latter are highly specialized; and unfortunately the arrangement of sinuses in their fossil relatives is unknown.

It is probably best to regard the sinus arrangement of *Merycoidodon* as primitive. It has no peculiarities to indicate the beginning of a trend to any one of the bizarre modifications of the system in late Tertiary Artiodactyla.

CIRCULATORY SYSTEM OF THE SKULL

In describing the bones of the skull, mention was made of all grooves, foramina, and canals that give evidence of the cranial circulation in *Merycoidodon*. This circulation will here be compared with that of other artiodactyls, and of various other mammals.

ARTERIES

The arterial system of *Merycoidodon* appears to have been in all but one respect the same as that of living Artiodactyla, both ruminant and non-ruminant (fig. 17). The difference was in the size and course of the internal carotid artery. This vessel is present and functional, but very small, in the Suidae (Sisson and Grossman, 1938) and the Camelidae (Lesbre, 1903); in the Tragulidae (Tandler, 1899) the internal carotid is better developed than in all other living ungulates. It is generally absent as a rule in other living Artiodactyla (Hofmann, 1900), but has been reported in *Cervus tarandus*, and probably exists in other genera,

as an essentially non-functional vestige (Tandler, 1899, p. 703).

The course of the internal carotid artery in *Merycoidodon* is very well indicated, and shows the artery to have been a large one (fig. 17, *ICA*). Undoubtedly it branched from the common carotid artery, as it does in living mammals, and extended dorso-laterally to the base of the skull. There the first evidence of its presence in *Merycoidodon* is seen.

A canal that passes dorso-laterally between the posterior extension of the tympanic and the pars petrosa of the periotic is identified as the posterior carotid canal. Its opening to the exterior is through the foramen lacerum posterius, and it is through this foramen that the internal carotid artery enters the skull (figs. 15–17, *FLP*).

After entering the foramen lacerum posterius, the internal carotid diverged from the other vessels that passed through the foramen, all of which ran medial, instead of lateral, to the pars petrosa. It then passed through the posterior carotid canal, and turned anteriorly into the tympanic cavity.

Although the internal carotid can be definitely traced into the tympanic cavity, there is no evidence as to its course through the cavity. Further proof that it crossed this region is, however, furnished by the large antero-medial opening in the bulla, just behind the ostium tympanicum tubae (fig. 15, *OTT*), which is obviously the anterior carotid foramen. Here the artery left the tympanic cavity, lay for a short distance between the bulla and basisphenoid, and entered the cranium through the foramen lacerum medius (fig. 17, *FLM*). It lay on the floor of the cranium in a groove (fig. 16) whose size indicates that the internal carotid artery was an important vessel in *Merycoidodon*. It did not divide to form a rete mirabile, or network of small arteries, but extended undiminished to the chiasma ridge, where it divided into the anterior and middle cerebral arteries. Posterior to the sella turcica, the internal carotid arteries of the two sides were connected by the posterior intercarotid artery (fig. 16). There is no groove in the base of the braincase to indicate the presence of an anterior intercarotid artery.

A comparison of the basis cranii of *Merycoidodon* with that of its probable ancestor, *Protoreodon* of the late Eocene, gives a clue as to the primitive position of the internal carotid artery in the Merycoidodontidae. In *Protoreodon* (M. C. Z. 5334), the posterior carotid canal opens on the base of the skull through a foramen independent of the foramen lacerum posterius, 3 mm anterior to it on the medial side of the posterior part of the bulla. This arrangement is the same as that in the living *Lepus* (Gregory, 1910, p. 329), the Creo-

donta (Matthew, 1910, p. 297), all Carnivora, and some Notoungulata (van der Klaauw, 1931). The anterior carotid foramen, present in *Merycoidodon* and in *Protoreodon*, and situated in the antero-medial wall of the bulla, is also reminiscent of these mammals.

In the few modern Artiodactyla that have an internal carotid artery, its path differs considerably from that in *Merycoidodon*, in which it traverses the tympanic cavity. The internal carotid in the non-Ruminantia describes a loop ventral to the auditory bulla, so that the first contact of the artery with the skull is at its entry into the foramen lacerum medius (Sisson and Grossman, 1938; van Kampen, 1905).

In the living Camelidae, the internal carotid artery is in a completely closed bony canal whose laterial wall is formed by the medial wall of the bulla, its medial wall by the basioccipital.

The internal carotid in the Tragulidae also lies along the medial wall of the bulla. In *Tragulus* it is enclosed in a canal formed entirely by the tympanic bone; in the other genera it simply lies in a shallow groove (van Kampen, 1905).

The above comparison of *Merycoidodon* with the living Artiodactyla shows that there are found, within this order, two of the three possible courses of the internal carotid through the tympanic region. The third course, with one branch of the artery passing through the bulla and another lying medial to it, is found only in the Muridae (van der Klaauw, 1931, p. 180).

Within the cranium, the groove for the internal carotid (fig. 16, *ICA*) is evidence for the statement that this artery was much larger than in living Artiodactyla. It also differed from the latter in the absence of a rete mirabile, as has been pointed out by Black (1921) on the basis of his study of natural endocranial casts. Thus the intracranial portion of the internal carotid in *Merycoidodon* resembles that of the Carnivora (see Ellenberger and Baum, 1891, p. 373), but differs from the latter, in the absence of the anterior inter-carotid artery.

VEINS AND VENOUS SINUSES

The system of vessels draining the blood from the cranium of *Merycoidodon* (fig. 17) was considerably more complicated than in present-day Artiodactyla, as it contained several additional vessels.

As is usual in the Mammalia, an important part in the head drainage in *Merycoidodon* was played by the venous sinuses, which are enclosed by dense membranes and usually lie in bony grooves. They consist of two groups, the dorsal and basilar sinus systems, and their attendant veins. A third venous system is that of the subsphenoid canals of the basisphenoid bone, a venous

arrangement here observed for the first time in the Artiodactyla.

DORSAL SINUS SYSTEM

The vessels of this group lie on the dorsal and dorso-lateral sides of the brain. The most anterior of them is the sagittal sinus, a median vessel lying directly above the longitudinal fissure of the brain and just below the sagittal crest (fig. 22, *SS*). Its length, as indicated by the groove it occupied in the roof of the braincase, was 4 mm.

No impressions in the braincase indicate the anterior and posterior connections of the sagittal sinus. We may assume, from the anatomy of modern Artiodactyla, that the sagittal sinus of *Merycoidodon* collected venous blood from the numerous small veins of the surface of the cerebral hemispheres, and transmitted it posteriorly into the transverse sinus, between the cerebrum and cerebellum.

Ventro-lateral to the sagittal sinus, on the side walls of the pyriform lobes, lies the vena collateralis cerebri, which is the only connection in *Merycoidodon* between the veins of the face and orbit and the dorsal sinus system. The presence of this vein is indicated by an antero-posterior groove in the side wall of the braincase (fig. 16, *VCC*).

The vena collateralis cerebri entered the cranium through the sinus canal (fig. 16, *PSC*), which carried it from its origin in the orbital venous plexus. The groove for the vena collateralis cerebri extends backward as far as the posterior part of the cerebrum where, presumably, it joined the transverse sinus near its entry into the temporal canal.

A vein almost identical with that indicated in *Merycoidodon* is found in many modern Insectivora. Gregory (1910, p. 248) reports it in *Solenodon*, *Microgale*, and *Erinaceus*; and Shindo (1915) notes its presence in *Talpa europaea*. In the last, however, the vena collateralis cerebri enters the cranium through the optic foramen rather than an independent canal. According to Shindo, this vein is a remnant of the anterior cerebral vein of the early embryonic stages. In some living mammals, the back part of the vena collateralis cerebri is present, but the anterior connection with the orbital plexus never develops. See *Lepus* (Shindo, 1915, p. 370).

In the possession of this vein in its entirety, *Merycoidodon* differs from all but the most primitive of living mammals.

The chief path by which the venous blood of the dorsal sinus system left the cranial cavity was the temporal canal (see p. 130). The blood passed from the transverse sinus into at least three veins, the supe-

rior cerebral, the vein of the postparietal canal, and the mastoid emissary.

The superior cerebral vein entered the temporal canal through a foramen between the pars petrosa and the endocranial surface of the squamosal. This foramen opened into the sinus venosus temporalis (fig. 20, *SVT*), which lies almost entirely in the squamosal. Besides receiving blood from the superior cerebral vein, this sinus undoubtedly collected it from the tiny veins filling the thick diploë of the squamosal. From the sinus the superior cerebral vein passed ventroposteriorly into the temporal canal (fig. 20, *TC;* fig. 21, *FJSP*), leaving it through the foramen jugulare spurium (figs. 15, 17, *TC*) to join the external jugular vein (fig. 17, *EJV*).

The foramen jugulare spurium is very small considering the size of the sinus venosus temporalis, which it drains but this disparity can be explained. Probably the temporal sinus served chiefly as a reservoir, in other words, the pressure of the blood therein was low. Besides, a posterior branch of the temporal canal (see below) relieved the foramen jugulare spurium of the necessity of transmitting all the blood in the temporal sinus.

Although it has not been reported in any living mammals, the sinus venosus temporalis cannot be regarded as a primitive structure. It is, however, an expression of the small size and correspondingly primitive condition of the cerebrum of *Merycoidodon*.

The temporal canal is present in the Ruminantia, but absent in the Non-Ruminantia.

The posterior branch of the temporal canal begins a few millimeters above the foramen jugulare spurium. Thence it extends postero-laterally to its exit from the skull through a foramen between the external auditory meatus and the postglenoid process (fig. 17, *PTC*). After leaving the skull, this vein also joined the external jugular. The vein homologous with this one is the only external orifice of the temporal canal in the modern Artiodactyla and the living Equidae and Carnivora (Dennstedt, 1903).

Another vessel that drained the transverse sinus of *Merycoidodon* was the vein of the post-parietal canal, which extended backward beneath the parieto-squamosal suture. Just before its exit from the skull, this vein in some cases divided into two or more small branches. It is represented in *Merycoidodon* by the post-parietal foramina (fig. 14, *FPP*). This vein is present in many modern mammals, including some Artiodactyla (see above).

Some distance ventral to the postparietal canal is the passage for another vein, the mastoid emissary. This leads from the temporal canal back to the mastoid fora-men on the occipital surface of the skull. It probably drained posteriorly into the vertebral or the deep cervical vein and thence to the anterior vena cava. The mastoid emissary vein is present in living Ruminantia; it is absent in the Non-Ruminantia, probably because the overlapping of the squamosal bone upon the occipital surface caused a rerouting of the blood by covering the area where the mastoid foramen lay.

The dorsal petrosal sinus is the last member of the dorsal sinus system of which traces are found in the skull of *Merycoidodon*. This vessel was, as in living mammals, a tributary of the superior cerebral vein, which it joined at its entrance to the sinus venosus temporalis. The dorsal petrosal sinus gathered venous blood from the lower part of the cerebral hemispheres and, before joining the superior cerebral vein, coursed posteriorly in a groove in the dorsal side of the pars petrosa. Judging from the depth of this groove, the sinus was rather small (fig. 21, *DPS*).

These vessels in *Merycoidodon*, as in modern forms, were much more closely connected with the anteroposterior drainage of the head than was the dorsal system. There is no evidence that the two systems were connected in any direct manner.

The basilar sinus system, judging from the condition in living mammals, received blood from the nasal cavity and maxillary region by way of the orbital venous plexus. From this plexus a large vein extended backward through the foramen lacerum anterius (fig. 15, *FLA*). Within the cranium it entered the cavernous sinus, which lay posteriorly in a groove on the cranial floor (fig. 16, *ICA*).

Behind the pituitary fossa (fig. 16, *PF*), the cavernous sinuses of both sides were connected by the posterior intercavernous sinus. In this respect *Merycoidodon* differs from *Sus* (Dennstedt, 1903) which has no posterior intercavernous sinus.

Merycoidodon had no anterior intercavernous sinus. In this it differs from *Bos* but resembles the Caprinae (Dennstedt, 1903).

The cavernous sinus debouched from the braincase through the foramen lacerum medius (fig. 15, *FLM*). Here it was continuous posteriorly with the inferior petrosal sinus, a large vessel that was contained in a groove formed dorsally by the pars petrosa and medially by the basioccipital bone. This groove is the petrobasilar canal (figs. 14, 16, *PBC*).

The internal carotid artery of *Merycoidodon* passed lateral to the pars petrosa, and the inferior petrosal sinus ventro-medial to it (fig. 17). As well as could be determined from study of the skull of *Camelus* (for

the literature is vague on this point) these two vessels in that genus run side by side in the petrobasilar canal. This is also true of the living Perissodactyla (Sisson and Grossman, 1938).

In the posterior third of its course (fig. 15) the petrobasilar groove in *Merycoidodon* lies medial to the pars petrosa, and is impressed in the basioccipital only. Beyond this groove, the extracranial part of the inferior petrosal sinus probably emptied into the inferior cerebral vein, and thence to the internal jugular (fig. 17).

The serial sections revealed a minute canal extending posteriorly in the backward extension of the alisphenoid bone above the auditory bulla (fig. 21, *VCL?*). This canal probably carried a vestigial vein, so small as to be non-functional, which branched from the cavernous sinus at the foramen lacerum medius and passed into the dorsal side of the tympanic cavity. This course suggests that it may be a remnant of the embryonic lateral head vein: it runs medial (although posterior) to the alisphenoid bone, which is the homologue of the lamina ascendens of the embryonic ala temporalis. The ala temporalis, in turn, is homologised by Broom (1907) with the reptilian epipterygoid. Furthermore, the position of this small vein dorsal to the auditory ossicles is equivalent to a location dorsal to the jaw articulation of the Reptilia, where the lateral head vein lay.

To return to the functional portion of the basilar sinus system, we find that the inferior petrosal sinus, slightly anterior to the beginning of its extracranial portion, emitted a branch, the condyloid vein, which continued posteriorly within the skull in a groove at the lateral side of the myelencephalic base. It found its exit from the skull through the condylar foramen (figs. 15, 16, *CF;* fig. 17 *CV*) and joined the occipital vein, which probably transmitted the blood to the deep cervical or the vertebral vein. This constituted the second of the two outlets of the basilar sinus system.

SUBSPHENOID VEINS AND THE SINUS VENOSUS OSSIS SPHENOIDALIS

The evidence for the presence of this most unusual set of veins, hitherto unrecorded in Artiodactyla or in most other mammalian orders, consists of the well-developed canals by means of which they passed through the basisphenoid bone of *Merycoidodon* (see p. 122, and fig. 17).

A survey of anatomical literature proves beyond a doubt that the cavity in the basisphenoid bone (fig. 17, *SVOS*) contained a venous sinus, and that the canals leading from it to the surface of the skull (fig. 17, *SSC*) conveyed blood into it from the orbital region and out of it posteriorly.

Such a venous cavity in the basisphenoid was first reported by W. Krause (1868; cited by Arai, 1907), who observed it in the human foetus and in 10 percent of new-born infants studied. Arai (1907) found the same structure in the adult *Lepus cuniculus*, and named it the sinus venosus ossis sphenoidalis (this rather cumbersome title is necessary to differentiate it from the sphenoidal pneumatic sinus). In *Lepus*, the upper wall of this sinus is open into the pituitary fossa, and the membranous wall of the venous sinus is in contact with the dura mater which surrounds the pituitary body. In *Lepus*, the venous sinus receives blood from the veins of the dura mater. In *Merycoidodon* there is no such connection between the sphenoidal venous sinus and the pituitary fossa. This venous sinus has been regarded by most anatomists (Arai, 1907; Waldeyer, 1907; Bovero, 1905) as a remnant of Rathke's pocket. Voit (1909), however, feels that it is too far posterior and must be a secondary structure. As the sinus is found in the embryos of many mammals that lack it in the adult stage, the first hypothesis seems the more likely.

As in *Merycoidodon*, Lepus has one or more canals leading into the sphenoidal venous sinus from the exterior of the basisphenoid bone. These are designated by Arai (1907) the foramina venosa but, since they are the openings of what he calls the subsphenoid canals, they are here given the more specific title of subsphenoid foramina.

A functional sphenoidal venous sinus with its associated subsphenoid canals is found in the adult stage in relatively few mammals. These are the Sciuromorpha and Myomorpha (Bovero, 1905), the Marsupialia (Gregory, 1910, p. 431) and the Lagomorpha (Arai, 1907).

The manner of circulation of the venous blood of the head in the above-mentioned groups indicates the part which the sphenoidal venous sinus of *Merycoidodon* played in its cranial circulation.

Anteriorly the subsphenoid canal must have received, as in these groups, a branch of the ophthalmic vein coming from the orbital plexus. Posteriorly, the vein passed out through a foramen in the anterior wall of the foramen lacerum medius (fig. 16, *FSP*). Thence the blood undoubtedly flowed into the posterior portion of the cavernous sinus, just anterior to the confluence of the latter with the inferior petrosal sinus.

It is apparent from the skulls of *Merycoidodon* which were dissected that the vessels of the sphenoidal sinus system were larger than the cavernous sinus and, therefore, that the sphenoidal vessels were among the most important paths by which the blood of the facial region in *Merycoidodon* was drained posteriorly. We have no way, of course, of knowing the size in this genus of

the external maxillary vein, which is the chief posteriorly directed vein leaving the facial region of living Artiodactyla.

The facts here set forth show that, despite the size of the temporal canal, the preponderant venous outlet of the skull of *Merycoidodon* was the internal jugular vein rather than the external jugular as in modern Artiodactyla (Bolk, Göppert etc., 1936). This fact is proved by the large size of the sinus venosus ossis sphenoidalis and of the inferior petrosal sinus, and by the small size of the opening of the temporal canal, which led to the external jugular vein (fig. 17).

The internal jugular, a remnant of the lateral head vein, is the more primitive means of drainage. In this respect, *Ovis* and *Bos* are mammals of the most advanced type. In these genera, the external jugular vein drains the skull, and the last vestige of the lateral head vein is lost.

In *Merycoidodon*, a large part of the blood from the face must have run posteriorly through the subsphenoid canals. In the more advanced Artiodactyla, the mechanical advantages of an extracranial route apparently prevailed; the subsphenoid canals degenerated, and the external maxillary vein carried the blood which they had once transmitted. This change in circulation took place much earlier in evolution than the equivalent one in the arterial system.

NERVES OF THE SKULL REGION

The nerves supplying the cranium of *Merycoidodon*, as described above from grooves and foramina in the skull bones, do not differ in any important characteristics from those of living Artiodactyla.

CRANIAL MORPHOLOGY OF *POEBROTHERIUM*

Poebrotherium is the genus which represented, in White River (Oligocene) time, the ancestral line leading to the modern camels and llamas. Like the other

extinct camel-like mammals, it is included with the living genera in the suborder Tylopoda.

For this study, serial frontal sections were made of a skull of *Poebrotherium wilsoni* Leidy, from Oligocene rocks exposed near James Creek, in the Hat Creek Basin, Sioux County, Nebraska. It was collected in 1922 by a party from the Walker Museum, University of Chicago. Study of the serial sections was aided by comparison with four other skulls of *P. wilsoni*, and with one of *P. eximium* Hay, a larger species. No skulls of *P. labiatum* Cope, the only other species of the genus, were available for study; but reference has been made to descriptions and plates of the skull of this species (Scott, 1891, 1940).

The anatomy of the skull of *Poebrotherium* will not be described here in as great detail as was that of *Merycoidodon*; it will suffice to point out some significant similarities and differences between the two, especially those made available for the first time by the use of serial sections.

BONES OF THE SKULL

As in *Merycoidodon*, the basioccipital, exoccipitals and supraoccipital are fused in *Poebrotherium* into an occipital bone (fig. 25, *OC*). The paroccipital process of this bone (fig. 25, *PPO*) is suturally attached for its entire length to the auditory bulla. This is due chiefly to the great inflation of the latter. Another result of this inflation is that the basioccipital is in contact with the medial wall of the bulla (fig. 26), there being no gap between them as in *Merycoidodon*.

Within the braincase, the course of the condyloid vein is indicated by an antero-posterior groove near the lateral edge of the basioccipital. This is present also in *Merycoidodon*.

The most striking characteristic of the basisphenoid bone (fig. 26, *BS*) is that, as in *Merycoidodon*, it contains a large sinus venosus ossis sphenoidalis, with its
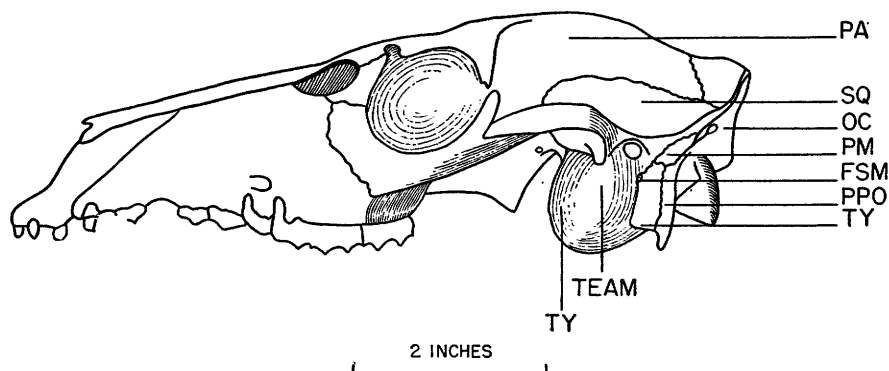

2 INCHES

FIGURE 25.—*Poebrotherium wilsoni*.   Lateral view of skull.   Modified after W. B. Scott.   × ½.

FSM, stylomastoid foramen.
OC, occipital bone.
PA, parietal bone.
PM, pars mastoidea of periotic bone.

PPO, paroccipital process of exoccipital.
SQ, squamosal bone.
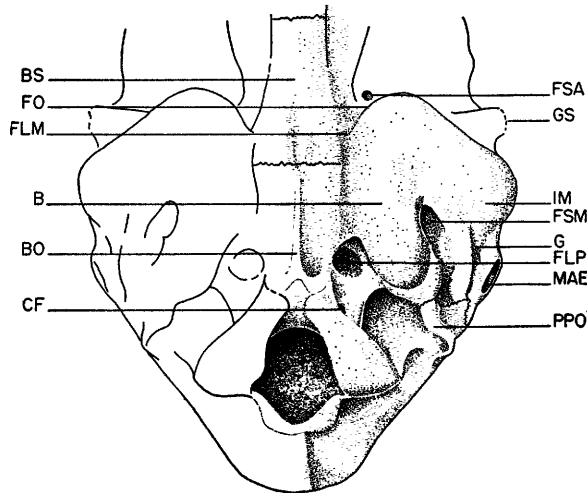*TEAM*, expanded external auditory meatus.
TY, tympanic bone.

FIGURE 26.—*Poebrotherium wilsoni,* ventral view of basis cranii. Composite, drawn from Princeton Museum no. 12692 and M. C. Z. 5998, × ½.

B, auditory bulla.
BO, basioccipital bone.
BS, basisphenoid bone.
CF, condylar foramen.
FLM, foramen lacerum medius.
FLP, foramen lacerum posterius.
FO, foramen ovale.
FSA, anterior subsphenoid foramen.
FSM, stylomastoid foramen.
G, groove separating bulla from external auditory meatus.
GS, glenoid surface of squamosal bone.
IM, inflated part of external auditory meatus.
MAE, external auditory meatus.
PPO, paroccipital process of exoccipital.

tributary subsphenoid canals (fig. 28, *SVOS*; cf. fig. 26, *FSA*). The sphenoidal venous sinus is larger than in *Merycoidodon* because of the greater dorso-ventral dimension of the basisphenoid. The sinus becomes narrower anteriorly, where the portions of the basisphenoid lateral to the sinus are filled with large-celled cancellous tissue. The sphenoidal venous sinus terminates anteriorly below the anterior end of the pituitary fossa; this differs from the condition in *Merycoidodon,* in which the anterior end of the sinus lies below the posterior end of the fossa.

Within the cranial cavity, the basisphenoid is excavated by the pituitary fossa, which is shallow, as in *Merycoidodon* and the living Tylopoda (Lesbre, 1903). The anterior end of the fossa is marked by an eminence which rises about 2 mm. above the floor of the braincase. At its posterior end are the posterior clinoid processes, whose bases are about 3 mm. apart. They are very delicate, and arch toward each other, almost touching at the midline of the skull.

Along either side of the pituitary fossa lie the grooves for the cavernous sinus and internal carotid artery and, lateral to these, the grooves for cranial nerves III, IV, VI, and the first two branches of nerve V. These pathways are separated by a very low ridge. Lateral to the groove which carries the cranial nerves is a higher, sharp ridge.

The alisphenoid bone of *Poebrotherium* differs from that of *Merycoidodon* in that it lacks a posteriorly projecting plate above the ostium tympanicum tubae. This function is taken over by the squamosal (see below). The posterior portion of the alisphenoid is in sutural contact with this horizontal plate of the squamosal, but does not reach backward as far as the ostium.

Within the cranium, a few millimeters medial to the alisphenoid-squamosal suture, a deep groove runs anteriorly from the region of the foramen lacerum medius to the foramen ovale (fig. 26, *FO;* hidden by the auditory bulla). Judging from its course, this must have borne the third (mandibular) branch of cranial nerve V.

The alisphenoid of *Poebrotherium* further differs from that of *Merycoidodon* in that the cavity for the sinus venosus ossis sphenoidalis extends laterally into it, as in the living Leporidae (Arai, 1907).

The deep, narrow presphenoid bone is of nearly the same shape as that of *Merycoidodon.* It is filled with cancellous tissue of much finer texture than that present elsewhere in the *Poebrotherium* skull.

At its anterior end the presphenoid is no narrower than in *Merycoidodon,* but, in contrast to this genus, it contains no pneumatic sinus.

On the external surface of the skull of *Poebrotherium,* the orbitosphenoid bone is in about the same position as in *Merycoidodon.* Within the cranium it shows an interesting difference in that its posterior root projects inward beneath the cerebrum as a curved, dorsally convex plate roofing the cranial nerves (IV, V_1, V_2, VI), which lay in a groove lateral to the pituitary fossa. In the anterior part of their intracranial course, therefore, these nerves were surrounded on all but the medial side by bone (fig. 28, *FLA*). This plate of the orbitosphenoid is probably a secondary ossification rather than a homologue of the lateral lamina of the sella turcica in *Merycoidodon.*

Where it forms part of the anterolateral wall of the cerebrum, the orbitosphenoid reaches its maximum thickness of 5 mm. This is the thickest part of the braincase wall, which as a whole is distinguished from that of *Merycoidodon* by its light construction. The thickened portion of the orbitosphenoid is solidly ossified, in contrast to the other bones of the *Poebrotherium* skull, which tend to be filled with large-celled cancellous tissue.

In the skull of *Poebrotherium* which was serially sectioned, almost no trace remained of the ethmoid bone. A small fragment of the bony nasal septum appears approximately in place in one section; it is only 1 mm thick.

The only evidence concerning the characteristics of

the turbinals is a sharp ridge projecting ventrally into the nasal cavity from each nasal bone. These projections run the entire length of the nasals, which are very long in this genus; they undoubtedly served as roots for the naso-turbinal bone or cartilage. It may be inferred, then, that these scrolls at least were well developed in *Poebrotherium*. Similar ridges are present in the living *Camelus*. They support a cartilaginous nasoturbinal scroll.

The nasal septum and turbinal scrolls were probably much less heavily ossified in *Poebrotherium* than in *Merycoidodon*.

The vomer was missing in the sectioned skull of *Poebrotherium*.

There is no separate ossification of the preinterparietal or interparietal in this skull.

The parietal bones are very long, and form almost the entire roof of the braincase. Posteriorly, the parietals conform much more closely to the shape of the brain (fig. 27) than do those of *Merycoidodon*. The vermis cerebelli of *Poebrotherium* was higher than that of *Merycoidodon*, projecting above the dorsal plane of the cerebrum, and very narrow. Its sides were nearly

vertical. These observations agree with the deductions drawn by Bruce (1883) and Scott (1940) on the basis of studies of damaged natural endocranial casts.

The posterior portions of the parietals are filled with diploë for about 10 mm on either side of the sagittal crest (fig. 27). The diploic layer is thin, however, and in this region the maximum thickness of the parietals is only 5 mm.

Over the junction of the cerebrum and cerebellum, the parietals become thicker, and their diploic cells increase in size to an average diameter of 2 mm. Here the diploë spreads farther laterally than over the cerebellum, extending about 18 mm ventrolaterally from the sagittal crest.

At their anterior termination, the parietals are again simple bony plates, devoid of cancellous tissue. This is true also of the posterior part of the frontal bone, dorsal to the anterior part of the cerebrum, which has an average thickness of only 2 mm.

The descending plate of the frontal, which forms part of the side wall of the braincase, is heavier than the dorsal plate and, in its posterior portion, consists of solid non-diploic bone like that of the orbito-
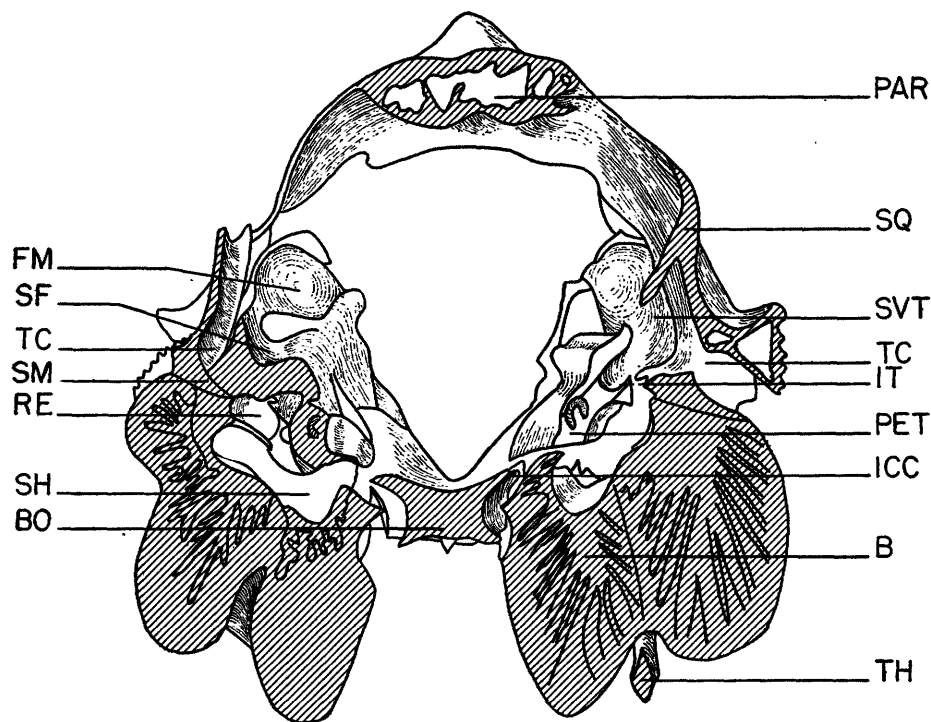
FIGURE 27.—*Poebrotherium wilsoni* Leidy. Thick section of skull, prepared from sections P 1–17, viewed posteriorly from level of vagina processus hyoidei. Natural size.

B, bulla.
BO, basioccipital.
FM, foramen magnum.
ICC, internal carotid canal.
IT, incisura tympanica.
PAR, parietal.
PET, pars petrosa.
RE, recessus epitympanicus.

SF, subarcuate fossa.
SH, hypotympanic sinus.
SM, superficies meatus.
SQ, squamosal.
SVT, sinus venosus temporalis.
TC, temporal canal.
TH, tympanohyal.

sphenoid, which adjoins it. Farther anteriorly the large diploic cells of the supraorbital process are continued ventrally into the lateral wall of the olfactory bulbs.

The supraorbital process of the frontal is very thick dorsoventrally, in marked contrast to the brain-case portion of the same bone. It is filled with large-celled diploic tissue. Between these processes, and dorsal to the anterior moiety of the olfactory bulbs, the horizontal plate of the frontal reaches its greatest thickness (5 mm) and is entirely cancellous in structure.

The olfactory lobes are somewhat larger than those of *Merycoidodon*, which has so often been cited as an extremely macrosmatic genus.

Comparison of the olfactory lobes of *Poebrotherium* with those of the living *Camelus* (Lesbre, 1903) indicates that, even considering the greater size of the neopallium of *Camelus*, the lobes of smell in *Poebrotherium* are nearly twice as large for the size of the brain.

The squamosal bone of *Poebrotherium* differs from that of *Merycoidodon* in that it is diploic only along its base (medial to the temporal crest and, farther forward, to the root of the zygoma). Above this the greater portion of the squamosal plate is very thin and conforms closely to the shape of the cerebrum (fig. 27). This bone is relatively much thicker in living Tylopoda.

The horizontal ventral plate of the squamosal is even more intimately involved in the structure of the middle ear in *Poebrotherium* than in *Merycoidodon*. The term "horizontal plate" is not applicable here in a strict sense, for parts of this structure are at a sharp angle with the horizontal.

A part of the ventral squamosal plate, the superficies meatus (fig. 27, *SM*) forms the roof of the external auditory meatus. It is a very thin plate of bone, lying in an almost vertical attitude due to the steep slant of the tube of the meatus. In *Merycoidodon* the superficies meatus is horizontal and about three times as thick as in *Poebrotherium*.

The superficies meatus extends ventromedially into the tympanic cavity, terminating 2 mm lateral to the promontorium, and dividing the front part of the tympanic cavity into dorsal and ventral cavities.

In the living Tylopoda, there is no such medially projecting plate of the superficies meatus (van Kampen, 1905). In *Merycoidodon* it projects medially in a horizontal direction and its medial end is in contact with the pars petrosa above the tympanic cavity.

A more truly horizontal part of the ventral plate of the squamosal is that which projects medially above the ostium tympanicum tubae. To its ventral side, lateral to the ostium, is attached the anterior part of the auditory bulla. Over the anterior end of the ostium, the squamosal plate meets the alisphenoid, and also extends behind it, where a gap between the squamosal and the basioccipital forms the foramen lacerum medius.

The squamosal therefore plays the part in *Poebrotherium* which, in *Merycoidodon*, is taken by the posteriorly projecting plate of the alisphenoid, which partially roofs the tympanic cavity.

The temporal canal, bearing the superior cerebral vein, is not contained, as in *Merycoidodon*, entirely within the squamosal, but is bounded only dorsolaterally by it (fig. 27, *TC*). This canal is further discussed below.

Like *Merycoidodon*, *Poebrotherium* possessed an anterior branch of the temporal canal; it ran entirely within the squamosal, however, and not between the squamosal and the tympanic. The vein which occupied this canal reached the surface just medial to the root of the zygoma through two foramina, the supraglenoid foramina of Cope (1880). Examination of other skulls of the genus reveals that either one or two supraglenoid foramina may be present and that the number may differ on the two sides of the same skull. The same is true of the living Tylopoda.

No supraglenoid foramen is present in *Merycoidodon*.

Poebrotherium possesses a maxillary pneumatic sinus along the medial side of the cheek-tooth row and dorsal to it, and projecting posterior to the third molar into the tuber maxillare (fig. 28). The sinus is almost square in frontal section, with a height of about 15 mm. Anteriorly it reaches as far as the fourth premolar, a distance of about 33 mm. The maxillary sinus ascends into the vertical plate of the maxilla, ventral to the lacrimal fossa. Probably the entrance of this sinus into the nasal cavity lay in the medial wall of this extension; this could not be definitely determined, however, because of the broken condition of the bone in this area.

The ventrally projecting vertical plate of the palatine bone is much heavier than in *Merycoidodon*. It is directed ventro-laterally and is in contact medially with the pterygoid bone, a slimmer plate that is oriented vertically. This union of the two bones forms a bifurcated process such as is also typical of living Tylopoda (fig. 28, *PAL*, *PT*).

TYMPANIC REGION
PARS PETROSA OF THE PERIOTIC BONE

An interesting feature of this bone in *Poebrotherium* is the extremely large subarcuate fossa that occupies its entire dorsal side. The front part of the fossa (fig. 27, *SF*) is a simple depression in the pars petrosa, such as was observed in *Merycoidodon*, but behind this it is a cavity whose floor is the dorsal side of the pars vestib-
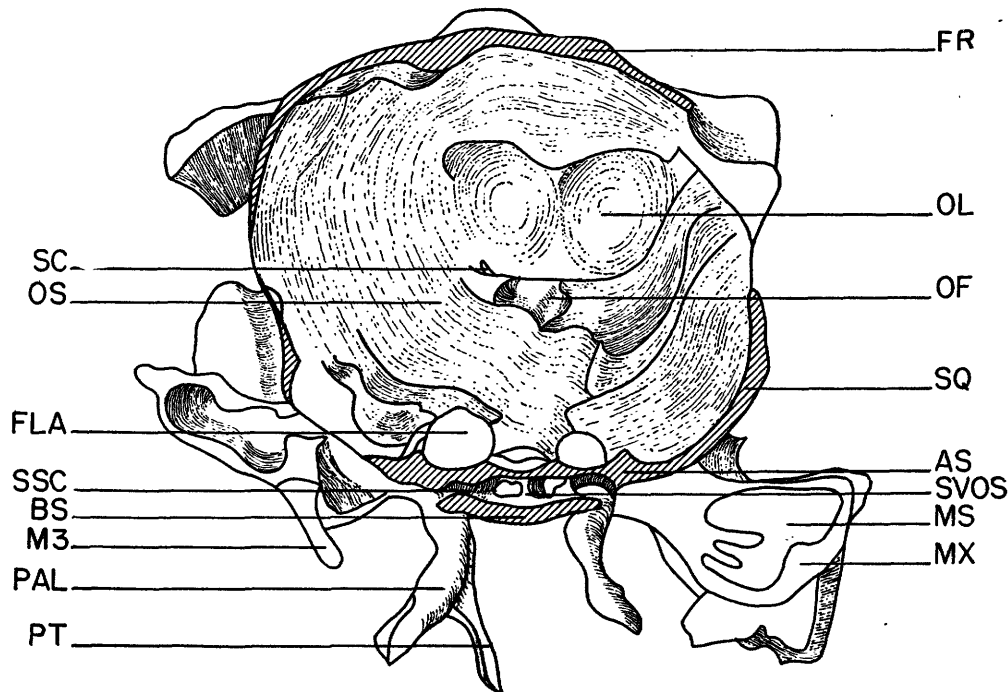
FIGURE 28.—*Poebrotherium wilsoni* Leidy. Thick section of skull, prepared from sections P 37–81, viewed anteriorly into olfactory lobes. Skull somewhat distorted. Natural size.

AS, alisphenoid.
BS, basisphenoid.
FLA, foramen lacerum anterius.
FR, frontal.
MS, maxillary sinus.
MX, maxilla.
M3, third molar.
OF, optic foramen.

OL, olfactory lobes.
OS, orbitosphenoid.
PAL, palatine.
PT, pterygoid.
SC, sinus canal.
SQ, squamosal.
SSC, subsphenoid canal.
SVOS, sinus venosus ossis sphenoidalis.

ularis, and whose side walls and roof are formed by the bony arch which housed the posterior semicircular canal (fig. 27, *F*). Its posterior wall is a part of the dorsal portion of the pars mastoidea of the periotic.

This fossa was the receptacle of the lobulus petrosus of the cerebellum, mentioned above in the discussion of *Merycoidodon*; the lobulus of *Poebrotherium* must have been at least three times this size.

The modern Lagomorpha have an identical fossa. Krause (1884, p. 182) described it, and designated it the fossa mastoidea. A very similar structure is reported by Elliot Smith (1903, p. 428) to exist in all Primates except *Simia*, *Anthropopithecus* and *Homo*.

For comparison with modern descendants of *Poebrotherium*, the writer examined the skulls of Tylopoda in the osteological collection of the Museum of Comparative Zoology at Harvard University. The roof of the braincase had been removed from only two skulls, specimens of *Lama huanachus* (M. C. Z. 1746, M. C. Z. 29878); and in both skulls the fossa mastoidea was identical with that of *Poebrotherium*. No mention of this fossa has been made in the literature but it seems safe to conclude that it is typical of modern Tylopoda.

Further examination of skulls of present-day Artiodactyla reveals that no others possess the fossa mastoidea. Its presence in the living Tylopoda contradicts the statement of Black (1921, p. 310) and Bolk (1906) that no modern ungulates possess the lobulus petrosus of the cerebellum.

MIDDLE EAR AND SURROUNDING STRUCTURES

The auditory bulla of *Poebrotherium* (fig. 26, *B*) is typical of Tylopoda—extremely large and filled with cancellous bone.

The relationships of the bulla to its surrounding structures differ from those of *Merycoidodon* largely because of its greater size, and agree correspondingly with those of the living Tylopoda.

The bulla projects posteriorly along the lateral side of the paroccipital process, to which it is attached. Ventrally, it overlaps the anterior part of the process. Dorsally, the main part of the bulla is in contact with the pars petrosa and the squamosal. It projects much farther anteriorly than in most mammals. The anterior part of the bulla in *Poebrotherium* is well inflated and entirely cancellous; it is laterally compressed to-

ward its dorsal side, and serial sections show its dorsal margin to be in contact with the suture between the alisphenoid and squamosal.

As in the living Tylopoda, the bulla of *Poebrotherium* is in contact medially with the pars petrosa but is not fused with it (fig. 27, *PET, B*). No gap exists between the two as in *Merycoidodon*.

Despite the great size of the *Poebrotherium* bulla, the hypotympanic sinus is no larger than that of *Merycoidodon* (fig. 27, *SH*). It is of relatively the same size and shape as that of *Lama* and *Camelus* (van Kampen, 1905, p. 594).

The ostium tympanicum tubae is longer than that of *Merycoidodon*, because of the greater anterior extension of the bulla. It is closed below by the contact of the bulla with the basisphenoid, and above by the horizontal plate of the squamosal bone. The living Tylopoda differ from *Poebrotherium* in that the ostium tympanicum tubae is roofed by the alisphenoid (van Kampen, 1905) as in *Merycoidodon*.

In *Poebrotherium*, the tympanic bone forms almost all of the medial wall in addition to the ventral and part of the lateral wall of the tympanic cavity. The pars petrosa is thus limited almost entirely to the roof of the cavity (fig. 14). The cavity is wider and shallower than that of *Merycoidodon*.

The epitympanic recess of *Poebrotherium*, instead of lying directly above the tympanic cavity as in *Merycoidodon* and *Camelus* (van Kampen, 1905), extends dorsolaterally above the external auditory meatus. It is very small, and is bounded laterally by the tympanic and squamosal, and dorso-medially by the pars petrosa of the periotic (fig. 27, *RE*).

Just behind the epitympanic recess and also dorsomedial to the external auditory meatus, lies the incisura tympanica (fig. 27, *IT*). As in other mammals, both its dorsal and ventral sides are formed by the squamosal bone; it is much larger than in most mammals, however. Comparison of the diameter of the medial end of the external auditory meatus with that of the incisura, reveals that, in *Poebrotherium*, the pars tensa of the tympanic membrane was very small, and the pars flaccida very large. The incisura tympanica is absent in the living Tylopoda (van Kampen, 1905).

The vagina processsus hyoidei is almost completely surrounded by the auditory bulla. In the vagina, sections show the tympanohyal (fig. 27, *TH*) which, as Scott (1940, p. 621) suggested, is not fused to the tympanic. This fusion is present in the adult modern Tylopoda (van Kampen, 1905, p. 598), in which the bulla completely encloses the vagina to form a true pit.

The stylomastoid foramen of *Poebrotherium* is the lateral opening of a nearly horizontal canal leading from the tympanic cavity to the posterolateral side of the bulla (fig. 26, *FSM*). Dorsally, this canal is bounded by the squamosal; it differs from the stylomastoid canal in *Merycoidodon* in that its ventral wall is formed by the laterally swollen bulla rather than by the paroccipital process of the exoccipital. The canal in *Camelus* is formed in the same way.

EXTERNAL AUDITORY MEATUS

At first glance the porus acusticus externus of *Poebrotherium* appears to open directly out of the tympanic bulla, with no intervening tubular meatus (fig. 26, *MAE*), but what appears to be the lateral portion of the auditory bulla is actually the inflated meatus (fig. 13, *IM*).

The external auditory meatus in *Poebrotherium* is surrounded anteriorly, ventrally, and posteriorly by the inflated tympanic bone, and dorsally by the superficies meatus of the squamosal, but in living Tylopoda, the meatus roof is formed by a thin plate of the tympanic, so that the meatus is a tube formed by this one bone. In both *Poebrotherium* and its living relatives the tube of the meatus slants sharply dorsolaterally from the tympanic cavity.

PARS MASTOIDEA OF THE PERIOTIC BONE

This bone is well exposed upon the lateral surface of the skull (fig. 25, *PM*), the exposed area being larger than in *Merycoidodon*. In *Poebrotherium*, the pars mastoidea is bounded anteroventrally by the tympanic portion of the auditory bulla, rather than by the squamosal, which in *Merycoidodon* overlaps its lower part (figs. 14, 25). In *Camelus* also (van Kampen, 1905) the squamosal covers the ventral part of the mastoid exposure. This appears to be another instance, like that cited above in the family Merycoidodontidae, of progressive covering, in the course of evolution of a group, of the pars mastoidea by neighboring elements.

PNEUMATIC SINUSES

The sinus system of *Poebrotherium* is less extensive than that of *Merycoidodon*, as no sphenoidal sinus is present. The frontal sinus is much smaller than that of *Merycoidodon:* instead of occupying the entire supraorbital process of the frontal bone, it is found only in the anteriormost part of this process. Its anteroposterior length is only about 4 mm., and it opens into the nasal cavity dorsal to the lacrimal fossa.

The maxillary sinus (fig. 28, *MS*) is considerably longer, but narrower, than that of *Merycoidodon*. Its greater extent as a cavity independent of the nasal cavity is due to the greater thickness in *Poebrotherium* of the palatine plate of the maxilla.

In *Camelus* (Aubert, 1929), in contrast to *Poebrotherium*, the maxillary sinus is absent and the sphenoidal sinus is well developed. This discrepancy in a supposed descendant of *Poebrotherium* (Scott, 1891) is easily explained: The development of larger cheek teeth would occupy the space in the maxilla formerly filled by the sinus, and the almost threefold increase in skull size would allow room for a sinus ventral to the olfactory lobes (compare *Merycoidodon*).

CIRCULATORY SYSTEM OF THE SKULL
ARTERIES

The internal carotid artery did not, as in *Merycoidodon*, traverse the tympanic cavity; instead it lay in a bony canal formed by the tympanic bulla and the basioccipital and basisphenoid (fig. 27, *ICC*).

As Scott (1891) first pointed out, the internal carotid entered this canal through a foramen anterior to the foramen lacerum posterius. The farthest posterior appearance of the carotid canal is, therefore, just anterior to this foramen and at the level of the vagina processus hyoidei. From this point the canal extends forward 4 mm. to an opening medial to the ostium tympanicum tubae. After leaving the canal, the artery entered the cranium through the foramen lacerum medius, which lies dorsal to the anterior end of the bulla (fig. 26, *FLM*).

The carotid canal in *Poebrotherium* differs from that of *Camelus* only in its less superficial position (because of the more swollen bulla of the former) and in the separation of its posterior foramen from the foramen lacerum posterius. In *Poebrotherium*, the size of the carotid canal indicates that the carotid artery was already, as it is in *Camelus*, relatively unimportant in supplying cranial blood, although still functional.

VEINS AND VENOUS SINUSES
DORSAL SINUS SYSTEM

Poebrotherium, like *Merycoidodon*, differed from living Artiodactyla in the possession of a venous tributary that passed from the orbital plexus through the sinus canal (fig. 15, *SC*) to the vena collateralis cerebri.

The superior cerebral vein in this genus ran ventro-laterally in a space between the ascending plate of the subarcuate fossa (near the anterior end of the pars petrosa) and the descending plate of the squamosal (fig. 27). At the base of the latter plate it entered a small (10 mm. in diameter), subspherical sinus venosus temporalis (fig. 27, *SVT*), whose medial and ventral walls were formed by the tegmen tympani of the pars petrosa and the dorsal side of the tympanic bulla. The size of this sinus is in distinct contrast to that of the homologous sinus in *Merycoidodon*.

The temporal venous sinus opens into the temporal canal, which, after coursing ventro-laterally, opens upon the surface of the skull in a foramen between the auditory bulla and the squamosal bone. This foramen is difficult to find because it is overhung by the root of the zygoma.

The anterior branch of the temporal canal was mentioned in the discussion of the squamosal bone.

BASILAR SINUS SYSTEM

The depth of the grooves that extend antero-posteriorly alongside the pituitary fossa indicates that the cavernous sinus was a relatively small vessel. So, too, was the inferior petrosal sinus, if it was present at all. The carotid canal (fig. 27, *ICC*) is so small that it could not have contained two functional blood vessels. The inferior petrosal sinus must, then, have been extracranial in its course, or absent. No detailed account of the venous system of *Camelus* is known to the author, and it was impossible to determine whether this sinus is present in living Tylopoda.

SINUS VENOSUS OSSIS SPHENOIDALIS

This venous sinus in *Poebrotherium*, with its tributary subsphenoid canals, differed from that of Merycoidodon only in that it extended laterally into the root of the alisphenoid bone (fig. 28, *SVOS, AS*). In figure 28 the anterior subsphenoid canals (*SSC*) are seen, extending transversely in the plane of the section from their openings at the sides of the basisphenoid bone.

The antero-posterior length of the sphenoidal venous sinus is about 5 mm.

Lesbre's illustration of a sagitally sectioned skull of *Camelus* (1903, p. 19) shows that the basisphenoid contains no cavities of any sort.

The above observations suggest that in *Poebrotherium* the dorsal sinus system was the main path of drainage of blood from the cranial cavity, and the venous blood from the facial region ran posteriorly through the sphenoidal venous sinus and extracranial paths, rather than through the cranium.

NERVES OF THE SKULL REGION

The arrangement of the cranial nerves of *Poebrotherium* differs from that of *Camelus* (Lesbre, 1903) only in the position of the optic nerves. These nerves lie very close together throughout their length, and the optic foramina (fig. 28, *OF*) are separated only by the thin medial bony plate formed by the two orbito-sphenoids. The great size of the orbits causes these bones to be closely pressed together in the midline of the skull—a condition common in small mammals, such

as the Lagomorpha, Tragulidae and Hypertragulidae.

Because of the larger size of the skull, the optic foramina of the living Tylopoda are separated by the sphenoidal pneumatic sinus, which lies between the orbitosphenoid plates.

CRANIAL MORPHOLOGY OF *LEPTOMERYX*

Leptomeryx is a member of the family Hypertragulidae, which is well represented in the fauna from the White River group. The members of this family bear a very close resemblance to the living Tragulidae and their relationships have long been a subject of controversy.

Serial sections of the skulls of the Hypertragulidae do not yield as much information as those of larger mammals, because their delicate bones retain fewer impressions of the endocranial soft parts.

Because well-preserved *Leptomeryx* skulls are rare, one skull was divided sagittally, the left half serially sectioned at 0.5 mm intervals, and the right half kept intact for reference.

The skull on which this study is chiefly based is one of *Leptomeryx evansi* Leidy, M. C. Z. 6566 (figs. 29, 30). It was collected by S. W. Garman in 1880, in the Bad Lands of northeastern Wyoming, and was given to the Museum of Comparative Zoology by Alexander Agassiz.

BONES OF THE SKULL

The supraoccipital portion of the coössified occipital bone is, unlike that of the Tragulidae, extended posteriorly into a nuchal crest, which is filled with diploë the size of whose cells resembles those of the Camelidae more than those of *Merycoidodon*.

The proportion of the occipital surface of the skull formed by the supraoccipital is less than in any other artiodactyl family, because the pars mastoidea is exposed on the occipital rather than the lateral surface of the skull (fig. 30, *M*).

The basisphenoid bone, like those of *Merycoidodon* and *Poebrotherium*, contains a cavity for the sinus venosus ossis sphenoidalis.

The sagittally sectioned skull reveals that the postclinoid processes are very high (3.5 mm) in proportion to the size of the skull, and that the pituitary fossa, as in the Camelidae and *Merycoidodon*, is shallow.

The alisphenoid bone has a posterior process that lies dorsal, not only to the Eustachian tube but also, behind this, dorsal to the tympanic cavity itself. This process thus reaches farther back than in *Merycoidodon*, where it lies dorsal only to the ostium tympanicum tubae. In *Tragulus* the alisphenoid seems, insofar as could be determined from external examination of skulls in toto, to have the same relationships as in *Leptomeryx*.

The subsphenoid canals, leading to the sinus venosus ossis sphenoidalis, lie for the most part in the alisphenoid, and their foramina open on its surface (fig. 30, *FSA*).

Considerable portions of the turbinal ossifications of the ethmoid bone were preserved in this specimen. In the back part of the nasal cavity are the roots of three turbinals thick enough to be tentatively termed endoturbinals. There may well have been more than three of these scrolls in life, but the three preserved apparently occupied more than two-thirds of the posterior part of the nasal cavity; it is therefore improbable that
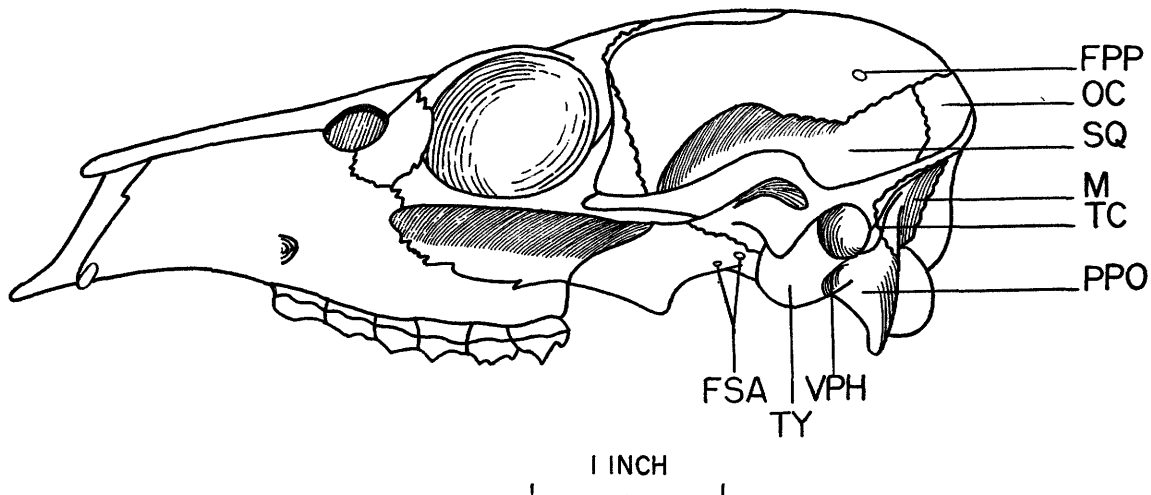
FIGURE 29.—*Leptomeryx evansi*, lateral view of skull. Modified after W. B. Scott. Natural size.

FPP, post-parietal foramen.
FSA, anterior subsphenoid foramen.
M, pars mastoidea of periotic bone.
OC, occipital bone.
PPO, paroccipital process of exoccipital bone.

SQ, squamosal bone.
TC, foramen jugulare spurium.
TY, tympanic bone.
VPH, vagina processus hyoidei.

wide, roofing the lateral portion of the tympanic cavity. There is no superficies meatus. The posterior horizontal process of the alisphenoid forms a larger area of the roof of the auditory bulla than in *Merycoidodon*.

TYMPANIC REGION
PARS PETROSA OF THE PERIOTIC BONE

This bone possesses several peculiarities which are not shared by the pars petrosa of most living Artiodactyla: unfortunately it was impossible to determine, either from the literature or from dried skulls, whether these are shared by the Tragulidae.

The ascending plate forming the lateral border of the subarcuate fossa is, in *Leptomeryx*, extraordinarily high. It reaches dorsally a distance of 7 mm. from the plane of the temporal ridge (almost one-half the height of the braincase), and serves as the medial wall of the proximal part of the temporal canal (fig. 31, *APP*).

Ventromedially, another process of the pars petrosa projects between the basisphenoid bone and the auditory bulla (fig. 31, *VPP*). Lull reports this feature in *Allomeryx planiceps* (1922). In most mammals the pars cochlearis lies in or near this postion; in *Leptomeryx* it lies dorsal to it, well within the braincase.

FIGURE 30.—*Leptomeryx evansi*, ventral view of basis cranii. M. C. Z. 6566. × 2.

B, auditory bulla.
CF, condylar foramina.
FLA, foramen lacerum anterius.
FLP, foramen lacerum posterius.
FO, foramen ovale.
FSA, anterior subsphenoid foramen.
FSM, stylomastoid foramen.
M, pars mastoidea of periotic bone.
OC, occiptal bone.
PBC, petrobasilar canal.
SQ, squamosal bone.
TC, foramen jugulare spurium.

Leptomeryx had the six endoturbinal scrolls of the modern Artiodactyla (including the Tragulidae).

Many delicate fragments of ectoturbinals can also be seen, but the number of these cannot be estimated.

The nasoturbinals (a single scroll) and the maxilloturbinals (a bifurcated scroll) are identical with those of the Tragulidae, being more heavily ossified than the ethmoturbinals.

The external surface of the parietal bone closely reflects the shape of the brain. It is cancellous only where it fills the gap between cerebrum and cerebellum; elsewhere it is little more than 1 mm thick.

Like the parietal, the part of the squamosal participating in the braincase wall is very thin and nondiploic.

The horizontal plate of the squamosal is, relative to the size of the vertical plate, much less well developed in *Leptomeryx* than in most other Artiodactyla. The facies epitympanica (fig. 31, *FE*) is a plate only 2 mm.

FIGURE 31.—*Leptomeryx evansi* Leidy. × 2. Thick section from sections L 14–36, viewed anteriorly from region of bulla.

APP, ascending process of pars petrosa.
AS, alisphenoid.
B, bulla.
BS. basisphenoid.
FE, facies epitympanica of squamosal.
FS, facial sulcus.
ICC, internal carotid canal.
PAR, parietal.
PET, pars petrosa.
PM, pars mastoidea.
SF, subarcuate fossa.
SQ, squamosal.
TC, temporal canal.
TT, tegmen tympani.
VPP, ventral process of pars petrosa.

The subarcuate fossa of *Leptomeryx* (fig. 31, *SF*) resembles that of *Merycoidodon* and the carnivores in being a definite but shallow depression in the dorsal wall of the pars petrosa. It is divided into two subequal portions by a low antero-posterior ridge, which may indicate that the fossa contained two cerebellar gyri. The subarcuate fossa bears no resemblance to that of the Camelidae.

The sulcus facialis of *Leptomeryx* lies in the extreme lateral side of the roof of the tympanic cavity (fig. 31, *FS*). It is separated from the squamosal by a ventrally projecting plate of the pars petrosa, the lower end of which is inserted in the stylomastoid foramen and extends to within a few millimeters of the ventral surface of the skull.

MIDDLE EAR AND SURROUNDING STRUCTURES

The epitympanic recess in *Leptomeryx* is, considering the size of the middle ear, a fairly long cavity (fig. 31). Its anterior part is covered chiefly by the tegmen tympani of the pars petrosa; laterally it is bounded by the squamosal and the tympanic. Farther anteriorly it is roofed entirely by the tympanic.

The epitympanic recess of *Tragulus* (van der Klaauw, 1931) is like that of *Leptomeryx*.

As in all Artiodactyla, no tympanic sinus is present.

The auditory bulla of *Leptomeryx* (fig. 17, *B*) is hollow, unlike that of most tragulid species. It is only moderately inflated, extending ventrally to the level of the basioccipital. It is in contact medially with the petrosal, a ventral process of which separates it from the basioccipital; dorsally with the posterior process of the alisphenoid (fig. 31) and laterally with the squamosal. It is fused to none of these elements.

The tympanic gap ("tympanicumdefekt" of Bondy, 1907), or dorsal opening in the inflated auditory bulla, is small in *Leptomeryx*. The tympanic bone arches dorsal to the lateral part of the epitympanic recess, so that the tympanic gap is only half as wide as in *Merycoidodon* and *Poebrotherium*. In *Leptomeryx*, the gap is closed partly by the pars petrosa, as is usual, and partly by the posterior process of the alisphenoid.

The tympanic gap does not extend to the anterior part of the bulla (fig. 31).

The incisura tympanica is absent in *Leptomeryx* as in the Tragulidae. In the former, the position usually occupied by the incisura, dorsal to the medial end of the external auditory meatus, is covered within the tympanic cavity by the ventro-lateral plate of the pars petrosa which serves as the lateral wall of the facial sulcus. *Leptomeryx* thus could not have possessed a pars flaccida of the tympanic membrane.

The stylomastoid foramen of *Leptomeryx* is, like that of the Tragulidae, situated between the paroccipital process, the pars mastoidea, the posttympanic process, and the tympanohyal bone (fig. 30, *FSM*). The tympanohyal separates the foramen from the bulla.

EXTERNAL AUDITORY MEATUS

The meatus is short, with a diameter almost as great as that of the bulla and twice as large as that of the Tragulidae. It slants posterodorsally. Its posterior wall is formed by the posttympanic process of the squamosal; the tympanic occupies the other three walls of the tube. In the Tragulidae, however, the tympanic forms the entire meatus.

PARS MASTOIDEA OF THE PERIOTIC BONE

As figures 29 and 30 (*M*) show, the pars mastoidea is extensively exposed upon the occipital surface of the skull as in the Carnivora, rather than on its lateral surface as in all other mastoid Artiodactyla, including the Tragulidae, and *Hypertragulus*. This characteristic of *Leptomeryx* is probably a primitive one; in this respect *Leptomeryx* resembles the hypothetical ancestor of the amastoid Artiodactyla postulated by Helga Pearson (1927, p. 456, 457).

The pars mastoidea is large, relative to that of *Merycoidodon* and *Poebrotherium* (fig. 31, *PM*). Here, in the back part of the bone, is a large cavity which, having no direct outlet, must be diploic in nature. In the front part, the mastoid cells are smaller.

As in the Tragulidae (Milne-Edwards, 1864), the mastoid process is separated from the bulla by the posttympanic process of the squamosal (fig. 29).

PNEUMATIC SINUSES

The maxillary pneumatic sinus is the only one present in *Leptomeryx*. This is also true of the Tragulidae (Aubert, 1929), and seems to be typical of small mammals. In *Leptomeryx* it lies above the cheek tooth row, and extends antero-posteriorly about 5 mm.

CIRCULATORY SYSTEM OF THE SKULL
ARTERIES

No separate posterior carotid foramen is visible on the basis cranii of *Leptomeryx* (fig. 30), but the serial sections indicate that here, as in *Poebrotherium*, *Protoreodon* and a few groups of living mammals, the internal carotid artery entered the carotid canal through an opening anterior to the foramen lacerum posterius.

A cross-section of the posterior portion of the carotid canal in *Leptomeryx* is seen in figure 31 (*ICC*), which shows a canal between the dorsomedial tympanic wall of the tympanic cavity and the ventral side of the

posterior process of the alisphenoid bone. Apparently the artery lies for a short distance in the posterior third of the petrobasilar canal (fig. 30, *PBC*), then enters the carotid canal near the dorsal edge of the medial wall of the bulla. The artery extends dorsal to the bulla for only about 2 mm, leaves the canal through the anterior carotid foramen, enters the cranium through the foramen lacerum medius, and extends anteriorly in a groove in the floor of the basis cranii.

The internal carotid artery in *Leptomeryx* was much less superficial in position than that of the Tragulidae, in which as a rule, it lies in a simple groove in the medial wall of the bulla.

VEINS

DORSAL SINUS SYSTEM

There is no indication in the *Leptomeryx* skull of the details of the dorsal cranial vessels anterior to the transverse sinus, but several of the distributaries of the sinus are well marked.

There was no temporal venous sinus in *Leptomeryx*, and the temporal canal, bearing the superior cerebral vein, was similar to that of the living Artiodactyla. The superior cerebral vein left the brain cavity high up on its lateral wall, extended ventrally in the temporal canal (fig. 31, *TC*), between the mastoid and squamosal bones, and left the skull through a foramen just behind the external auditory meatus (fig. 30, *TC*).

As in most Artiodactyla, an anterior branch of the temporal canal passed anteriorly in the temporal crest to a foramen on its dorsal side in the region of the root of the zygoma.

The transverse sinus of *Leptomeryx* was also drained by a vein that occupied the post-parietal canal, which extends posteriorly in the parietal bone and opens upon the dorsal surface of the braincase through the post-parietal foramen (fig. 29, *FPP*).

BASILAR SINUS SYSTEM

Other than the groove in the cranial floor for the cavernous sinus, and the petrobasilar canal for the inferior petrosal sinus (fig. 30, *PBC*), there is no evidence as to the condition of this system in *Leptomeryx*.

SINUS VENOSUS OSSIS SPHENOIDALIS

This sinus in *Leptomeryx* was about 3 mm long. It differed from those of *Merycoidodon* and *Poebrotherium* chiefly in that the associated subsphenoid canals extended laterally into the alisphenoid bone (fig. 30, *FSA*).

MORPHOLOGICAL CONCLUSIONS

The studies upon which this paper is based have yielded a number of new facts concerning the endocranial anatomy of Oligocene Artiodactyla. Some of these observations add to the existing information concerning evolutionary trends in this order; others, because of the lack of sufficient data for comparison, can only be recorded in hopes that further studies, bridging the gap between the Oligocene and Recent epochs, will give them significance.

The characteristics observed may be divided into three categories:

(a) Primitive characteristics.

(b) Characteristics whose significance is doubtful, but which are noted because they have never before been observed.

(c) Anatomical peculiarities indicating the habits of the genus involved, evolutionary tendencies within the artiodactyl group to which it belongs, or its relationships to other artiodactyl groups.

The characteristics to which the first two categories may be applied are listed under the headings used above for subdividing the morphological discussions, then the diagnostic anatomical features are discussed individually.

BONES OF THE SKULL

PRIMITIVE CHARACTERISTICS

1. In *Merycoidodon*, the pituitary body was contained between two thin, longitudinally oriented, bony plates. These represent the taenia interclinoidalis, the primitive lateral wall of the braincase.

2. In *Merycoidodon* and *Poebrotherium* the superficies meatus of the squamosal is wide and heavily ossified as compared to that of *Leptomeryx* and the living Artiodactyla. The reduction of the superficies in living genera is concomitant with the shortening and lightening of the bony meatus.

3. *Merycoidodon* is unique among the Artiodactyla in that the posttympanic process of the squamosal participates in forming the ventral wall of the external auditory meatus.

CHARACTERISTICS OF DOUBTFUL SIGNIFICANCE

1. The mesethmoid bone of *Merycoidodon* is very heavily ossified midway between the cribriform plate and the anterior nares. This suggests that the mesethmoid and presphenoid bones in this genus ossified separately. If this were the case, this genus would be sharply differentiated from the other Artiodactyla. It is probable, however, that the thickness of the mesethmoid is simply a part of the heavy ossification of the entire nasal region in *Merycoidodon*.

2. The posterior horizontal process of the alisphenoid of *Leptomeryx* extends far enough posteriorly to close the anterior part of the tympanic gap. This is apparently most unusual among Artiodactyla, but comparative data are incomplete.

TYMPANIC REGION

PRIMITIVE CHARACTERISTICS

1. The tympanohyal bone of *Merycoidodon*, *Poebrotherium*, and *Leptomeryx* was inserted loosely into the vagina processus hyoidei. This is in contrast to the living Artiodactyla, in which the tympanohyal is fused to the tympanic in the fundus of the vagina.

2. The tympanic gap of *Merycoidodon* is larger than that of living Artiodactyla or of *Leptomeryx*. This is regarded as primitive because it more closely approximates the primitive ring-form of the tympanic (van der Klaauw, 1931) than does the condition in which the bulla is partly closed dorsally.

The size of the tympanic gap determines the composition of the roof of the epitympanic recess. If it is small, as in *Leptomeryx* and most living Artiodactyla, the tympanic itself forms most of the roof. If it is large, as in *Merycoidodon* and the Tylopoda, the pars petrosa is the important element involved.

CHARACTERISTICS OF DOUBTFUL SIGNIFICANCE

1. In *Merycoidodon*, the fissura glaseri is almost entirely surrounded by the tympanic bone. This is not the case in any living artiodactyl (van Kampen, 1905), or in *Poebrotherium* or *Leptomeryx*. It may, at least until further information becomes available, be regarded as a structure characteristic of *Merycoidodon*.

2. An entotympanic bone is present in *Merycoidodon*. Because of the sparseness of knowledge concerning this bone, even in Recent Artiodactyla, speculation on this fact is useless.

3. The meaning of the presence or absence of the incisura tympanica is often difficult of interpretation. It is missing in *Leptomeryx* and the Tragulidae, probably because the relatively large size of the tympanic annulus, together with the great reduction of the horizontal plate of the squamosal, leaves no room for such a structure. The lack of the incisura in these genera is due to the small size of their skulls.

The condition in the Tylopoda is, however, puzzling. The incisura tympanica is missing in the living members of the suborder (van Kampen, 1905), but well developed in *Poebrotherium*. Only one explanation can at present account for this discrepancy. In the living Tylopoda a portion of the tympanic bone forms the roof of the external auditory meatus, and thus the superficies meatus of the squamosal, which performed this function in *Poebrotherium*, is excluded from its participation in the attachment of the tympanic membrane. This membrane in modern Tylopoda is, therefore, attached throughout its circumference to a ring of bone; in *Poebrotherium*, due to a gap in this ring, it was possible for a dorsal portion (the pars flaccida) of the membrane to be attached to a process of the squamosal below which lay the incisura tympanica.

This evolutionary trend in the Tylopoda conforms with the already mentioned tendency in all mammals toward closure of the tympanic gap.

4. *Leptomeryx* differs from all other mammals observed by the writer or mentioned in the literature in the extreme height of the ascending plate of the pars petrosa, which serves as the lateral border of the subarcuate fossa. In this genus, this plate composes almost the entire medial wall of the temporal canal. It probably appears unusually high simply because of the small size of the skull. This supposition is borne out by the large size of the pars petrosa as a whole in proportion to the size of the *Leptomeryx* skull. It is a recognized fact that, in small mammals, the organs of sense occupy, comparatively, a greater space than in larger ones.

5. A characteristic which, in the present state of knowledge, distinguishes *Leptomeryx* from all other Artiodactyla is the great ventral extent of that plate of the pars petrosa which forms the lateral wall of the facial sulcus. No functional reason for this condition is evident, nor is it a stage in any known evolutionary trend in skull development. It is not present in the Tragulidae, so that it would not seem necessarily associated with small skull size. It is therefore here tentatively suggested that this peculiarity may be a hypertragulid (or perhaps only a leptomerycid) characteristic.

PNEUMATIC SINUSES

PRIMITIVE CHARACTERISTICS

In their small extent and number, and in the lack of any interconnections between them, the pneumatic sinuses of the three Oligocene genera here discussed are primitive. This is most strikingly apparent in *Merycoidodon*, whose thick cranial bones were capable of housing a much more complicated sinus system than the animal possessed. This bears out Paulli's statement (1900) that the complicated sinus system of modern type did not appear until late in the Miocene epoch.

ARTERIES

PRIMITIVE CHARACTERISTICS

1. In the three Oligocene genera studied, evidence was found that the internal carotid artery was functional, a primitive condition in the Artiodactyla. The artery was relatively much smaller in *Poebrotherium* than in *Merycoidodon* or *Leptomeryx*.

2. The absence in *Merycoidodon* of a rete mirabile of the intracranial part of the internal carotid artery is, in all probability, also primitive.

VEINS AND VENOUS SINUSES

PRIMITIVE CHARACTERISTICS

1. The sinus venosus ossis sphenoidalis and the sub-sphenoid canals, possessed by all three of the Oligocene genera studied here, were part of an archaic type of venous cranial circulation. This conclusion is based upon their absence in living Artiodactyla as opposed to their apparently widespread occurrence in Oligocene time, and also upon their presence in primitive living mammals: the Insectivora and Marsupialia, as well as the Lagomorpha and some Rodentia. The conclusion that these blood vessels are primitive in character is further borne out by their absence in the Merycoidodontidae after the late Oligocene.

2. The vein of the sinus canal, which was possessed by *Merycoidodon* and *Poebrotherium*, was another primitive artiodactyl characteristic. The same evidence contributes to this conclusion as was cited in the case of the sinus venosus ossis sphenoidalis.

3. The presence of a temporal venous sinus in *Merycoidodon*, and to a far lesser extent in *Poebrotherium*, is due to the fact that the small size of the brain relative to skull size leaves space available for the sinus.

4. The vestigial vena capitis lateralis, observed in *Merycoidodon*, was probably merely a relic from the embryonic stage, various manifestations of which are often encountered in adult modern Mammalia.

ANATOMICAL PECULIARITIES INDICATING HABITS, EVOLUTIONARY TRENDS, OR RELATIONSHIPS

Mesethmoid ossification in Merycoidodon.—As has been discussed at length above, the extremely strong bony nasal septum of this genus resembles closely that of the peccary, and indicates similar rooting habits.

The thickness and extensive development of the turbinal bones of this genus were undoubtedly the result of the unusual degree of ossification of the septum.

Tendency of Selenodontia to approach the amastoid condition.—Comparison of *Poebrotherium* with the living Tylopoda, and especially of *Merycoidodon* with the later Merycoidodontidae, reveals a progressive and distinct reduction in the area of the pars mastoidea exposed upon the surface of the skull. This does not diminish the value of the mastoid-amastoid distinction drawn by Pearson (1927); it simply points out that the mastoid and amastoid Artiodactyla differ in this respect only in the degree of advancement of a trend that is present in both.

Absence of the epitympanic sinus.—In this characteristic, the three Oligocene genera examined resemble the living Artiodactyla. In mammals as a whole, the absence of the epitympanic sinus is also the rule rather than the exception.

Course of the internal carotid artery.—In *Merycoidodon*, this artery courses through the auditory bulla as in the Carnivora; in this it differs from all other Artiodactyla in which the internal carotid is known. Probably this is true of all the Merycoidodontidae.

The other two Oligocene genera studied possessed a carotid canal medial to the bulla, as in the living Tylopoda and Tragulidae.

In the study of various phylogenetic lines of the Artiodactyla there was observed a tendency to posterior migration of the posterior carotid foramen: in other words, the length of the carotid canal progressively increased. This backward migration culminates when the posterior carotid foramen merges with the foramen lacerum posterius.

Migration of the posterior carotid foramen was completed early in the evolution of the Merycoidodontidae, much later in the Camelidae.

Tendency toward reduction of the internal carotid artery in the Artiodactyla.—The internal carotid, absent or non-functional in almost all living Artiodactyla, was present and well developed in some Oligocene members of the order, according to the observations recorded here. It was strong in *Merycoidodon* and *Leptomeryx;* in *Poebrotherium*, oddly enough, it was relatively no larger than in the living *Camelus*. This suggests that, in the Oligocene ancesters of the Tylopoda, the reduction in size of this artery may have progressed further than in *Merycoidodon* and *Leptomeryx*, which apparently represented more archaic sidelines of artiodactyl phylogeny.

Internal jugular vein replaced by external jugular as dominant efferent cranial vessel.—In *Merycoidodon* especially, and to a less degree in *Poebrotherium*, most of the blood from the facial region and the braincase found its exit from the skull by way of the basilar sinus system and the sphenoidal venous sinus, and thence to the internal jugular vein. In the course of evolution to the modern artiodactyl condition, the sphenoidal venous sinus disappeared and the ventral petrosal sinus lost some of its tributaries. The result was that blood from the face adopted a course outside the cranium, while most of the endocranial blood was drained off through the superior cerebral vein. Both these vessels are tributary to the external jugular vein.

The lobulus petrosus of the cerebellum.—This lobule of the brain is absent in all but a few living Artiodactyla. In two of these, *Oreamnos* and *Sus*, it is very small. In the modern Tylopoda, on the other hand, it is well developed, and is enclosed dorsally by the arch of the posterior semicircular canal. This is also the case in the Oligocene *Poebrotherium*. In *Leptomeryx* and *Merycoidodon* of the Oligocene the lobulus was

present and very large; it resembled that of the living Carnivora in being housed in a deep fossa in the dorsal side of the pars petrosa. It was not arched over by the semicircular canal as in the Tylopoda.

The strong similarity, amounting almost to identity, between the lobulus petrosus of the Tylopoda and those of the Lagomorpha and some Rodentia is difficult to explain, especially as the function of this lobule is not definitely known. The consensus of opinion seems to be that it functions in maintaining proper static and kinetic conditions in a fluid medium, since it is highly developed in the Pinnipedia. It may be that this type of lobule in the Lagomorpha serves in maintaining equilibrium in jumping, and that in the Tylopoda it is a relic of ancestral leaping habits in the Artiodactyla, such as are suggested by the double rollers possessed by the artiodactyl astragalus.

PHYLOGENETIC CONCLUSIONS

Study of the cranial anatomy of *Merycoidodon*, *Leptomeryx* and *Poebrotherium* reveals that these three genera (and, presumably, most other early Oligocene Artiodactyla) possessed structures which are found today only in the Marsupialia, Insectivora, Lagomorpha, and some Rodentia. These characteristics are evidence of the fact that Oligocene artiodactyls were nearer in structure to their primitive, insectivorelike ancestors than might be judged from their superficial appearance. Investigation of the cranial anatomy of Artiodactyla from the Wasatch, Bridger, and Uinta formations is likely to give further information concerning the steps involved in the gradual loss of primitive mammalian cranial characteristics by the artiodactyls. It may even yield specific information concerning the stem group from which the Artiodactyla sprang, presumably in the Paleocene.

The crania of the Oligocene Artiodactyla also possess some details of structure which add to the body of knowledge from which, in turn, can be derived a partial understanding of the interrelationships of the various artiodactyl families and suborders. The conclusions resulting from this evidence are discussed below.

TYLOPODA

Poebrotherium was an advanced artiodactyl by early Oligocene standards, as is shown particularly by the pattern of its cranial circulation. Its relatively advanced state of evolution facilitates comparison with living Tylopoda and the establishment of *Poebrotherium* as one of an almost direct line leading to the modern genera.

One of the most striking pieces of evidence linking *Poebrotherium* with the living Tylopoda is its peculiarly constructed subarcuate fossa, which is identical in the genera of Oligocene and modern times and occurs in no other Artiodactyla, living or fossil. The great antiquity and unique character of this structure is strong evidence of the long independent existence of the suborder, which must have separated from the other artiodactyl lines in the middle Eocene at the latest.

Most cranial features of *Poebrotherium*, such as its inflated, cancellous bullae, carotid canal and the structure of the middle ear region, bear out the opinion of previous authors that this genus was a direct ancestor of modern Tylopoda.

The living Tylopoda, as is shown by their many resemblances to their Oligocene relative, are no longer advanced members of the artiodactyl fauna. This reflects the fact, evident in postcranial as well as in cranial structures, that tylopod evolution was rapid in the early Tertiary and proceeded at a much more leisurely rate thereafter.

MERYCOIDODONTIDAE

Merycoidodon has the greatest number of primitive cranial features of the Oligocene genera examined; it may therefore be regarded as an archaic member of the artiodactyl fauna of the White River group. This agrees with the degree of advancement observed in other merycoidodont genera as compared to that of their contemporaries.

The structure of the subarcuate fossa in *Merycoidodon* is also important taxonomically. Although well developed, it is smaller than that of *Poebrotherium*, and is formed in an entirely different manner. This fact supports the majority of paleontologists in denying Rütimeyer's and Scott's hypothesis that the Merycoidodontidae are closely related to the Tylopoda.

The subarcuate fossa of *Merycoidodon* differs only in size from that of *Oreamnos* (one of the Capridae); in other living Pecora this structure has disappeared. This evidence is not cited to prove *Oreamnos* a close relative of *Merycoidodon;* rather, it is cited as proof that the Pecora once possessed a subarcuate fossa of the type found in *Merycoidodon*, and that this fossa has been, since the Oligocene, reduced and finally lost.

It may therefore be concluded on the basis of evidence now available that the Merycoidodontidae belong near the base of the phylogenetic tree of the suborder Pecora.

Before the above conclusion can be regarded as final, much further investigation will be necessary. The problem of the origin and relationships of the Merycoidodontidae apparently will depend for its solution upon the unearthing of more details concerning the morphology of other primitive selenodonts and bunoselenodonts of the lower Tertiary. Particularly im-

portant in this respect are the Anthracotheriidae, Caenotheriidae, Anoplotheriidae, and Homacodontidae. It is possible that research into the cranial anatomy of these primitive families will establish their taxonomic positions more definitely.

LEPTOMERYCINAE

The cranial morphology of *Leptomeryx* and related genera strongly supports including them in a subfamily of the Hypertragulidae, equal in status to the subfamily Hypertragulinae. The diagnostic cranial features of the Leptomerycinae are the exposure of the pars mastoidea upon the surface of the occipital plate (a feature otherwise unknown in Selenodontia) and the presence of a ventral process of the pars petrosa separating the basioccipital bone from the auditory bulla. Both these characteristics are found in *Allomeryx*, of the John Day formation of early Miocene age, a fact that proves that the leptomerycine line survived as long or longer than that of the Hypertragulinae.

The simple subarcuate fossa of *Leptomeryx* reinforces other cranial evidence in suggesting Pecoran affinities. Again the theories of Rütimeyer and Scott are contradicted, for these authors believed the Hypertragulidae, like the Merycoidodontidae, to have been closely related to the Tylopoda.

No conclusive evidence has been adduced concerning the relationship between the Hypertragulidae and the Tragulidae. Many similarities exist between the extinct family and the living one, but probably most of these are due to small skull size.

SUMMARY OF PHYLOGENETIC CONCLUSIONS

1. The early Oligocene Artiodactyla were not far removed from an ancestral group resembling the Insectivora.
2. The Tylopoda represent an evolutionary line that has been independent of all other Artiodactyla since the middle Eocene, at least.
3. The Hypertragulidae are members of the suborder Pecora; the Merycoidodontidae belong close to the base of the phylogenetic tree of this suborder.
4. The Hypertragulidae consist of two subfamilies, the Hypertragulinae and Leptomerycinae, both of which survived from early Oligocene into early Miocene time.

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Shorter Contributions

to General Geology

1952

UNITED STATES DEPARTMENT OF THE INTERIOR

Douglas McKay, *Secretary*

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