GEOLOGICAL SERIES
OF
FIELD MUSEUM OF NATURAL HISTORY

Volume VI CHICAGO, DECEMBER 28, 1937 No. 19

SOME NOTOUNGULATE BRAINCASTS

BY BRYAN PATTERSON
ASSISTANT CURATOR, PALEONTOLOGY

RESULTS OF THE MARSHALL FIELD PALEONTOLOGICAL EXPEDITIONS TO ARGENTINA AND BOLIVIA, 1922–27

In a recent paper of this series I published the results of a study of the middle ear structure of representative notoungulates (1936). This investigation was made in an attempt to discover heritage characters of possible phylogenetic and taxonomic importance. The results obtained were important enough to warrant testing them against evidence derived from another deep-seated structure—the brain. The results here presented are derived from a study of braincasts of several important genera, and extend the excellent work of Simpson (1933a, b), who has described representative genera of several notoungulate families.

Before describing the specimens, the technique employed in obtaining the casts may be briefly explained. With one exception these are artificial and were made by the use of a liquid rubber preparation. The extreme flexibility and ease of application of this substance render it ideal for the purpose. Liquid rubber is more convenient than glue or gelatine for this type of work, as it requires no heating and contains no water that would affect plaster joints in the specimen. No separator is needed. In dealing with friable bone, however, the surface to be cast should be thoroughly hardened with shellac or bakelite. The rubber penetrates every minute crack and crevice and is for this reason very hard to pull away from untreated porous bone, and may even take away with it sections of such bone. Two to three coats of the liquid rubber are applied evenly to the bone with a brush. In dealing with a complete cranial cavity, the rubber may be poured in, rolled, and drained out. Each coat will dry within three or four hours. After application of the third or fourth coat, pulverized cork is dusted on to the wet rubber and allowed to dry with it. Successive coats of rubber and cork are applied until a thickness of a sixteenth to an eighth of an inch (2 to 4 mm.), depending upon the size of the specimen, has been reached. The cast is then allowed to dry for some twenty-four hours before removal.

After being pulled, the cast is filled with plaster to preserve its shape while a mold of it is being made, preparatory to the making of permanent plaster casts. The durability of the rubber casts is not known. Some of those described here were prepared more than a year ago and appear to have suffered no deterioration. The liquid rubber solution used was obtained from a local firm, Devoe & Raynolds Company, 29 South Wabash Avenue, Chicago, at a cost of $1.55 per pint.

I wish to express my thanks to Mr. Elmer S. Riggs for editing copy, to Mr. James H. Quinn for his skilful preparations, and to Mr. Frank H. Letl for introducing me to the liquid rubber technique. I am, as always, deeply indebted to Mr. Carl F. Gronemann for his painstaking work on the illustrations.

Notohippidae Ameghino

Rhynchippus Ameghino (fig. 75).

Two braincasts of *R. equinus* Ameghino are available. The first is an excellent artificial cast taken from F.M. No. P13410 in which only the olfactory bulbs are imperfect; the second is a poor artificial cast taken from F.M. No. P13420, which has fairly good olfactory bulbs. Some notes are given below on a natural cast described by Professor Loomis under the name of *Eutrachytherus spegazzinianus*, but which unquestionably belongs in the Notohippidae. The Field Museum specimens were collected from the Deseado beds at Cabeza Blanca, Chubut, Argentina by the late Mr. J. B. Abbott.

The total length of the skull of P13410 is 245 mm.; that of the braincast, exclusive of medulla, is approximately 93 (olfactory bulbs restored from P13420). The index is 38, and the ratio of olfactory bulbs: cerebrum: cerebellum is about 3: 11: 5. Exposure of the olfactory bulbs, extent of overlapping of the cerebellum by the cerebrum, and degree of flexure are comparable to the conditions seen in *Hegetotherium* (Simpson 1933b).

The rhinencephalon is well developed, but differs in details from that of most notoungulate braincasts hitherto described. In contrast to the typotheres and in agreement with *Rhyphodon* (Simpson

1933a) and *Toxodon* (Gervais 1872), the prominent olfactory bulbs are completely separated by a deep groove, which, however, does not affect the heavy deep peduncles, and is not continuous with the longitudinal scissure dorsally. The bulbs are laterally compressed and much deeper than wide, a marked difference from those of *Rhyphodon*. In this character there is an approach to *Toxodon*, but in the Pampean form the bulbs are more widely separated. An interesting feature that has been noted is the presence of a foramen in the posterior part of the orbit, on the level of the optic foramen, which enters the olfactory fossa low on its lateral side. This foramen has been observed on both sides of P13410 and on the left side of P13420 (the right side is broken). From its position, it would seem possible that it transmitted the ethmoidal artery or arteries and perhaps the nasal nerve, if this nerve re-entered the cranial cavity in notoungulates.

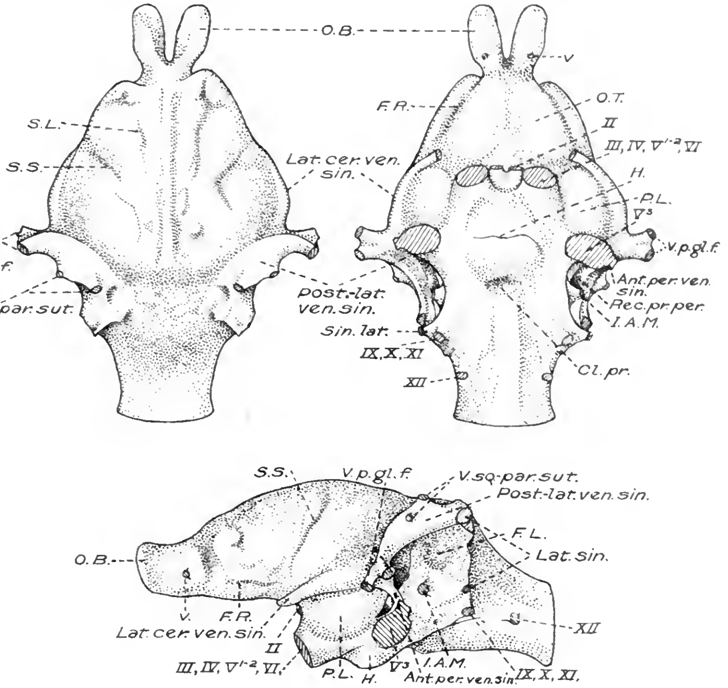

FIG. 75. ***Rhynchippus equinus*** **Ameghino. Dorsal, ventral, and left lateral views of braincast. F.M. No. P13410. Olfactory bulbs in part restored from F.M. No. P13420. For abbreviations see p. 301. ×½.**

The olfactory tubercles are prominent, but not quite so conspicuous as in *Hegetotherium.* The pyriform lobes are large, but not visible in dorsal view. In outline and proportions they resemble those of *Rhyphodon* more closely than any form already described, and are not as expanded medially as those of *Hegetotherium.* They are notably shallower than the neopallium.

In outline, the neopallium is roughly triangular, but it is relatively wider anteriorly than that of *Hegetotherium.* It definitely extends back beyond the pyriform lobes. The rhinal fissure is distinct anteriorly, but is concealed posteriorly by the large lateral cerebral venous sinus. No fossa Sylvii can be seen. The fissura Sylvii of the right side curves upward and backward almost in a semicircle; on the left side the posterior portion is lacking. In contrast to the typotheres, there appears to have been no suprasylvian sulcus. The sulcus lateralis is well defined anteriorly, poorly so posteriorly, and is completely interrupted in the middle of the cerebrum. It is somewhat curved, being closer to the longitudinal scissure at its center than at either extremity. Short crescent-shaped sulci are present in the coronal area, evidently homologous with the similarly situated depressions of *Hegetotherium.* The one on the right side is aligned antero-posteriorly with the horns of the crescent facing laterally, and is joined by the sulcus lateralis. The left sulcus is aligned transversely, with the horns facing anteriorly. The sulcus lateralis falls well short of it. The right coronal area extends further forward than the left. Between the coronal sulcus and the fissura rhinalis on the right side is an S-shaped, laterally-facing sulcus. On the left side there is only a small pit in this position. These depressions, and similarly situated ones in *Nesodon* and *Adinotherium* correspond, at least topographically, to the anterior portion of the sulcus in *Proterotherium* provisionally regarded by Simpson (1933b, p. 10) as ectosylvian. The longitudinal scissure is filled for its entire length by the external longitudinal sinus. The convolution pattern of *Rhynchippus* is about as definite as that of *Hegetotherium,* different in some features, and perhaps slightly more complex. It compares quite closely with that of *Adinotherium* to be described below. A striking feature of the cast at hand is the marked differences between the sulci on the two sides of the neopallium. This feature is perhaps abnormal, but the perfect preservation of the skull indicates that it is not artificial.

The hypophysis is nearly circular in outline, large, and very deep. It extends ventrally well below the pyriform lobes and the fillings of the anterior lacerate foramina. Immediately behind it is a sharply defined concavity for the posterior clinoid process.

Almost no structural details of the dorsal and occipital faces of the cerebellum can be seen. The dorsal exposure is narrow antero-posteriorly and wide transversely, equalling in width the anterior part of the neopallium. The occipital face slopes downward and backward at an angle of about 45°, and is gently convex transversely. Definite indication of lobes is lacking, and the postero-external angle is obscured by a thin lateral extension of the cast—the filling of a narrow gap between the postero-internal angle of the periotic and the supra- and exoccipital—which runs down to the foramen lacerum posterius. The lateral face is rough and rather complex. The internal auditory meatus is situated beneath the posterior extremity of the cerebrum. The ascending crus of the formatio vermicularis cannot be made out; the descending crus is stout. The "flocculus" is large and directly above the internal auditory meatus. Due to the fact that the dorsal portion of the medial face of the periotic slopes outward, the ascending crus and flocculus extend laterally over the internal auditory meatus. Anteriorly the periotic is produced into a stout medially expanded process which points downward and forward, forming a large cavity in the cast in front of the flocculus and meatus.

In the region of the pons is a long gently convex area which fades away posteriorly at the level of the posterior lacerate foramina. The medulla is broader than deep and presents no structural peculiarities.

The nerve exits are all well preserved. The optic chiasma is stouter and much broader than in *Hegetotherium*, and is notably retracted above the fillings of the anterior lacerate foramina. The passages for III, IV, V^{1-2}, and VI are very large and in the usual position. The foramen ovale (V^3) is equally large, and, as described below, transmitted a large vein in addition to the nerve. The position of the internal auditory meatus (VII, VIII) with respect to the posterior extremity of the cerebrum has been noted above. It is definitely on the lateral surface of the cast, a resemblance to *Rhyphodon*. IX, X, and XI were transmitted, as usual, through the foramen lacerum posterius. XII is single, of medium size, and further from the lacerate foramen than in *Rhyphodon*.

The vascular sinuses are more conspicuous on this cast than on that of any notoungulate yet described. The large lateral cerebral venous sinus runs along the rhinal fissure, as in the typotheres but, in contrast to these forms, it passes to the outside of the skull through a foramen situated above the foramen opticum. This somewhat resembles the condition in *Rhyphodon* which, although lacking a lateral cerebral venous sinus, has a prominent vascular exit near to and above the optic and anterior lacerate foramina. The periotic of *Rhynchippus* is not united dorsally with the cranial roof, and in consequence a cavity exists above and lateral to it, which was not filled by any part of the brain, but which housed the very large postero-lateral venous sinus. The cast of the sinus is crescent-shaped with the horns of the crescent extending laterally and posteriorly. At its lateral extremity it receives two veins from the post-glenoid drainage. The lateral cerebral venous sinus enters anteriorly, and at the same point a sinus is given off ventrally which runs down to the foramen ovale. Two veins are received dorsally which enter the sinus through foramina opening externally along the squamoso-parietal suture. The posterior extremity leads to the mastoid foramen. Beneath the posterior extremity a poorly defined sinus leads ventrally, posterior to the periotic, to the foramen lacerum posterius where it undoubtedly passed to the internal jugular vein. The superior longitudinal sinus is visible along the entire length of the longitudinal scissure. At its posterior extremity it tends to bifurcate; this tendency is stronger on the Amherst cast, and is fully completed in the young *Adinotherium* described below. The two branches presumably joined the postero-lateral sinuses either directly or by joining a sinus running across the cerebellum, for there must have been one or more of these connecting the postero-lateral sinuses behind the blunt inconspicuous tentorium. One certainly connected, either directly across or via the postero-lateral sinuses (judging from the specimen, the latter alternative is more probable), the two sinuses which descend, posterior to the periotic, to the posterior lacerate foramina. This arch is unquestionably the homologue of the lateral (transverse) sinus of other mammals. This and the superior longitudinal are the only venous sinuses occurring in notoungulates that can be certainly homologized at present. To the others topographic names may be assigned. Simpson has already named the lateral cerebral and the postero-lateral. The sinus running down to the foramen ovale, I name anterior periotic. This appears to be the equivalent, if not the homologue, of the superior petrosal in man. The foramen, probably arterial, opening out of the olfactory fossa has been described above.

The brain of *Rhynchippus* appears to be approximately as progressive as those of the typotheres, but is of a somewhat different type. The major distinctions of *Rhynchippus* are:

1. Olfactory bulbs completely separated.
2. Some differences in cerebral convolution pattern.
3. Pyriform lobes not as much expanded toward the mid-line.
4. Hypophysis much larger.
5. Lateral cerebral venous sinus passing anteriorly to the outside of the skull.[1]
6. A venous sinus passing down to the foramen ovale.
7. Postero-lateral venous sinus widely open medially, due to failure of periotic to reach cranial roof.
8. Large anterior process of periotic.

No. 8 is so far unknown in other notoungulates, 7 occurs in *Oldfieldthomasia* (Simpson 1936, p. 27); the remaining distinctions are all shared with *Nesodon* and *Adinotherium*. Nos. 1 and 3, and in part 5, are seen in *Rhyphodon;* Nos. 1, 3, 5, and 6 are shared with *Homalodotherium*. Ameghino placed the Notohippidae in his order Hippoidea, but the characters of the braincast just described do not indicate any relationship to the Equidae.

MEASUREMENTS IN MILLIMETERS

Total length of skull	245
Length of brain, oblique, including medulla (olfactory bulbs restored from P13420)	109
Length of brain between verticals, excluding medulla (olfactory bulbs restored from P13420)	93
Length of olfactory bulbs (P13420)	17
Width across olfactory bulbs (P13420)	15
Length of cerebrum between verticals	54
Width of cerebrum	55
Length of cerebellum between verticals	25
Width of cerebellum across flocculi	41

NOTES ON THE AMHERST CAST (Fig. 76)

This specimen, a fairly complete natural cast with the dorsal surface of the cerebrum well preserved, was referred to *Trachytherus* (=*"Eutrachytherus"*) *spegazzinianus* by Professor Loomis (1914, pp. 77–80, fig. 47) on the basis of some associated fragments of the skull which are not now preserved. This identification is entirely

---

[1] Not, perhaps, an important difference. Although the sinus apparently does not pass directly to the outside in typotheres, vascular foramina in the vicinity of the Sylvian fossa that may bear some relation to the sinus occur in several forms (Simpson 1936, p. 27).

understandable, for parts of the skulls of *Trachytherus* are very similar to those of notohippids. I was able to show previously (1934, p. 126) that this cast was not referable to *Trachytherus*. The series of casts prepared for this paper has now revealed its family position. The Amherst specimen was also collected at Cabeza Blanca, Chubut.

The structure of the neopallium is sufficiently similar to that of the *Rhynchippus* just described that it will suffice to point out the distinctions. The fossa Sylvii appears to be faintly indicated. The fissura Sylvii is not semicircular and runs into the sulcus lateralis; those of the two sides are symmetrical. The sulcus lateralis is continuous on the right side, interrupted on the left; on both sides it runs forward into the coronal area. The left coronal area extends farther forward than the right. The longitudinal scissure is not obscured by the superior longitudinal sinus. Posteriorly the bifurcation of this sinus can be seen. The posterior extremity of the neopallium slopes downward toward the tentorium much more sharply than in the cast described above. The cerebrum as a whole is longer and relatively narrower.

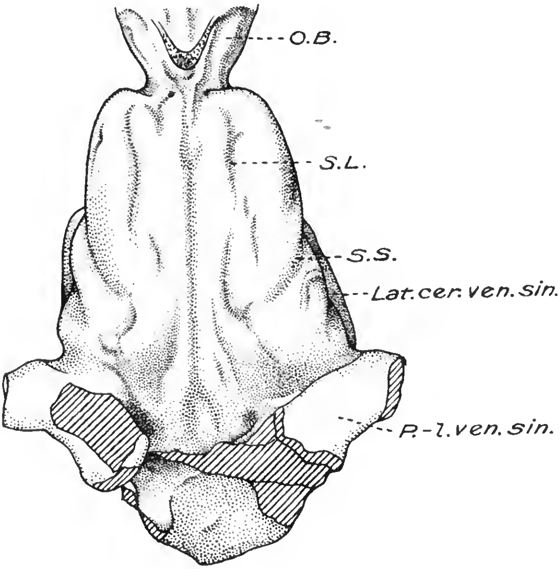

FIG. 76. Notohippidae, gen. et sp. indet. Dorsal view of braincast. Amherst College Museum specimen. For abbreviations see p. 301. ×⅔.

Very little of the cerebellum is preserved, but what remains compares closely with that of *Rhynchippus*. The anterior process of the periotic is present and enclosed in the cast—a most important resemblance between the two specimens. Above this process the postero-lateral venous sinus is widely exposed. It is flatter than that of *Rhynchippus*, and does not show any indication that veins entered it dorsally. Professor Loomis interpreted this structure as the epitympanic sinus in the squamosal, but, as shown by many specimens, this cavity has no direct connection with the brain case in notoungulates. The lateral cerebral sinus is fairly well shown, but the sinuses anterior and posterior to the periotic are not preserved. The only nerve exits remaining on the cast are the fillings of the optic and anterior lacerate foramina, and the internal auditory meatus; these are identical with those of *Rhynchippus*.

Every feature of this specimen, and particularly the anterior process of the periotic and the open posterolateral venous sinus, indicates that it should be referred to the Notohippidae. Generic identification is not possible at present. Although the extent of individual variation in *Rhynchippus* is not known, and the distortion, if any, undergone by the skull from which the Amherst cast came will never be known, the specimen can hardly be referred to this genus. Several notohippids—*Morphippus*, *Argyrohippus*, *Coresodon*, etc.—to which it might be referable occur in the Deseado. Until more information is available, the specimen must be referred to as Notohippidae, gen. et sp. indet.

Toxodontidae

Nesodon Owen (fig. 77).

An artificial braincast has been taken from F.M. No. P13076, referred to *N. imbricatus* Owen, and collected by Mr. G. F. Sternberg from the Santa Cruz beds on the Atlantic coast eight miles South of the Río Coyle. The specimen has suffered a little lateral compressure, which seems to have slightly increased the height and decreased the width of the cast. The amount of distortion cannot be gauged accurately and has, therefore, not been corrected in the drawings.

The total length of the skull is 473 mm., that of the braincast, enclusive of medulla, 118. The index is 25, and the ratio of olfactory bulbs: cerebrum: cerebellum is approximately 3: 13: 7. Taking into account the large size of the skull and the relatively shorter olfactory bulbs—factors tending to give a low index—the brain of

Nesodon appears to be somewhat more advanced than that of *Rhynchippus,* and less macrosmatic. As stated previously (Riggs and Patterson 1935, p. 191), the toxodontid skull is cyptocephalic, i.e., the basifacial axis is bent down upon the basicranial. The occiput is pitched forward. As a result of this bending down of the facial region and of the inclination of the occiput, the cerebrum is inclined upward and quite strongly arched, much of the neopallium is dorsal to the cerebellum, and the dorsal exposure of the cerebellum slopes downward and backward.

The olfactory bulbs are short in comparison with those heretofore described, deep, and narrow transversely. As in *Rhynchippus* they are separated by a groove which neither splits the peduncles nor joins the longitudinal scissure. Resemblance to *Toxodon* is close, with the exception that in the Pampean genus the bulbs are farther apart. The olfactory peduncles are large and long. The pyriform lobes are relatively small; structurally they are very similar to those of *Rhynchippus.* They are lateral in position, invisible in dorsal view, and little conspicuous in ventral view. This is perhaps a little accentuated by the slight distortion of the skull, but it is certainly a natural feature of the brain and is related to the upward inclination of the cerebrum and the large size of the hypophysis.

The neopallium is similar in outline to that of *Toxodon.* It is somewhat wider anteriorly than that of *Rhynchippus* and notably more so than those of the typotheres. The anterior portion of the fissura rhinalis is very distinct, but posteriorly it is, as usual, concealed by the lateral cerebral venous sinus. The fossa Sylvii is in the usual position, but very poorly defined. The fissura Sylvii is very distinct, as in *Toxodon,* and rather undulating. The short sulcus situated dorsal to the anterior part of the rhinal fissure is longer than in *Rhynchippus,* extending posteriorly to the sylvian fissure. The longitudinal scissure is filled by the superior longitudinal sinus which is prominent anteriorly, as in *Toxodon,* and medianly. No other sulci can be seen on the dorsal surface of the cerebrum, and the same seems to be true of *Toxodon,* to judge from Gervais' figure. The cerebrum of the young *Adinotherium ovinum* described below shows that these conditions are due to lack of impression of the sulci on the roof of the brain case, and not to extreme simplicity of pattern in the family.

The hypophysis is enormous and very deep, deeper even than in *Rhynchippus.* It extends ventrally far below the pyriform lobes, well below the fillings of the anterior lacerate foramina, and forward

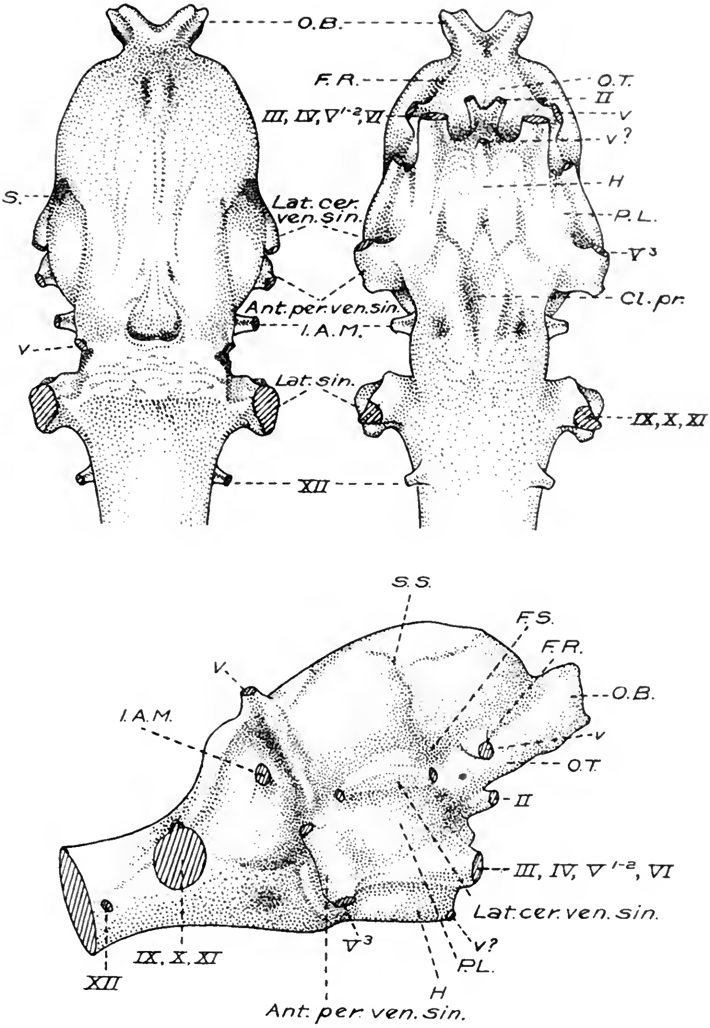

FIG. 77. *Nesodon imbricatus* Owen. Dorsal, ventral, and right lateral views of braincast. F.M. No. P13076. The olfactory bulbs may not be quite as divergent as represented. For abbreviations see p. 301. ×½.

between these fillings. Between the anterior extremity of the hypophysis and the fillings of the anterior lacerate foramina are two deep concavities in the cast caused by bony processes extending back from the sides of the optic chiasma. A foramen, probably vascular, leads forward from the mid-line of the ventral extremity of the hypophysis. The posterior clinoid process is elongate and flanked on either side by depressions which appear on the cast as ridges.

The tentorium of *Nesodon* is a rather narrow blunt process situated on the mid-line of the skull and not extending completely across the roof of the cranial cavity. It forms a large depression in the cast, on either side of which the dorsal surfaces of the cerebrum and cerebellum appear as though confluent. The cerebellum is narrower than the anterior portion of the cerebrum. The occipital face slopes downward and backward at about the same angle as that of *Rhynchippus*. Due to the upward inclination of the cerebrum, the dorsal face is not horizontal, as it is in other notoungulates (*Toxodon* excepted) hitherto described, but also slopes downward and backward, although at a more gentle angle than the occipital face. As in *Rhynchippus*, no traces of structure are apparent. Also as in this genus, the periotic is not firmly united postero-internally with the supra- and exoccipital. A narrow gap is thus left in the cranial wall which was probably not occupied by any part of the brain, but which is represented on the cast by a thin postero-lateral extension. In contrast to *Rhynchippus*, the internal face of the periotic is smooth and vertical. The formatio vermicularis is not apparent, and the flocculus is indicated only by a very faint convexity above the internal auditory meatus.

The pons is very similar to that of *Rhynchippus* but occupies a rather more posterior position in relation to the periotic. The medulla is somewhat longer, and shallower dorso-ventrally.

All nerve exits are preserved. The optic chiasma is situated more in advance of and above the anterior lacerate foramina than in *Rhynchippus*, due to the upward inclination of the cerebrum. The passages for III, IV, V^{1-2}, and VI are somewhat higher on the sides of the cast and are more widely separated than in the last mentioned genus. They are much more widely separated than in any known typothere or in *Notostylops*, and resemble those of *Phenacodus* (Simpson 1933a, figs. 1–2) in this respect. The filling of the foramen ovale (V^3 and the anterior periotic venous sinus) is narrow antero-posteriorly and extends out for some distance from the body of the cast. The internal auditory meatus (VII, VIII) is situated high on the side of the cast and nearly in the center of the periotic face of the cerebellum. It extends far into the periotic before the nerves separate. Above the foramen lacerum posterius (IX, X, XI) is a large irregularly shaped recess to be described below. The exit for XII occupies the same position with relation to the filling of the lacerate foramen as does that of *Rhynchippus.*

The vascular sinuses present some differences from those of *Rhynchippus,* but the general similarity is very close. The lateral cerebral venous sinus is in its usual position on the posterior half of the rhinal fissure, and opens anteriorly above the filling of the foramen lacerum anterius. In contrast to *Rhynchippus,* it does not join the anterior periotic venous sinus on the cast, the two sinuses evidently uniting within the cranial wall. A conspicuous anterior vascular opening is present in the anterior half of the rhinal fissure, a structure not present in *Rhynchippus.* The periotic of *Nesodon* differs from that of the last named genus in being closely approximated to, although not fused with, the cranial roof. As a result, the postero-lateral venous sinus is not open internally. However, due to the imperfect union of periotic and cranial roof, a thin superolateral extension of the cast projects for a short distance between the two. This space was evidently not occupied by any part of the brain, but it seems to have provided passage for a sinus or sinuses (fig. 77). A peculiar feature of the cast is the greatly expanded recess above the foramen lacerum posterius, a structure not encountered in the other forms studied, but clearly shown in Roth's excellent sagittal section figures of *Toxodon burmeisteri* (1898, pls. 5, 6). This recess was evidently filled in life by nerves IX, X, and XI, the internal jugular vein, and part of the lateral sinus. The last named may have been unusually large. In addition, a vascular tract, possibly part of the inferior periotic sinus, runs backward and slightly downward from the upper part of the recess to the hypoglossal canal. The superior longitudinal sinus has been mentioned in the description of the neopallium. Many small blood vessel impressions may be seen on the dorsal surface of the cerebrum. Several of these unite to form two moderately large vascular tracts which run posteriorly, one on either side of and close to the superior longitudinal sinus.

The fundamental similarities of the braincast of *Nesodon* to that of *Rhynchippus* have been given above (p. 279) The chief characters in which *Nesodon* differs from *Rhynchippus* are as follows:

1. Smaller olfactory bulbs.

2. Cerebrum higher, more arched and inclined upward.
3. Dorsal exposure of cerebellum sloping downward.
4. A vascular opening on the anterior portion of the rhinal fissure.
5. Lateral cerebral and anterior periotic sinus meeting outside the cerebral cavity.
6. A large recess dorsal to the foramen lacerum posterius.

Of these, 2 and 3 are to be correlated with the cyptocephalic skull, and may be regarded as habitus distinctions. No. 5 is caused by the periotic reaching the cranial roof and shutting off the posterolateral venous sinus from the cranial cavity. As stated above, the open condition of the sinus is a peculiarity of *Rhynchippus*, and may well be a family character. Nos. 1, 2, 3, and 6 will probably prove to be family characters of the Toxodontidae. These differences between *Rhynchippus* and *Nesodon* are of less importance than the resemblances common to both, which are listed on p. 279. They do not oppose the conclusion that the two genera are fundamentally similar in brain as well as in ear structure.

An important fact brought out by this investigation is the revelation of the very close resemblance, almost amounting to identity, between *Nesodon* and *Toxodon* in endocranial structure. The shape of the cranial cavity of *Toxodon*, as shown by Roth's admirable figures (1898, pls. 5, 6), reveals that the cerebrum was inclined dorsally and arched, more so indeed than that of *Nesodon;* that the dorsal exposure of the cerebellum sloped downward; that a large recess was present above the foramen lacerum posterius; and that the olfactory bulbs were proportionately the same size as in *Nesodon*. In short, the evidence of endocranial anatomy is decidedly opposed to recognition of a distinct family, Nesodontidae.

MEASUREMENTS IN MILLIMETERS

Total length of skull	473
Length of brain, oblique, including medulla	150
Length of brain between verticals, excluding medulla	118
Length of olfactory bulbs	14
Length of cerebrum between verticals	69
Width of cerebrum	58
Length of cerebellum between verticals	35
Width of cerebellum above I. A. M.	31

Adinotherium Ameghino (fig. 78).

An incomplete cast of the cerebrum was obtained from F.M. No. P13107, a young individual of *A. ovinum* (Owen) which has yielded valuable information concerning details of the ear structure (Patterson 1936, p. 214, fig. 50). It was collected by Mr. Abbott from the Santa Cruz beds five miles south of Coy Inlet. The right side of the cast is well preserved; the left is considerably distorted. The importance of the specimen lies in the fact that it reveals almost the entire cerebral convolution pattern which is not well shown in Gervais' specimen of *Toxodon,* nor in the cast of *Nesodon* described above.

The outline of the neopallium is essentially the same as in *Nesodon.* The rhinal fissure is obscured anteriorly by crushing, and posteriorly by the lateral cerebral venous sinus. As in *Rhynchippus,* the fossa Sylvii cannot be seen. The fissura lateralis is similar in general to that of *Rhynchippus,* but is more definite, more curved, and more erratic in its course. It does not extend to the coronal area, in which there is, on the right side at least, a slight depression. The sulcus situated between the anterior portions of the fissurae lateralis and rhinalis is practically identical with that of *Nesodon.* The longitudinal scissure is visible anteriorly, but is completely concealed posteriorly by sinuses. The close agreement of this convolution pattern with that of *Rhynchippus* strengthens the belief expressed above concerning the close relationships of the Toxodontidae and Notohippidae.

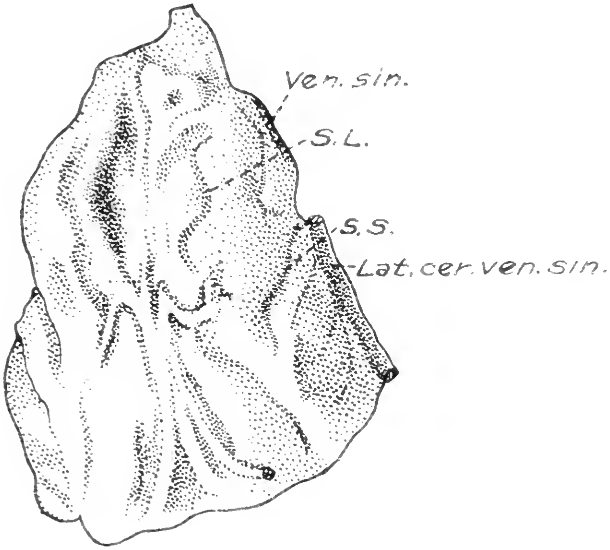

FIG. 78. *Adinotherium ovinum* (Owen). Dorsal view of cast of cerebrum of young individual. F.M. No. P13107. For abbreviations see p. 301. $\times\frac{1}{1}$.

The cast shows certain of the venous sinuses and their tributaries extremely well. The lateral cerebral is in its usual position along the posterior portion of the rhinal fissure. Near its anterior exit it receives two dorsal tributaries. The anterior of these, which is almost as large as the sinus, divides into four small branches at a point seven mm. above the junction. Two of these branches extend forward, one extends upward, and the fourth and longest extends upward and backward. The posterior tributary is small and divides almost immediately into two branches, one of which roughly parallels the sinus, the other the long branch of the anterior tributary. A small sinus with an anterior exit is situated beneath the small sulcus between the fissurae lateralis and rhinalis. This may be the homologue of the vascular opening on the anterior half of the rhinal fissure in *Nesodon*, but there can be no certainty on this point due to the obscuring by crushing of this fissure on the cast at hand. The superior longitudinal sinus is more complex (or perhaps more detail in preserved) on this specimen than on any other yet described. It is apparent on the posterior half of the cerebrum only, becoming indistinct near the center of the longitudinal scissure. At this point it receives a large tributary on the left side which proceeds for a short distance antero-externally before fading from view. This tributary in turn receives a small but sharply defined branch which runs postero-externally for some seven mm. before suddenly ending. Some six mm. posterior to the point of entry of the left tributary, the sinus receives a tributary on the right side. This extends forward, then loops backward, and then loops forward again to disappear on the fissura lateralis. On the posterior third of the longitudinal scissure, the sinus divides into right and left portions which curve externally around the median parts of the posterior extremities of the cerebral hemispheres. The right is lower than the left, and receives a well defined tributary which parallels it for its entire length and passes out of the cranial cavity into the cranial roof.

Homalodotheriidae Ameghino

Homalodotherium Flower (fig. 79).

The partial skeleton of *H. cunninghami* in the Field Museum collections, No. P13092, was recently mounted by Mr. Quinn, and advantage was taken of further preparation of the skull to obtain an excellent braincast. This fine specimen, collected by Mr. Riggs in the vicinity of Cape Fairweather, Santa Cruz, has already been

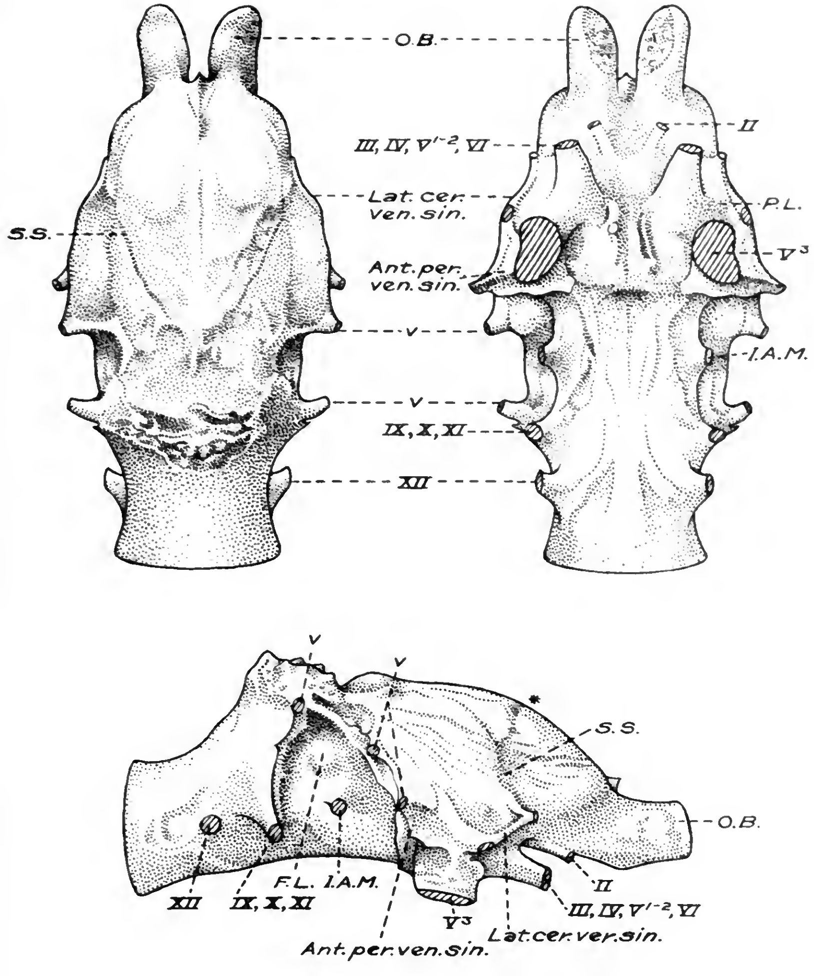

FIG. 79. *Homalodotherium cunninghami* Flower. Dorsal, ventral, and right lateral views of brain-cast. F.M. No. P13092. The asterisk indicates the position of the posterior extremity of the frontal sinus. For abbreviations see p. 301. ×½.

described in several publications, and it is a pleasure to record here a highly important, hitherto unknown part of its anatomy.

The length of the skull is 411 mm., that of the braincast exclusive of medulla 136. The index is 33, and the ratio of olfactory bulbs: cerebrum: cerebellum is approximately 3: 11: 4. The serial arrangement and degree of flexure are about as in *Rhynchippus*, with the conspicuous exception that the olfactory bulbs are greatly depressed and the optic chiasma is not retracted. The position of the bulbs is similar to that seen in the Musters homalodotherid *Rhyphodon.*

The olfactory bulbs are relatively as large as those of *Rhyphodon,* but are somewhat deeper dorso-ventrally, and more compressed ventro-medially—dorso-laterally. The surfaces applied to the cribriform plates face inward and downward. The bulbs are separated by a deep, wide fissure which runs between the peduncles on the ventral surface. The olfactory tubercles are very poorly defined. The pyriform lobes are less prominent than in *Rhyphodon,* due to greater expansion of the neopallium, and are not visible in dorsal view. The lobes extend laterally, as in *Rhyphodon* and the casts described above, rather than posteriorly as in *Notostylops* and the typotheres.

The neopallium is quadrangular in outline and rather wider posteriorly than anteriorly, the outline more nearly resembling that of *Nesodon* than that of *Rhynchippus.* This neopallium is clearly a derivative from the *Rhyphodon* type, over which it is advanced in antero-posterior and transverse expansion. The convolution pattern is very obscure. The fissura rhinalis and fossa Sylvii are not apparent on the cast, although almost certainly present on the brain proper. A poorly defined fissura Sylvii, similar in its course to those of *Rhynchippus* and *Nesodon,* is the only sulcus that can be seen. This fissure is absent in *Rhyphodon.* No trace occurs of a lateral or ?suprasylvian sulcus, the latter being present in *Rhyphodon.* It cannot be determined at present whether this simplicity of pattern is real, or due merely to lack of impression of detail on the bone surface. The anterior third of the cerebrum is strongly depressed. The hypophysis is large but very shallow; in comparison with the hypophyses of *Rhynchippus* and *Nesodon* it is merely a slight swelling. The shallowness of the hypophysis, and the depressed condition of the olfactory bulbs and the anterior part of the cerebrum are due, as in *Rhyphodon,* to the presence of a very large frontal sinus. This sinus is also present in the genera described above but is smaller and situated more anteriorly. The depression occupied by the posterior clinoid process is in the same position as that of *Rhynchippus,* but is shallower.

The cerebellum is approximately as wide as the anterior portion of the cerebrum, and is much shorter antero-posteriorly than that of *Rhyphodon.* As in the casts described above, almost nothing of the structural details can be seen. A high antero-posteriorly compressed posteromedian lobule which slopes down at a sharp angle to the medulla is the only recognizable feature of the dorsal and occipital faces. The irregular dorsal exposure slopes downward and forward. The occipital exposure is more rounded transversely than that of *Rhynchippus* and *Nesodon.* As in the latter genus, postero-lateral and supero-lateral extensions of the cast occupy gaps in the cranial wall around the periotic. The internal face of the periotic is vertical and comparatively smooth. The flocculus is slight and is situated above and slightly behind the internal auditory meatus. This is a decided difference from *Rhyphodon,* in which there is a cerebellar lobule behind the meatus but no flocculus. No clear traces of the formatio vermicularis can be detected.

There is no appreciable convexity in the region of the pons. The medulla is notably smaller than in *Rhyphodon* although larger than in either *Nesodon* or *Rhynchippus.* It is broader than deep.

All cranial exits are preserved. The optic chiasma is not apparent on the cast. The optic nerves are not retracted, are well separated, and run forward for some distance before leaving the cranial cavity. This is in decided contrast to the other casts described here. In *Rhyphodon* the optic nerves leave the cranial cavity through the anterior lacerate foramina. Non-retracted and well separated optic nerves occur in *Phenacodus* (Simpson, 1933a, p. 6, fig. 1). The similar conditions seen in *Homalodotherium* may be interpreted as a primitive character that has become "fixed" due to the enlargement of the frontal sinus, which inhibited dorsal expansion of the anterior part of the brain. An analogous case is presented by the giant panda (*Ailuropoda melanoleucus*), in which the frontal sinus is of enormous size and the brain sharply depressed anteriorly, whereas in its close relative, the little panda (*Ailurus fulgens*) the sinus is small and the cerebrum expanded dorso-anteriorly (Gregory 1936, p. 22, figs. 17, 18). As in *Rhyphodon,* the fillings of the anterior lacerate foramina extend considerably further forward than in other notoungulates. The foramen ovale (V^3 and sinus) is situated somewhat more anteriorly than in the casts previously described. The internal auditory meatus, foramen lacerum posterius, and condylar foramen are essentially as in *Rhynchippus.*

In contrast to *Rhyphodon,* a lateral cerebral venous sinus is present although not as prominent as in *Nesodon* and *Rhynchippus.* It is situated lower on the cast than in these genera and appears to overlie part of the pyriform lobe. It has an anterior exit in the region of the fossa Sylvii, and a second exit situated above and slightly in front of the filling of the foramen ovale. It receives one or more vaguely defined dorsal tributaries. A poorly defined structure which appears to correspond to the anterior periotic sinus of *Rhynchippus* and *Nesodon,* runs down from the lateral cerebral sinus to the foramen ovale. Two vascular openings occur along the anterior face of the periotic. The lower of these, and possibly the upper as well, connects the lateral cerebral and anterior periotic sinuses with the postero-lateral sinus. As in *Nesodon,* a conspicuous vascular opening is present above the periotic at the lateral extremity of the cerebellum. The superior longitudinal sinus is obscurely visible along the longitudinal scissure, and numerous very fine vascular markings may be seen on several parts of the neopallium. Vascular tracts on the ventral surface and sides of the medulla are interpreted as the courses of the intracranial portions of the vertebral arteries and their branches.

The braincast of *Homalodotherium* differs from that of its earlier relative *Rhyphodon* in a number of features, as follows:

1. More expanded neopallium.
2. Greater depth of the brain as a whole.
3. Shorter cerebellum.
4. Olfactory bulbs more compressed, and deeper.
5. Smaller medulla.
6. Optic nerve separate and leaving the cranial cavity through the optic foramen.
7. Presence of the lateral cerebral venous sinus.
8. "Flocculus" in the usual position, no cerebellar lobule in petrosal posterior to internal auditory meatus.

Nos. 1 to 5 may be regarded as evolutionary advances, but No. 6 is a fundamental difference, and Nos. 7 and 8 probably fall into this category also. *Rhyphodon,* although structurally ancestral to *Homalodotherium* in its broader features, is aberrant in these characters and probably represents a non-ancestral side branch of the family. *Homalodotherium* agrees with *Rhynchippus* and *Nesodon* in Nos. 6, 7, and 8, and Simpson (1933a, p. 16) has recognized a separate optic foramen in *Pleurostylodon*. The bearing of the braincast of *Homalodotherium* on notoungulate taxonomy is discussed below under Conclusions.

MEASUREMENTS IN MILLIMETERS

Length of skull	411
Length of brain, oblique, including medulla	152
Length of brain between verticals, excluding medulla	127
Length of olfactory bulbs	22
Width across olfactory bulbs	35
Length of cerebrum between verticals	76
Width of cerebrum	64
Length of cerebellum between verticals	29
Width of cerebellum across flocculi	48

Typotheriidae

Typotheriopsis[1] Cabrera and Kraglievich (fig. 80).

An imperfect natural braincast was obtained by Mr. Quinn from F.M. No. P14420, referred to *T. internum* (Ameghino); the ventral surface is lacking, but most of the sides, the dorsal surface, and most of the olfactory bulbs are well preserved. The specimen was collected by Mr. Robert C. Thorne from the Araucanense beds near Puerta de Corral Quemada, Catamarca.

The total length of the skull in this specimen cannot be given; the estimated length of a well preserved skull (lacking premaxillaries) of the same species and of similar size, F.M. No. P14477, is 265 mm. The estimated length of the braincast (the olfactory bulbs are not quite complete anteriorly) is 95 mm. (excluding the medulla). The approximate index is 38; omitting the olfactory bulbs it is 31. These indices are considerably lower than those of *Hegetotherium* and *Protypotherium*. This condition seems to be due to the larger size of *Typotheriopsis*, and does not in itself indicate a less effective brain. Comparisons with *Trachytherus* are very inexact, since both skull and braincast of *T. spegazzinianus* are imperfect anteriorly, but the index in this genus can be very roughly estimated to be

---

[1] This genus has been described only briefly in a preliminary note (Cabrera and Kraglievich 1931, p. 111) and has never been figured. The type species, *T. chasicoensis* C. and K. is from the Chasicó beds, lower Pliocene, placed by Kraglievich (1934, p. 119) between the Paraná and Mesopotamian. Kraglievich noted (1934, p. 34) that Ameghino and Rovereto were probably incorrect in their references of the species *internum* and *studeri* to *Eutypotherium* (=*Tachytypotherium*, "*Trachytypotherium*"). He believed that these species should be placed in *Typotheriopsis* or, and more probably, in *Pseudotypotherium*. Excellent specimens referred to *internum* in the Field Museum collections show conclusively that they cannot be referred to the latter genus. They agree with the published description of the former, but this is so brief that the identification cannot at present be regarded as definitely established.

about 32. The facial region is longer than in *Typotheriopsis*, a factor which tends to give a lower index. The brain of the Pliocene genus is certainly greater in volume, however; this indicates, providing that *Trachytherus* is on or near the main line of descent and not a conservative, surviving side branch, that a certain amount of brain evolution has taken place in the family since Oligocene times.

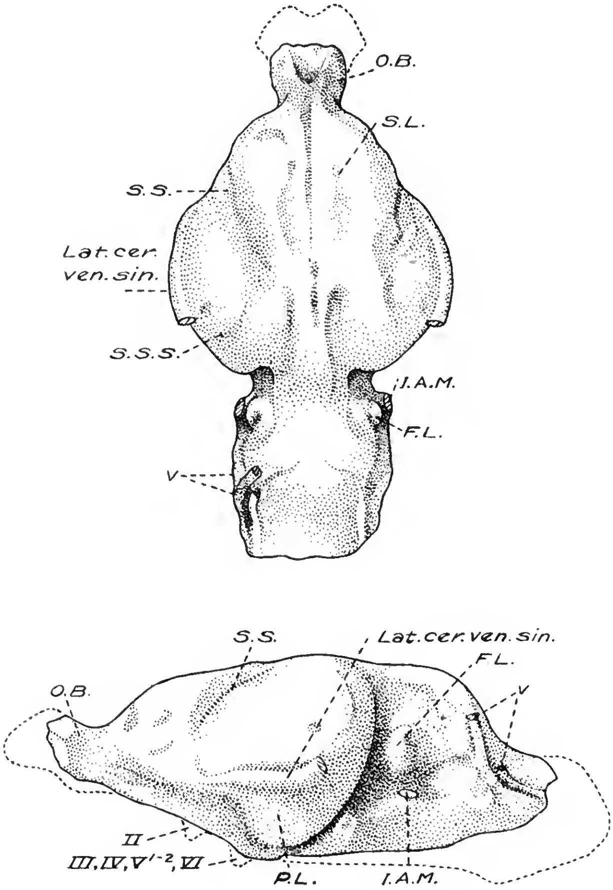

FIG. 80. *Typotheriopsis internum* (Ameghino). Dorsal and left lateral views of incomplete brain-cast. F.M. No. P14420. For abbreviations see p. 301. ×⅔.

The olfactory bulbs are fully exposed, the midbrain was certainly covered, but the cerebrum has barely begun to overlap the cerebellum. The flexure is definitely slighter than in *Hegetotherium*, and agrees closely with that seen in *Trachytherus*. The brain appears to have been shallower than that of *Hegetotherium,* as is also true of *Typotherium,* to judge from a section of the cranium given by Gervais (1867, pl. 23, fig. 4). The ratio of cerebrum to cerebellum is approximately 2:1, as in *Trachytherus;* restoring the olfactory bulbs, the ratio was probably about 4:11:5, slightly less advanced than that of *Hegetotherium.*

The rhinencephalon is as well developed as in other known typotheres. The olfactory bulbs are united in the parts preserved, and were probably separated only at their extremities. The peduncles, and probably the bulbs also, are narrower than those of *Hegetotherium;* they are also somewhat longer.[1] In *Protypotherium* the peduncles agree in length with those of *Typotheriopsis,* but are somewhat wider, although narrower than those of *Hegetotherium.*

The olfactory tubercles are not preserved. The pyriform lobes are largely destroyed, but enough remains to show that they were similar to those of *Trachytherus* and *Hegetotherium.*

The outline of the neopallium is similar to that of *Protypotherium,* but is slightly narrower posteriorly than in this genus or in *Hegetotherium.* The rhinal fissure is concealed by the postero-lateral cerebral venous sinus. The fossa Sylvii has been somewhat obscured by slight distortion but appears to have been small. The fissura Sylvii is well marked and runs upward and backward. The sulcus lateralis is rather poorly defined and, in contrast to *Hegetotherium,* does not have curving ends. As in this genus, there are pits in the coronal area anterior to the sulcus lateralis. The longitudinal scissure is very distinct anteriorly; posteriorly the superior longitudinal sinus is plainly visible, and broad. The suprasylvian sulcus is very slight and, as in *Protypotherium,* has no anterior part. The sulci as a whole are not as well defined as those of *Hegetotherium,* resembling those of *Protypotherium* in this respect. They are, however, much plainer than in Gervais' specimen of *Typotherium,* as figured (1872, pl. 21, fig. 11).

The cerebellum, as a whole, is not as low relative to the cerebrum as is that of *Hegetotherium.* The occipital exposure is much more sloping than in the last named genus; there is no apparent separation between the dorsal and occipital faces. Very little detail is apparent; the occipital face shows a broad posteromedian lobule similar to that of *Hegetotherium.* The lateral surfaces of this face are obscured

---

[1] If *Typotheriopsis* is a reliable criterion, the restored olfactory peduncles in the published figure of *Trachytherus* (Patterson 1934, fig. 28) are too wide.

by the sinuses described below. The lateral face is, as a whole, decidedly convex. The formatio vermicularis is prominent, the descending crus and flocculus being more definite than in *Hegetotherium.* The flocculus is directly above the internal auditory meatus, as in *Trachytherus.* The periotics of *Typotheriopsis* are closer to the midline of the skull than in *Hegetotherium* and *Protypotherium,* and the cerebellum is consequently narrower anteriorly.

The internal auditory meatus is the only nerve exit preserved. This opening and the flocculus are rather closer to the cerebrum than are those of *Trachytherus,* but, in contrast to *Hegetotherium,* are still not beneath the posterior end of the cerebrum.

The posterolateral venous foramen leading from the cerebral cavity is not as large as in *Hegetotherium,* nor is it situated as high nor as far back. The venous sinus running from it turns down quite sharply after leaving the foramen, and then runs forward along the fissura rhinalis. No traces of minor veins leaving the foramen or entering the sinus can be detected either on the cast or on the inside of the brain case. On the posterolateral angle of the cerebellum is a conspicuous, dorso-ventrally aligned sinus which emerges from a foramen situated slightly above the level of the flocculus. Ventrally it continues in the direction of the foramen lacerum posterius (not preserved on the cast). From its relations, this sinus would appear to be the homologue of that regarded as the lateral in the casts described above. At the level of the internal auditory meatus it gives off a branch which runs posteriorly along the side of the medulla oblongata. This branch receives a somewhat smaller tributary which, at first appearing near the junction of the medulla with the occipital face of the cerebellum, runs parallel to and slightly above it for a short distance. The cast is not complete enough to follow this branch for its entire course. Judging from other skulls it appears to end in the vicinity of the condylar foramen. It is probably homologous, therefore, with the vascular tract which runs back toward this foramen in *Nesodon* (see p. 285). The periotic of *Typotheriopsis* is closely united with the roof and sides of the cranial cavity.

The brain of *Typotheriopsis* is in general very similar to those of other typotheres that have been described. It appears to be somewhat more primitive than that of *Hegetotherium,* although from a considerably more recent horizon, in a few features such as slightly lesser depth, lesser degree of flexure, and more sloping occipital face of cerebellum. In all parts in which comparison is possible, the braincast agrees closely with that of *Trachytherus,* thus further confirming the reference of this genus to the Typotheriidae. I have previously stated (1936, p. 224) that in some characters the Interatheriidae and Typotheriidae were closer to each other than to the Hegetotheriidae. Simpson has listed (1933b, pp. 6–7) the few characters in which the braincast of *Protypotherium* differs from that of *Hegetotherium. Typotheriopsis* resembles *Protypotherium* in these characters, with the exception of 3, which is not a structural difference. Sagittal sections of *Protypotherium* and *Interatherium* show that these genera agree with *Typotheriopsis* and differ from *Hegetotherium* in having a shallower brain, a slighter degree of flexure, and a higher cerebellum. The observed differences between the Hegetotheriidae on the one hand and the Typotheriidae-Interatheriidae on the other are not striking, however, and from the available evidence it would appear that the Typotheria, as currently recognized, form a compact uniform group in brain structure. The possibility that this observed uniformity does not indicate taxonomic unity is discussed below.

MEASUREMENTS IN MILLIMETERS

Total length of skull (estimated, from P14477)	265
Length of brain between verticals, excluding medulla (olfactory bulbs estimated)	95
Length of cerebrum between verticals	55
Width of cerebrum	52
Length of cerebellum between verticals	21
Width of cerebellum	28

CONCLUSIONS

Study of the middle ear structure in the Notoungulata (Patterson 1936) has indicated that, as far as this highly important region is concerned, the families Toxodontidae, Leontiniidae, and Notohippidae (the suborder Toxodonta of various authors) form a natural group. It has also been shown that *Homalodotherium,* generally regarded as the typical representative of the suborder Entelonychia, is clearly referable to this group on the evidence of middle ear structure. The families Typotheriidae and Interatheriidae have been found to possess several important characters in common, characters in which both of them differ from the Hegetotheriidae. The validity of the Entelonychia, and the unity of the suborder Typotheria, as currently recognized, have thus been called into question. The bearing of evidence derived from the braincasts described above on these problems may now be reviewed.

The close agreement in brain structure of the Notohippidae and Toxodontidae, as exemplified by *Rhynchippus*, *Nesodon*, and *Adinotherium*, and their common divergence from the typotherian brain type have already been discussed, and require no further comment. *Homalodotherium* agrees with these genera in the majority of the characters in which they differ from the typotheres (p. 279), namely, separation of olfactory bulbs, position and expansion of pyriform lobes, and relations of lateral cerebral and anterior periotic venous sinuses. The hypophysis is not expanded ventrally in *Homalodotherium*, but it may be noted that the space between the fillings of the anterior lacerate foramina is fully as large as in *Nesodon*. The non-expanded condition may perhaps be correlated with the large size of the frontal sinus. The cerebral convolution pattern of *Homalodotherium* is unfortunately unknown, and may or may not have been similar to the toxodontid-notohippid pattern. *Rhyphodon* displays some differences from this pattern, but it has been shown above that this genus is aberrant in certain features. Therefore, it may not be typical of the homalodotherid pattern.

The notable characters in which *Homalodotherium* differs from *Nesodon* and *Rhynchippus*—depressed olfactory bulbs and anterior portion of cerebrum, and non-retracted optic nerves—are correlated with the early development of a large frontal sinus in the family, and hence do not, in my opinion, offset the positive resemblances that have been noted between the three casts. I believe, therefore, that the evidence obtained from this study supports the conclusion reached from middle ear structure that "the homalodotherids stand in about the same relation to the Toxodonta as the chalicotherids do to the less aberrant perissodactyls." This conclusion carries with it the implication that the suborder Entelonychia should no longer be recognized, and that its component families Homalodotheriidae and Isotemnidae should be transferred to the Toxodonta. Simpson has recently shown (1936b) that the peculiar skeletal modification of the homalodotherids has been acquired since Musters time, the earlier members of the family having skeletons of more generalized type. This seems to be in keeping with the subordinal assignment made here. It may be necessary to separate the homalodotheres from the remaining toxodonts either as an infraorder or as a superfamily, but this question is beyond the scope of the present study.

If the views expressed here are correct, the braincasts of *Rhynchippus*, *Nesodon*, and *Homalodotherium* should be structurally derivable from a common stem type. Recognition of such a type will be greatly impeded by the major gap in the South American record that exists between the Musters of middle or upper Eocene age and the Deseado of middle or upper Oligocene age. The importance of this unrecorded interval is admirably demonstrated by the homalodotherids which, on present evidence, appear to have undergone practically their entire profound skeletal modification during it. As stated above, *Thomashuxleya* and *Periphragnis* of the Casamayor and Musters are generalized notoungulates in skeletal characters (Simpson 1936 b, p. 12), whereas *Asmodeus* of the Deseado is about as fully specialized as *Homalodotherium* (Loomis 1914, figs. 94–99, and original specimens). The same probably holds true for other notoungulate groups, all of which undergo only relatively minor modifications in post-Deseado time. In studying the braincasts of *Rhynchippus*, *Nesodon*, and *Homalodotherium*, we are dealing with fully specialized representatives of three divergent families, and have no present opportunity adequately to trace the early stages of the divergence. In spite of these difficulties, I am, nevertheless, inclined to believe that the braincast of a generalized toxodont such as the Casamayor isotemnid *Pleurostylodon*, should present a fairly close approximation to the hypothetical prototype. The braincast of *Rhyphodon* probably approaches this ideal, but it is definitely homalodotherid in some features and seemingly aberrant in others, and accordingly does not fulfill the necessary requirements.

The known typotherian braincasts are all of similar type, whereas the middle ear structure of these animals indicates a division into two groups. The known toxodont braincasts exhibit a considerable degree of divergence, whereas the middle ear structure is very uniform throughout. This apparent contradiction might be considered as invalidating the conclusions arrived at above. I do not believe that this is the case, however. The brain, being the dominant organ of the body, is more liable than the middle ear to modification in response to varying modes of life. The Hegetotheriidae, Interatheriidae, and Typotheriidae have in common a remarkably rodent-like habitus. Simpson (1933a, b) has demonstrated that the braincast of *Notostylops* of the Notioprogonia, also a rodent-like form, is fundamentally similar to the typotherian type. It seems entirely possible, therefore, that the Hegetotheriidae on the one hand and the Typotheriidae-Interatheriidae on the other, may have descended independently from notioprogonian ancestors, and that the close similarity they display in braincast structure may be in part convergent, due to the acquisition of almost identical habitus, and in part common heritage. The proper taxonomic position of the Hegetotheriidae cannot be decided, however, on the evidence at present available.

REFERENCES

Cabrera, C. and Kraglievich, L.

1931. Diagnosis previas de los ungulados fósiles del Arroyo Chasicó. Notas prelim. Mus. La Plata, **1**, 107–113.

Gervais, P.

1867–9. Recherches sur différents groupes de mammifères fossiles de l'Amérique méridionale. Zool. Paléont. générales, 129–147, 252–254, pls. 22–25, 27.

1872. Mémoire sur les formes cérébrales propres à différents groupes de mammifères. Journ. Zool., **1**, 425–469, pls. 20–23.

Gregory, W. K.

1936. On the phylogenetic relationships of the giant panda (*Ailuropoda*) to other arctoid carnivora. Amer. Mus. Novit. No. 878, 1–29, figs. 1–22.

Kraglievich, L.

1934. La antigüedad pliocena de las faunas de Monte Hermoso y Chapadmalal, deducidas de su comparación con las que precedieron y sucedieron. Imprenta "El Siglo Illustrado," Montevideo. Pp. 1–136. A posthumous work, pp. 1–16 being devoted to a brief obituary notice and a bibliography.

Loomis, F. B.

1914. The Deseado formation of Patagonia. Amherst, 1–232, frontispiece, text-figs. 1–160.

Patterson, B.

1934. *Trachytherus* a typotherid from the Deseado beds of Patagonia. Geol. Ser. Field Mus. Nat. Hist., **6**, 119–139, text-figs. 24–28.

1936. The internal structure of the ear in some notoungulates. Ibid., 199–227, text-figs. 44–54.

Riggs, E. S. and Patterson, B.

1935. Description of some notoungulates from the Casamayor (*Notostylops*) beds of Patagonia. Proc. Amer. Phil. Soc., **75**, 163–215, text-figs. 1–4, pls. 1–5.

Roth, S.

1898. Catálogo de los mamíferos fósiles conservados en el Museo de La Plata. Grupo Ungulata, orden Toxodontia. Rev. Mus. La Plata, **8**, 33–160, text-figs. 1–81, pls. 1–8.

Simpson, G. G.

1933a. Brain casts of *Phenacodus*, *Notostylops*, and *Rhyphodon*. Amer. Mus. Novit. No. 622, 1–19, text-figs. 1–3.

1933b. Brain casts of two typotheres and a litoptern. Ibid., no. 629, 1–18, text-figs. 1–3.

1936a. Structure of a primitive notoungulate cranium. Ibid., No. 824, 1–31, text-figs. 1–11.

1936b. Skeletal remains and restoration of Eocene Entelonychia from Patagonia. Ibid., No. 826, 1–12, text-figs. 1–2.

ABBREVIATIONS ON FIGURES

II	Optic nerve
III, IV, V^{1-2}, VI	Filling of foramen lacerum anterius, the common exit of these nerves
V^3	Mandibular nerve
IX, X, XI	Filling of foramen lacerum posterius, the common exit of these nerves
XII	Condylar foramen (hypoglossal canal)
Ant. per. ven. sin.	Anterior periotic venous sinus
Cl. pr.	Depression caused by posterior clinoid process
F. L.	"Flocculus"
F. R.	Fissura rhinalis
F. S.	Fossa Sylvii
H.	Filling of fossa hypophyseos
I. A. M.	Internal auditory meatus (nerves VII, VIII)
Lat. cer. ven. sin.	Lateral cerebral venous sinus
Lat. sin.	Lateral (transverse) sinus
O. B.	Olfactory bulb
O. T.	Olfactory tubercle
P. L.	Pyriform lobe
P.-1. [post-lat.] ven. sin.	Postero-lateral venous sinus
Rec. pr. per.	Recess formed by anterior process of periotic
S. L.	Sulcus lateralis
S. S.	Fissura Sylvii
S. S. S.	Suprasylvian sulcus
Sin. lat.	Lateral (transverse) sinus
V.	Vascular opening
V. p.gl. f.	Veins passing to postglenoid drainage
V. sq.-par. sut.	Veins passing to foramina along the squamoso-parietal suture
Ven. sin.	Venous sinus