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BRAINCASTS OF TWO TYPOTHERES AND A LITOPTERN[1]

By George Gaylord Simpson

In the preceding paper of this series (Simpson 1933), the braincasts of *Phenacodus*, *Notostylops*, and *Rhyphodon* were described and illustrated. In this paper this research will be completed, so far as now possible to me, by the description of braincasts of *Hegetotherium*, *Protypotherium*, and *Proterotherium*, and the general results will be summed up. The introductory remarks and acknowledgments of the previous paper apply equally to this.

Hegetotherium

This braincast is taken from a skull of *Hegetotherium mirabile*, Amer. Mus. No. 9223, found by Barnum Brown in 1899 in the Santa Cruz Formation at Halliday's Estancia, Río Gallegos, Santa Cruz. This fine skull was described and figured by Sinclair, but the braincast was not taken. No Santa Cruz notoungulate braincast has been previously described. The cast is very good, including all the features of the left side and extending beyond the midline.

The total length of the skull is 115 mm. and of the brain (exclusive of medulla) 59 mm., giving an index of 51, slightly greater than in *Notostylops* (about 48). The figures are comparable as the skulls are of nearly the same size and rostral development. If the olfactory bulbs be omitted from the length, the index for *Notostylops* is about 37 and for *Hegetotherium* about 43. Due to the greater flexure and much greater depth of the present brain, its volume is even larger relative to that of *Notostylops*. *Hegetotherium* does seem to represent a real advance over the earlier genus in effective brain size.

The olfactory bulbs remain fully exposed, but the midbrain was surely completely covered dorsally and the cerebrum has even begun definitely to overlap the cerebellum. The arrangement can no longer be called serial, and the flexure is greater than in *Notostylops*. As a whole, the brain is relatively shorter and wider, and also much deeper, especially in the cerebellum. The ratio of the exposed, dorsal parts of olfactory

[1]Publications of the Scarritt Patagonian Expedition, No. 16.

bulbs, cerebrum, and cerebellum is about 2:7:3, decidedly different from *Notostylops* and expressive of great reduction of the olfactory bulbs, expansion of the cerebrum, and overlapping, shortening, and deepening rather than reduction of the cerebellum.

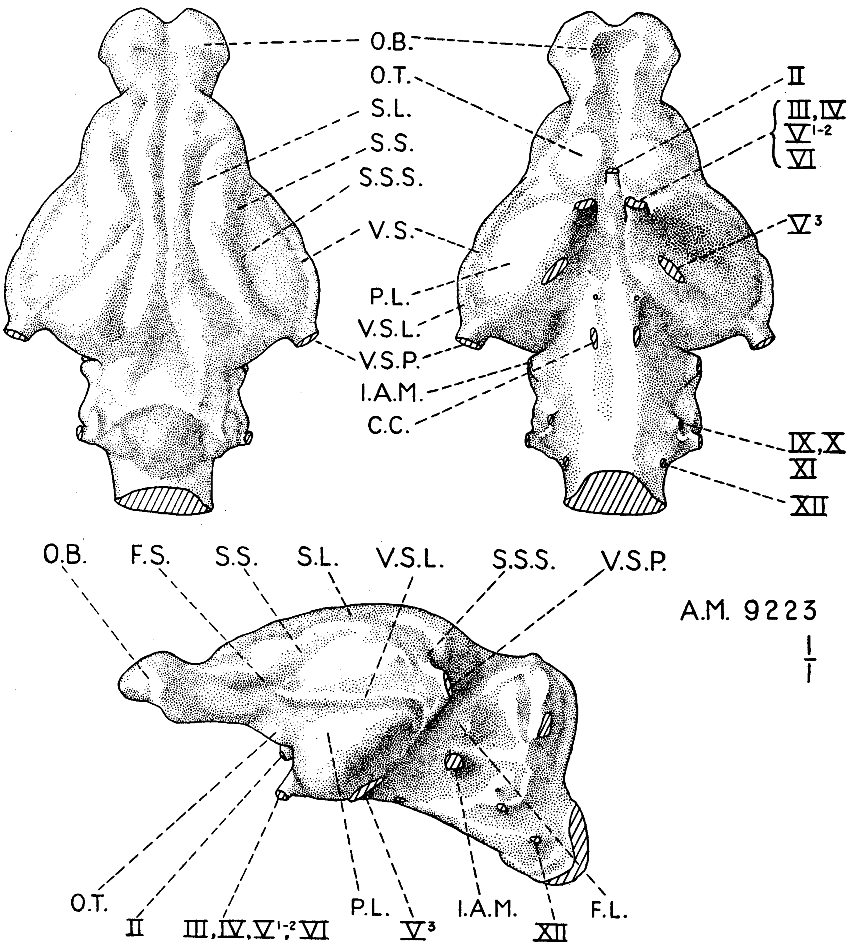

Fig. 1. *Hegetotherium mirabile.* Braincast from Amer. Mus. No. 9223. Dorsal, ventral, and left lateral views. For abbreviations see p. 17. Natural size.

The rhinencephalon, as a whole, is well developed, but in a different way from either *Phenacodus* or *Notostylops.* The olfactory bulbs have become smaller, not only relatively but even absolutely. Shape and proportions are more like *Phenacodus* than *Notostylops*, each bulb about as broad as long and somewhat compressed dorsoventrally. The fila originated on almost the whole ventral surface, which is inclined forward. The bulbs were separate only at the tips. The peduncles are short and even stouter, relatively, than in *Phenacodus*.

The olfactory tubercles are not significantly different from those of *Notostylops*. The pyriform lobes are very large but are purely ventral, not visible at all in dorsal view. Their maximum width is almost exactly that of the neopallium, but, in marked distinction from *Notostylops*, they do not extend as far posteriorly as does the neopallium. Expressed differently, presupposing an ancestral condition near *Notostylops*, the neopallium has expanded somewhat laterally and decidedly posteriorly. The pyriform lobes have, however, expanded downward and forward, and also are crowded toward the midline.

The outline of the neopallium is not greatly unlike that of *Notostylops*. The anterior end has expanded only slightly, and posterior and posterolateral expansion has been proportionate, retaining the triangular contour. But whereas the most posterior point on the cerebrum of *Notostylops* was lateral, it is here nearly median. The rhinal fissure is largely obscured by a large venous sinus and foramen, but there is no doubt that it lay approximately along this sinus. The part anterior to the fossa sylvii is clearly visible. The fossa sylvii is much as in *Notostylops*, but relatively slightly smaller and more anterior. From it a distinct fissura sylvii runs upward and backward. There is a sharp sulcus lateralis, sagittal but with its ends curving slightly outward and terminating in distinct pits. Another sulcus, less definite, which may be called suprasylvian for descriptive purposes (perhaps not strictly homologous with that sulcus in any other mammals), begins near the posterolateral corner and runs anterointernally past the upper end of the fissura sylvii, where it seems to be slightly interrupted, and on the left side, but not the right, runs into the sulcus lateralis. Anterior to the sulcus lateralis, in the coronal region, there is a depression, like a dimple, but it can hardly be called a sulcus. This convolution pattern is certainly more definite and perhaps more complex than those of *Phenacodus* or *Notostylops*, but there is no basic difference beyond the natural further differentiation and deepening of the sulci, and even this may be more apparent than real, so far as the underlying brain itself was concerned.

There is a swelling in the region of the hypophysis, but the expansion of the pyriform lobes toward the midline has crowded this so that it is not distinctly bounded.

The occipital exposure of the cerebellum is large, particularly deep. The dorsal exposure, in a limited sense, separated from the occipital exposure by a raised transverse ridge, is very small relatively, and considerably wider than long. This space is almost featureless (except for the sinus descending from the longitudinal scissure of the cerebrum). Possibly it represents a broad anterior lobe, while the following transverse ridge is perhaps all or part of a lobulus simplex. On the occipital face there is a large, simple, convex, vertically elongate posteromedian lobule with faint traces of transverse sulci. On each side of this is another smaller vertical convexity, presumably a paramedian lobule. Superolateral to this is a squarely truncated, dorsoventrally elongate projection, which, if not due to crushing, at least was in all probability not closely occupied by a part of the brain. Anteroinferior to this, on the lateral surface of the cerebellum, is a prominent formatio vermicularis with a short, nearly vertical ascending crus and a more oblique descending crus ending in a large, roughly circular projection, lodged in the petrosal and doubtless representing, at least in part, the flocculus. This cerebellum as a whole is clearly much more progressive, or more highly differentiated, than those of *Phenacodus* or *Notostylops*.

The nerves are arranged much as in *Notostylops* but with modifications correlated with the different development of the cortical areas. The optic chiasma, lying above the closely crowded anterior lacerate canals, is hardly visible. The optic nerves are so closely approximated that they appear as one on the cast, the thin plate of bone between them being broken on the skull. The most ventral parts of the pyriform lobes are more pointed and shorter, making the passages for III, IV, V_{1-2}, and VI shorter, and are crowded toward the midline, bringing these passages within about 2 mm. of each other. V_3 occupies the same relative position as in *Notostylops*, but, due to the shortening of the pyriform lobe, is nearer the foramen lacerum anterius.[1] The internal auditory meatus, VII and VIII, has the usual relationships, but here, due to the cerebral expansion, is at the vertical level of the posterior end of the cerebrum, instead of far posterior to this as in *Phenacodus* or, still more, *Notostylops*. The posterior lacerate foramen, IX, X, XI, is small but otherwise quite usual. The hypoglossal canal, XII, seems to be single.

The large posterolateral venous opening into the cerebral cavity, already noted for *Notostylops*, is here more lateral and even larger. From it a very prominent venous sinus runs anteriorly near or along the fissura rhinalis to the fossa sylvii. Posterior to the fissura rhinalis it gives off a

[1]On the cast the size of V_3 is much exaggerated by breakage around the foramen.

small dorsal tributary. Another larger tributary runs upward and forward from near the large foramen, and a smaller vein, independent of the large lateral sinus, passes directly upward and forward from the foramen, and another, longer, straight downward and forward.

There is a small pair of foramina between V_3 of the two sides, and one still smaller in the periotic immediately dorsoanterior to the posterior lacerate foramen. The entocarotid enters the cranial cavity about 3 mm. from the midline between the levels of V_3 and VII–VIII, a position almost exactly as in *Phenacodus* and presumably primitive but secondarily lost in *Notostylops* (as in most notoungulates, being crowded out of position by the expanded bulla).

In a few points, such as entocarotid or the shape of the olfactory bulbs, *Hegetotherium* resembles *Phenacodus* more than it does *Notostylops*. These perhaps are among the characters distinguishing the Notostylopidae from the generalized notoungulate ancestry. In general, however, *Hegetotherium* shares with *Notostylops* the principal points by which the latter differs from *Phenacodus*.

The brain of *Hegetotherium* differs from that of *Notostylops* in many respects, but with few probable exceptions these are due to evolutionary advance, and could be, with considerable probability were, derived from the *Notostylops*-like type. Among the outstanding distinctions of *Hegetotherium* are:

1. Brain length and, to greater degree, brain volume relatively greater.
2. Midbrain fully and hindbrain partly excluded from dorsal exposure.
3. Olfactory lobes relatively much smaller than in *Notostylops* and of somewhat different form.
4. Pyriform lobes not visible dorsally, expanded antero-medio-ventrally.
5. Neopallium relatively and absolutely larger, expanded laterally and, especially, posteriorly.
6. Sulci perhaps more complex.
7. Cerebellum considerably more highly differentiated, relatively shorter and deeper.
8. Optic nerves retracted above the approximated anterior lacerate canals.
9. Entocarotid more as in *Phenacodus*.

The principal dimensions are:

Length of skull	115	mm.
Dorsal length of brain, oblique, including medulla oblongata	61	mm.
Dorsal length between verticals, excluding medulla	59	mm.
Length olfactory bulbs	9.5	mm.
Width across olfactory bulbs	15	mm.
Length cerebrum	35	mm.
Width across cerebrum	40	mm.
Length cerebellum (exposed dorsal part)	14	mm.
Width across cerebellum (flocculi)	21	mm.

Protypotherium

This braincast is taken from a skull of *Protypotherium* sp., Amer. Mus. No. 9246, found by Barnum Brown in 1899 in the Santa Cruz Formation at Felton's Estancia, Río Gallegos, Santa Cruz. The cast lacks much of the olfactory bulbs, all of the ventral surface, and the occipital surface. Although thus very imperfect, it serves to show that the better cast of *Hegetotherium* is not exceptional but is typical of at least the typotheres at this stage of development.

The cast is smaller than that of *Hegetotherium*, but belongs to a smaller animal and had about the same size relations to the skull and to

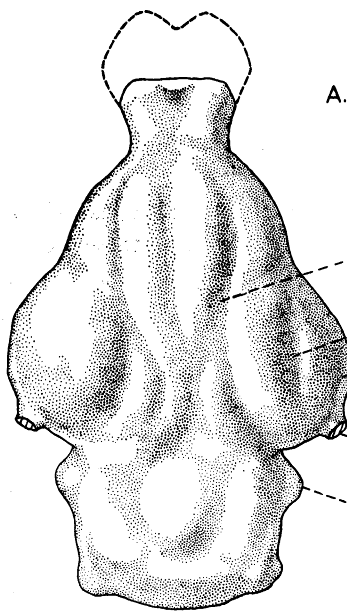

Fig. 2.—*Protypotherium* sp. Braincast from Amer. Mus. No. 9246. Dorsal view. For abbreviations, see p. 17. One and one-half times natural size.

the animal. Its general characters are those of *Hegetotherium* and it suffices to point out the principal differences:

1. The cerebellum is slightly less covered by the cerebrum and hence has a relatively very slightly longer dorsal exposure.

2. The neopallial sulci are less deeply marked, but have nearly the same pattern, except that, as in *Notostylops*, the anterior part of the suprasylvian sulcus is weak or absent and there is no sulcus or depression in the coronal area.

3. The anterior lobe of the cerebellum is more clearly divided into central and

lateral parts (a difference not structural but due to its being less obscured by venous sinuses and cerebrum).

4. The tentorium was more nearly vertical, and the internal auditory meatus more nearly directly beneath the flocculus.

Judging from the foramina and form of complete skulls, the ventral characters were not more distinctly different from *Hegetotherium*, except that the entocarotid did not enter by a separate canal. The brain of *Protypotherium* is clearly very similar to that of *Hegetotherium*, but is slightly more primitive. It is very much closer to *Hegetotherium* in grade of development than to *Notostylops*. The dental and osteological anatomy agrees with this general impression, showing that *Protypotherium* is rather closely allied to *Hegetotherium*, although placed in a separate family, and is in a nearly comparable stage of evolution but retaining a few more primitive characters.

NOTES ON THE NOTOUNGULATE BRAINCASTS DESCRIBED BY GERVAIS

Gervais (1872, pp. 426–436; Pl. xx; Pl. xxi, Fig. 11) described braincasts of *Toxodon* and of *Typotherium cristatum* from the Pampean. Each cast was figured in dorsal view only. Edinger (1929, pp. 194–195, Figs. 184–185) reproduced stipple copies of Gervais's lithographs and briefly referred to the morphology.

In *Toxodon*, the olfactory lobes are relatively small but fully exposed, widely separated from each other, and compressed laterally. In the general outline of the cerebrum, the striking features are the relatively posterior position of the sylvian emargination and relatively great width of the anterior part of the neopallium. In other words, the presylvian part of the cerebrum has increased in size (from a condition more like the early notoungulates here described) relatively faster than has the posterior part. There were apparently more sulci than in the other forms described here, but they cannot be traced or identified on Gervais's figure. The cerebellum was depressed and almost fully exposed. A prominent but relatively narrow vermis is seen in the figure. It seems that the brain of *Toxodon* has been modified by change of habits, by increased size of the animal, and to some extent by evolutionary advance, although even in this very late notoungulate it cannot be called a very progressive brain. These changes have masked any special resemblance to early notoungulates in the parts shown. It is probable that the lateral and ventral sides would show clearer traces of an ancestral structure more like that of, for instance, *Hegetotherium*. No earlier toxodont braincast is at present available to me.

The braincast of *Typotherium*, in dorsal view, is remarkably like that of *Hegetotherium* or *Protypotherium*. The outline and proportions are nearly identical, and the only significant difference to be observed in Gervais's figure is the lesser development of the dorsal sulci. The difference is apparently not due to any real difference of pattern, and probably is merely due to the less exact impression of the sulci on the overlying bones.

The braincasts of *Toxodon* and of *Typotherium* are so unlike that Gervais considered these animals as unrelated to each other. But the early forms are so similar in dental and skeletal structure that toxodonts and typotheres are now believed to be closely related. Probably when early toxodont braincasts are available, these, too, will be much like those of typotheres. The toxodont brain underwent more modification than did that of the typotheres.

Proterotherium

An artificial braincast of *Proterotherium cavum* has been prepared from Amer. Mus. No. 9245, found by Barnum Brown in 1899 in the Santa Cruz Formation at Felton's Estancia, Río Gallegos, Santa Cruz. This splendid skull was fully described and figured by Scott, but the braincast has not hitherto been described in any member of the Order Litopterna. By utilizing cracks already present, it was possible to open the cranium transversely across the cerebral hemispheres, and so to add to the value of the specimen by the preparation of this excellent and unique braincast without any permanent damage to the skull.

The total length of the skull is 180 mm., and of the brain, exclusive of medulla, 91 mm., giving an index of 51. In an animal of larger size and longer rostrum, both tending to give a low figure, this indicates a brain effectively distinctly larger than that of *Notostylops*, with an index of 48, and probably even effectively larger than that of *Hegetotherium*, which also has an index of 51 but is somewhat smaller and has a shorter rostrum. This is substantiated by the anatomical features, and both in effective size and in structure the brain is more highly evolved than the others here described.

Axial flexure is somewhat less than in *Hegetotherium*. The olfactory bulbs are fully visible dorsally and the cerebellum is only very slightly overlapped, but the midbrain was wholly concealed. The ratio of olfactory bulbs, cerebrum, and cerebellum is about 1:5:3. The exposed length of the cerebellum is greater, relative to the cerebrum, than in *Hegetotherium* and not markedly different from the early notoungulates or

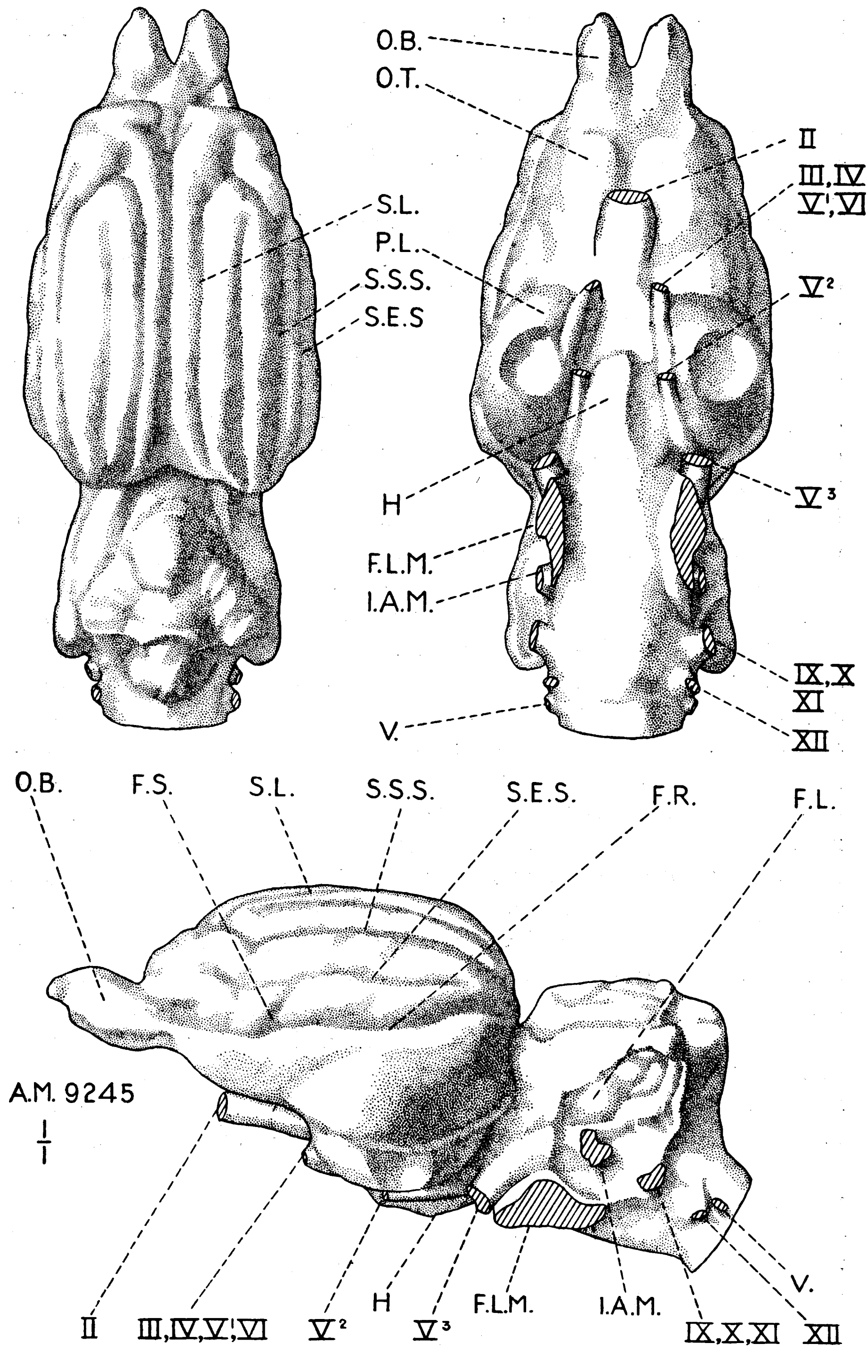

Fig. 3.—*Proterotherium cavum*. Braincast from Amer. Mus. No. 9245. Dorsal, ventral, and left lateral views. For abbreviations, see p. 17. Natural size.

Phenacodus, but the olfactory lobes are much smaller relatively than in any other cast here described. Olfactory bulbs and cerebellum are slightly and about equally depressed below the dorsal level of the neopallium.

The olfactory bulbs are unlike those of the other genera here described in being compressed laterally, the depth of each nearly equal to the length but the width considerably less. They are separated by a deep notch, continued into a median sulcus between the peduncles ventrally but not continuous with the longitudinal scissure dorsally. The olfactory tubercles seem to have been developed about as in *Notostylops*, somewhat more swollen but not relatively larger than in *Phenacodus*. The pyriform lobes are about equal to the neopallium in width, not or scarcely visible in dorsal view, but they are very deep, deeper than the neopallium. This expansion is almost purely vertical, less anterior than in *Hegetotherium*, less posterior than in *Notostylops*, and less lateral than in *Phenacodus*. On the ventral surface of each pyriform lobe there is a prominent circular pit, the significance of which is not clear.[1]

The shape of the neopallium is unlike that of any of the other casts here described, most nearly resembling *Phenacodus* except for its greater length and slightly less disparity in anterior and posterior widths. It is about one-fourth longer than wide, pyriform and with the greatest width posterior to the middle, but less triangular than the other casts and with the width more nearly the same throughout. The surface features are more clearly marked than on any other of this series of casts, even better than in *Hegetotherium*, and must reproduce the actual brain convolutions very closely. The brain is rather strongly gyrencephalic, and the presence of four sulci and the rhinal fissure on each side, all nearly straight and parallel to each other and to the longitudinal scissure, give it a very peculiar, almost mechanical or artificial appearance.

The rhinal fissure is very clearly and deeply impressed, becoming a little vague only anterior to the fossa sylvii, and is almost horizontal and straight in lateral view. The fossa sylvii is small and not very distinct. It does not form a lateral emargination to the same degree as in *Notostylops*, for instance. From it a short sulcus runs obliquely upward and backward, terminating at the most ventral of the longitudinal sulci. The latter, descriptively and perhaps functionally ectosylvian, is the least uniform of the series and is formed by a line of depressions rather loosely united into a longitudinal groove beginning near the pos-

[1]For possible future students of the cast, it should be noted that the still larger pit on the lateral surface of the left pyriform lobe is an artifact. It has been omitted in the drawings.

terior border and running forward to within about 7 or 8 mm. of the frontal pole. Above this is a nearly straight and even longitudinal sulcus, nominally suprasylvian, similar in character to and only very slightly shorter than the sulcus lateralis. These two, suprasylvian and lateral, are joined between their anterior ends by an obliquely transverse sulcus, from which another very short but (on the right side, at least) deep sulcus directed anteriorly also arises. This complex, uniting the lateral and suprasylvian sulci, produces somewhat the effect of coronal or coronal and ansate sulci in some other groups of mammals, but the relations in detail are unlike those on any other brain known to me, and it is highly probable that these sulci (and others, except probably the sulcus lateralis and possibly the suprasylvian) do not have any real homologues in any other mammalian order. Between the lateral and suprasylvian sulci there is another, nominally ectolateral, parallel to them and of similar character except that it is shorter, not reaching the transverse "corono-ansate" sulci and hence leaving the gyri above and below it continuous around its anterior end. These three longitudinal sulci all end freely and independently near the posterior border.

The fossa hypophyseos has been crushed so that its mold appears as a high sharp ridge on the cast. Apparently it was rather prominent.

The separation of the cerebellum is very deep and clear-cut, even more than in *Phenacodus*, the skull having a very strongly developed tentorium. In its gross modeling, the cerebellum shows considerable resemblance to *Phenacodus*, less to the other casts of this series. Its details are clearer and probably its structure was really more complex, although even in this case it is impossible to work out detailed relationships and divisions. Anteriorly there is a median lobe with no clear evidence of convolution, divided (probably by the fissura prima) into a small anterior lobe, almost hidden in the deep cleft formed by the tentorium, and a larger posterior part, probably the lobulus simplex. Posterior to this the dorsal portion of the cast becomes trifid. The lateral portions, apparently highly foliated, pass backward, slightly outward, and, particularly in their more posterior parts, downward. They probably are or include ansiform and paramedian lobules. The posteromedian lobule, with rather vague traces of convolution, forms an almost pyramidal point at the occipital pole and then sinks vertically to the medulla, very much as in *Phenacodus*. Lateral to the lobulus simplex and perhaps pertaining to it but separated by longitudinal grooves, are smooth hemispheres. Lateral to all these parts and much obscured by peri-petrosal fissures and postmortem crushing, is a looped projection, in part or wholly a formatio vermicularis, apparently with a short nearly vertical posterior crus and a more expanded and more oblique anterior crus. Much of the latter, undoubtedly more than a flocculus strictly speaking, is lodged in a shallow excavation in the petrosal, but this part is less sharply defined and considerably less salient than in *Notostylops*, for instance.

The nerve exits can all be unmistakably identified. The large optic nerves are confluent on the cast, due to postmortem destruction of the intervening septum, and are well in advance of and slightly above the following passages. The confluent casts of the other orbital nerves, III, IV, V_1, and VI, are relatively rather small (doubtless because the large maxillary nerve is not included with them), and occupy the usual position between the anterior ends of the pyriform lobes. V_2 can be closely traced, arising medial to V_3, running downward and forward, and becoming free of the cast (entering its separate canal) 7 or 8 mm. posterior to the single exit of III, IV, V_1, and VI. This separate exit of V_2 is a marked distinction from the other casts of this series.[1] The brain-cast representation of V_3 is also very peculiar and unlike any other cast here described. On the other casts, this nerve is represented by a stalk on the ventroposterior part of the pyriform lobe (far removed from the true point of origin of this nerve on the original brain). In other words, the internal opening of the foramen ovale in these forms is anterior to the tentorium osseum. In the present case, on the contrary, the very large V_3 arises on the cast on its cerebellar portion, anterior to and slightly below the internal auditory meatus, at what must have been the actual point of origin on the brain itself. It runs downward and forward, in the same direction as V_2 but leaving the cast long before the latter. The foramen ovale is posterior to the tentorium.

Loss of the tympanic has left a large gap on the skull at and posterior to the position of the median lacerate foramen and represented on the cast by a heavy triangular stalk. The internal carotid doubtless entered the skull somewhere along this gap. The internal auditory meatus is near the middle of a large petrosal fossa on the cast, well posterior to the cerebrum. The filling of the posterior lacerate foramen (IX, X, XI) is posterior and ventral to the internal auditory meatus, and at about an equal distance from the former, in the same direction, is the exit of XII. On the skull dorsoposterior to the latter and enclosed with it (the con-

[1]Scott stated that foramen ovale and foramen rotundum are confluent in the Litopterna. I have elsewhere suggested that this is highly improbable, *a priori*, and that the foramen rotundum was probably confluent with the anterior lacerate foramen. The endocranial anatomy proves that the latter is the true condition. What can only have been V_2 leaves the endocranial cavity separately, but its external exit is confluent with the anterior lacerate foramen, and very distant, at least 22 mm., from the foramen ovale.

dylar foramen) in a common pit, is a vascular foramen leading into the cancellae of the occipital bones.

This brain is, on the whole, a progressive one, but progressive in a direction not exactly paralleled in any other group. It thus accords with the other indications of affinity of the Santa Cruz litopterns, the only unexpected feature being the suggestion of more progressive development than in the associated typotheres. The effective size of the brain is relatively great, the olfactory bulbs are small, the neopallium (particularly its anterior part) is expanded and rather richly convoluted, and the cerebellum is large and complex. Correlated with osteological evidence of a fleet and at least superficially progressive plains-dwelling animal, the brain suggests in general intricate muscular coördination and dominance of visual, tactile, and kinesthetic senses over the more primitive olfactory and related sensual and cerebral organs.

So far as indications of affinity go, they are chiefly negative. The brain adds its evidence against the now universally abandoned theory of perissodactyl relationships for the Litopterna. It has no special resemblance to any perissodactyl brains known to me, and perhaps least of all to the early horses (*Mesohippus* has been compared). It also opposes any close union with the Notoungulata, differing in various fundamental features from any of the notoungulate braincasts yet available. On the positive side, the braincast of *Proterotherium* might easily be fitted into a preconceived theory, or one based on other evidence, but in fact is quite inconclusive. Thus it could very well have been derived from a brain like that of *Phenacodus*, but, in accord with its much younger age, it is decidedly more progressive and is too deeply modified from the *Phenacodus* stage, if it did pass through it, for any certain and objective recognition of affinity. Good evidence on this point could come only from older braincasts, of *Notostylops* or *Astraponotus* age, but there is no immediate prospect of obtaining these.

The principal dimensions follow:

Length of skull	180 mm.
Length of brain exclusive of medulla	91 mm.
Length of olfactory bulbs (dorsal)	10 mm.
Width across olfactory bulbs	15 mm.
Dorsal length of cerebral hemispheres	51 mm.
Width across cerebral hemispheres	40 mm.
Length of cerebellum	28 mm.
Width across cerebellum	29 mm.

CONCLUSIONS AND SUMMARY

Something is now known of characteristic braincasts of the more common and important South American ungulates.[1] This information is inadequate for any final conclusions, but does lead to some preliminary suggestions.

The oldest notoungulate braincasts, and the only ones that seem to be sufficiently unmodified to give some idea of ancestral structure in the group, are those of *Notostylops*, *Oldfieldthomasia*, and *Rhyphodon*. *Notostylops* and *Rhyphodon*, although apparently equally primitive, differ more than would have been anticipated, particularly as they are commonly referred to the same suborder. It is a reasonable theory that the characters shared by these casts probably nearly represent the ancestral notoungulate characters in general. The more important of these characters are:

1. Brain arrangement nearly serial.
2. Olfactory bulbs and cerebellum fully exposed dorsally, and midbrain partly exposed.
3. Olfactory bulbs very large, about one-half to one-third as long as the cerebral hemispheres, and cerebellum (in dorsal exposure) varying from as long as the olfactory bulbs to about twice their length.
4. Olfactory tubercles rounded swellings, low but distinct.
5. Pyriform lobes very large but shallow, visible in dorsal view laterally or posterolaterally.
6. Cerebral hemispheres as a whole triangular, much narrower anteriorly than posteriorly, shallow and somewhat flattened dorsally.
7. Rhinal fissure nearly or quite continuous and approximately horizontal.
8. Distinct sylvian fossa, placed well forward, and causing a lateral emargination in the cerebral outline.
9. Slightly gyrencephalic. Sulci poorly impressed on bone and probably shallow. A short sylvian fissure, a posterior suprasylvian sulcus, and a lateral sulcus probably primitive for the group.[2]
10. Fossa hypophyseos variable but not very deep or sharply defined in any case.
11. Cerebellum with relatively very large vermis, divided serially into two or more lobules, and rising to a node, of varying prominence, at the top of the occiput.
12. Lateral lobules or cerebellar hemispheres small and probably poorly subdivided or differentiated.
13. Formatio vermicularis, or its apparent gross anatomical equivalent, roughly in the form of an inverted V, the posterior crus longer than the anterior, the angle between them variable.
14. Despite the condition in *Rhyphodon*, it is highly probable that the lodging

[1]The rarer Astrapotheria and Pyrotheria are still quite unknown in this respect, but each of the other major groups is now represented by at least one typical example.

[2]One or the other of the two latter may have been absent in *Rhyphodon*, but this is quite uncertain, and it seems highly probable both were present in the ancestral notoungulates or appeared very early in the various groups.

of a nominal "flocculus" in a petrosal fossa anterior to the meatus is primitive for the group.

15. Cranial nerves, as they appear in the cast, grouped as follows: (a) I (multiple exits); (b) II[1]; (c) III, IV, V_{1-2}, VI; (d) V_3; (e) VII, VIII; (f) IX, X, XI, and (g) XII.

16. II between, slightly above, and anterior to the common canal of III, IV, etc. The latter at the anteromedian point of the pyriform lobe.

17. V_3 appearing on cast as a nearly vertical stalk on the posteroventral part of the pyriform lobe.

No important common features of the endocranial circulation are observed. Both *Notostylops* and *Rhyphodon* have peculiar and very prominent vascular exits from the cerebral fossa, but they are not homologous in the two cases and the primitive condition cannot be inferred.

Most of these characters are doubtless primitive in a general sense, yet it is surprising how distinctive they are in aggregate. Checking over the known braincasts,[2] with a single exception there is not one that could be confused with the inferred ancestral notoungulate type. It does seem, therefore, that these data give an adequate and distinctive definition on endocranial characters of a natural group of mammals. For instance, even the earliest known artiodactyl (Lower Eocene) or perissodactyl (Middle Eocene) braincasts are obviously and fundamentally different from the notoungulate type. This is likewise true, although to less degree in various points, even of such archaic ungulates as the amblypods (*sensu lato*) so far as these are known.

The exception to this exclusion from the notoungulate braincast type is of extraordinary interest and possibly of essential phylogenetic significance. *Phenacodus* has every one of these characters and cannot be separated from the Notoungulata on the basis of the endocranium. This appears also to be true of other genera, e.g. *Pleuraspidotherium* (see Edinger, 1929), which are also placed in the Condylarthra, but they are inadequately known. The theory is quite justified and seems to be supported by excellent, if not conclusive, evidence that the notoungulate brain evolved from a type otherwise known only in the condylarths and quite distinct from any others known, even those of comparable or greater age and comparably or more primitive in general structure.

The evidence of the braincast is not more certain than any other sort of evidence, belongs to no different category, and involves quite as

[1]II appears to have no separate exit in *Rhyphodon*, but its older allies show that this is anomalous or secondary.

[2]Particularly Edinger, 1929, also Tilney, and the literature cited by those authors. There are also a few braincasts in the American Museum which are not included in these general reviews or have not been described at all.

much personal judgment. It is not the hoped-for but probably non-existant datum that might reduce the large subjective element in phylogeny and improve the character of this very inexact science. Its value is in multiplying the data on which conclusions can be based and thus giving better grounds for personal opinion. Also, like other sorts of characters, it sometimes preserves clues which have been lost or disguised in other parts of the anatomy. The present case, with its clear suggestion of derivation of the Notoungulata from the Condylarthra, may be an example of this, but of course must be thoroughly correlated with all the other evidence before a final conclusion is drawn.

Turning to the Typotheria, the development of their brains from the primitive notoungulate type as outlined above seems fairly clear. Their dentitions became rapidly and profoundly modified between *Notostylops* and Santa Cruz time, but otherwise they were a conservative group. Directly ancestral stages are not known, but the series *Notostylops-Hegetotherium-Typotherium*, Eocene-Miocene-Pleistocene, represents a tentative structural sequence probably valid in a broad way. This sequence suggests that during the period of their most rapid dental evolution, Eocene to Miocene (or into the Oligocene when the advanced dental type was already fairly established), the brain also advanced, chiefly by reduction of the olfactory bulbs and moderate expansion and differentiation of the neopallium, but not enough to conceal its ancestral characters. From Miocene to Pleistocene the brain seems to have been relatively static. Even in the latest typotheres, the brain was of very low type (note Gervais's confusion of it with the rodent brain). As nearly as one can make such a comparison, the latest and most specialized typotheres stood about on the same level of brain development as the earliest and least specialized artiodactyls and perissodactyls.

The braincasts suggest considerably closer relationship between *Notostylops* and the typotheres than between either of these and *Rhyphodon*.

While it has the distinctive notoungulate stamp, the braincast of *Rhyphodon* is peculiar. It suggests, but on evidence inadequate for any positive assertion, that the homalodontothere brain diverged decidedly from those of other notoungulates and was conservative or even degenerate. *Homalodontotherium* itself, relatively gigantic in size, probably had brain modifications, not necessarily progressive, such as invariably accompany great skull size regardless of the factors of true neurological or mental advance.

For the toxodonts, *sensu stricto*, we have as yet only the inadequate data given by Gervais for the last of this line, *Toxodon* itself. Here the effects of gigantism, a rather broad massive braincast and increased convolution, are visible and tend to obscure more fundamental characters. Also the great time gap from Eocene to Pleistocene corresponds with evolutionary change which makes the braincast of *Toxodon,* so far as it is known, practically unrecognizable as being notoungulate. This does not oppose the general conception of a notoungulate brain type and its differentiation, but merely demands intermediate material for elucidation.

The braincast of *Proterotherium* is somewhat more progressive than that of contemporaneous typotheres, is developing along different lines, and shows no evidence of special relationships to the notoungulates. Common origin from a condylarth type is a possibility, but is not an inevitable conclusion on the available data. *Proterotherium* seems to be quite distant from the typotheres and probably from notoungulates in general, a member of a very distinctive order, and the braincast of this relatively late form suggests no definite connection with any other group.

Abbreviations on Text Figures

II—Optic nerve (filling of optic canal).
III, IV, V_{1-2} [or V_1], VI—The common canal of these nerves, the anterior lacerate foramen.
V_2—Maxillary nerve.
V_3—Mandibular nerve.
IX, X, XI—Common canal of these nerves (posterior lacerate foramen).
XII—Hypoglossal canal (condylar foramen).
C.C.—Carotid canal.
F.L.—"Flocculus," or cerebellar lobule lodged in petrosal.
F.L.M.—Foramen lacerum medium.
F.R.—Rhinal fissure.
F.S.—Fossa sylvii.
H.—Filling of fossa hypophyseos.
I.A.M.—Internal auditory meatus (nerves VII–VIII).
O.B.—Olfactory bulb.
O.T.—Olfactory tubercle.
P.L.—Pyriform lobe.
S.E.S.—"Ectosylvian" sulcus.
S.L.—Lateral sulcus.
S.S.—Sylvian fissure.
S.S.S.—Suprasylvian sulcus.
V.S.L.—Lateral cerebral venous sinus.
V.S.P.—Posterior venous passage from cerebral fossa.

NOTE

Loomis (The Deseado Formation of Patagonia, 1914, p. 79) has figured a braincast of *Eutrachytherus*. Although they probably will necessitate no essential modification of the views here expressed, the characters of the brain of this aberrant genus are so difficult to ascertain and interpret from the illustrations and brief description available that discussion is deferred and not attempted in this preliminary paper.

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