6. The Brains of three Pontian Ovibovinae from China.

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(4 Figs.)

Differences between the three genera.

The external differences between the skulls of the Pontian *Ovibovinae,* great though they are, are mere consequences of the position and direction of their horns (BOHLIN 1935 a, p. 60). *Urmiatherium* (with anteriorly growing bases of horns which point backwards) and *Plesiaddax* (with bases spreading between, behind and in front of horns which point outwards) are, moreover, members of the same type of *Hipparion*-fauna; in one of their habitats, Lok. 30_5 (Shansi province), both occur together. They were apparently fairly similar in size, bigger than a sheep but a good deal smaller than the living musk-ox:

Skull-length:

Plesiaddax depereti	204—263 mm
Urmiatherium intermedium	220—254 »
Adult Musk-oxen (ALLEN)	390—494 »

The scarce remains of *Tsaidamotherium* (with horn-base posterior to horns) belong, however, to a fauna whose species, apart from an indeterminate *Hipparion,* differ from those found with the North China *Hipparion,* and appear more primitive (BOHLIN 1937, p. 106—107). Nevertheless this fauna, since it includes *Hipparion,* is also Lower Pliocene and scarcely, if at all, older than the North Chinese; BOHLIN suggests that the specific differences may be due to different environment, Tsaidam having been a highland steppe. *Tsaidamotherium* may have been a somewhat but surely not essentially smaller animal than its contemporaries *Pl.* and *Urm.* Unfortunately, nothing but two incomplete neurocrania are preserved of the *Tsaid.* skull. The distance of the anterior orbital margin from the posterior end of the occipital condyles could only be approximately estim-

ated in *Tsaid.*: 120 mm (*Pl.*: 145—158; *Urm.*: 147—180) so that actually only the rather insignificant — or even misleading — postorbital (= greatest) breadth can be compared in fact:

Tsaidamotherium hedini (minimum)	124
Plesiaddax depereti	133—161
Urmiatherium intermedium	105—152
Pleistocene *Ovibos* (ANDREE)	110—168
Living *Ovibos* (ALLEN)	108—149

List of brain specimens.

On BOHLIN's suggestion, casts were taken of the interior of several skulls in the Upsala Palaeontological Institute, and kindly entrusted to me for description. My thanks are due, furthermore, for the drawings to G. WINTER-V.MOELLENDORFF, Frankfurt a. M. and E. EBERSTADT, London; for working facilities and the loan of specimens to Dr. EDWARDS, British Museum (N. H.), to Prof. BEATTIE and Dr. CAVE, Royal College of Surgeons.

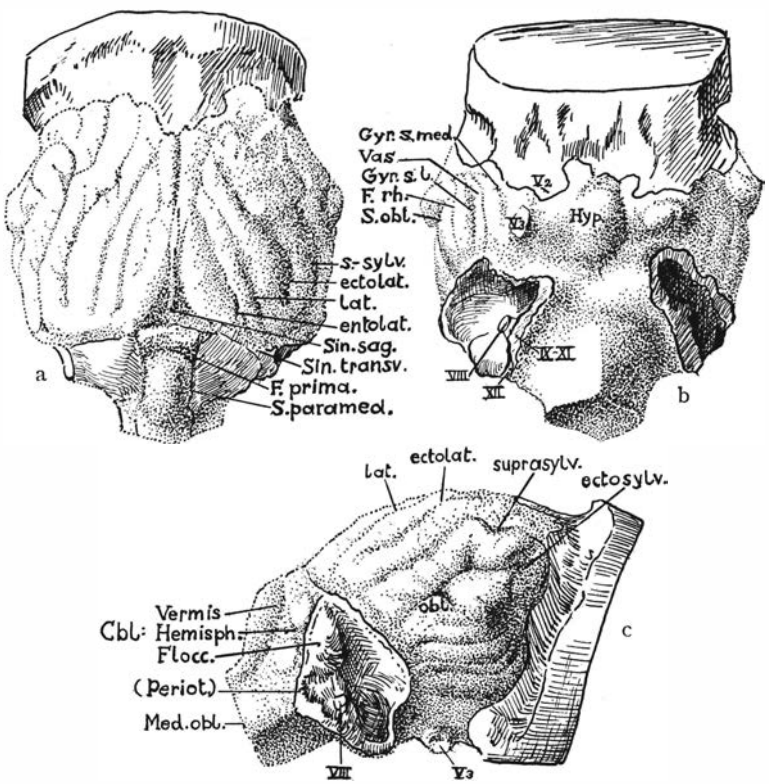

Fig. 1. *Tsaidamotherium hedini* BOHLIN. Plaster-cast of the posterior brain-cavity; 2/3, natural size. a) from above, b) from below, c) from right side.

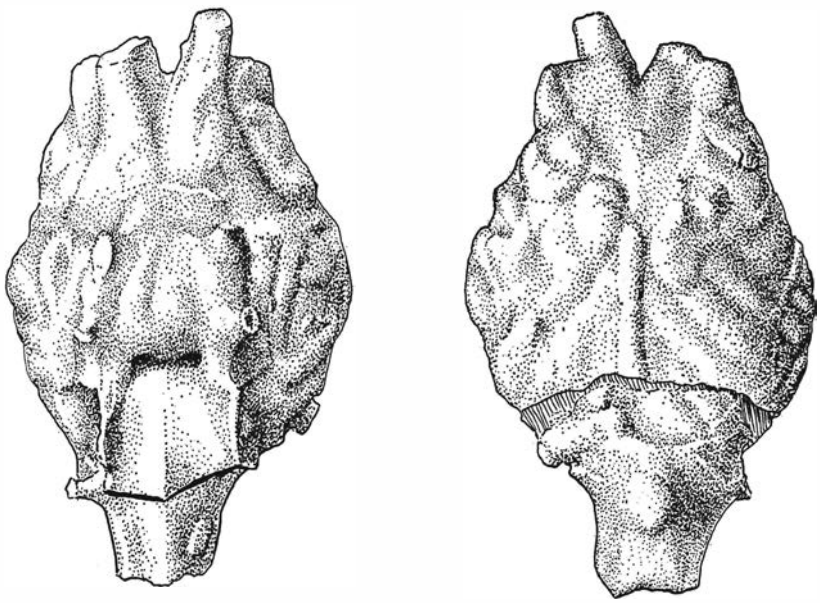

Fig. 2. *Plesiaddax depereti* SCHLOSSER. Plaster-cast of brain-cavity (No. I); $^2/_3$ natural size, right from above, left from below. The fissures are indistinct and displaced and have therefore not been named.

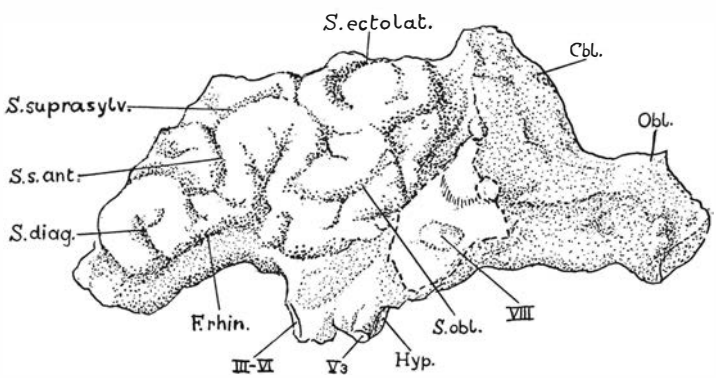

Fig. 3. *Plesiaddax depereti* SCHLOSSER. Plaster-cast of left half of brain-cavity (No. III), side-view, $^2/_3$ natural size.

a) *Tsaidamotherium hedini,* skull I (BOHLIN 1935 b, figs. 1—4). In the front view of this fragment (BOHLIN l. c., fig. 4), the lateral margins of the widely open brain-cavity are seen to converge slightly towards the base, which is notched on both sides: the skull is broken away at the contraction which (as a cerebral jugum) filled the Fossa Sylvii, and below which the canal for the second trigeminal branch pierces the basicranium. Hence the incompleteness of the »brain» shown in fig. 1: the praesylvian portion of the *Tsaidamotherium* brain remains unknown.

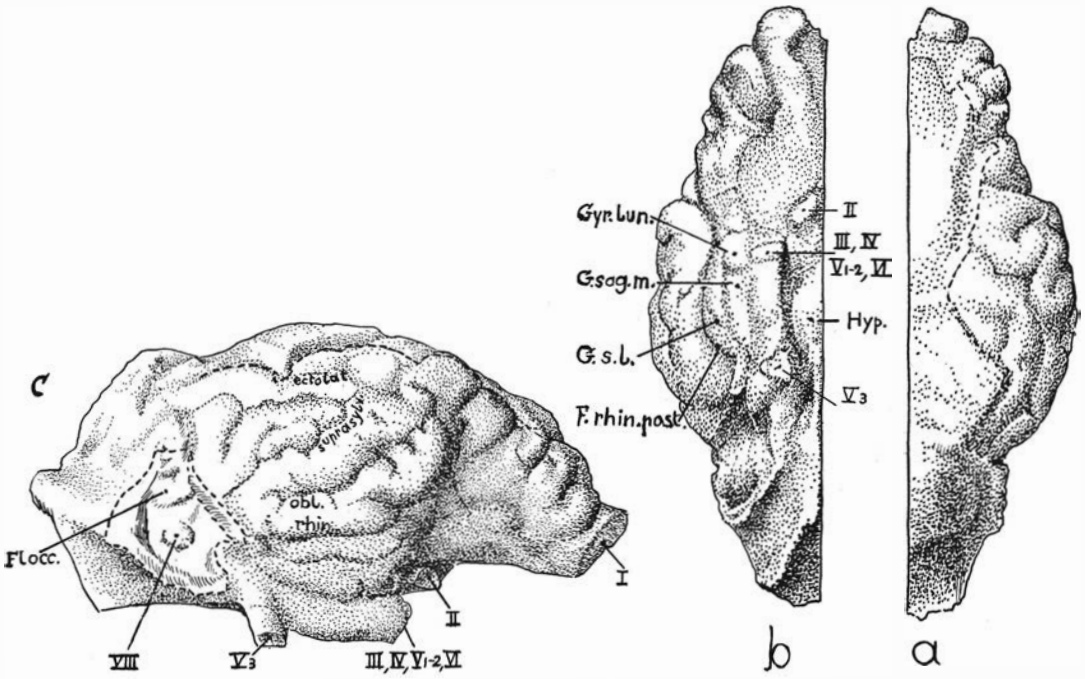

Fig. 4. *Urmiatherium intermedium* (SCHLOSSER). Plaster-cast of right half of brain-cavity; ⅔ natural size. a) from above, b) from below, c) side-view.

b) *Plesiaddax depereti.* I: complete cast of the interiorly distorted skull BOHLIN 1935 a, fig. 40; present fig. 2.

II: Complete cast of an even more crushed brain-cavity, BOHLIN's Ex. 45, mentioned p. 41.

III: Cast of the skull BOHLIN 1935 a, fig. 39; representing left half

	Total length	Forebrain + Cerebellum	Forebrain length		Breadth at temp. Gyri		Bulbi olf.	
			total	postsylv.	sup.	inf.	height	breadth
Ovibos								
Brain (RETZIUS)	130	115	91	50	83		10	10
Cast (Upsala)	164	128	111	60	88		24	7
Cast (New Haven)	163	120	106	60	82		29	14
Urmiatherium	115	98	79	48	~70	~67	16	10
Plesiaddax								
I	136	96	75	41	68	65	17	8
II	132	—	76	40	—	—	—	—
III	122	92	71	40	—	—	19	7
Tsaidamotherium	—	—	—	38	61	66	—	—

of brain with well-marked fissuration, which is effaced, however, along the midline (fig. 3).

c) *Urmiatherium intermedium*. Cast taken from the skull BOHLIN 1935 a, fig. 9 a (Ex. 11), representing right half of brain but not accurately along the midline (fig. 4).

d) *Ovibos moschatus*. Cast taken from the left half of a musk-ox skull, including the whole sinus sagittalis. Much more distinct than on this cast is the fissuration found on a musk-ox cast in the Senckenberg-Museum, Frankfurt a. M. (M. 3924), obtained from the Peabody Museum, New-Haven, Conn. (859), at present no more at my disposal; measurements of this cast are included in the table, p. 136.

Cerebral morphology.

Apart from size and fissuration (in their joint relation to phylogeny) very little in these casts merits attention; as comments upon our illustrations, however, brief mention will be made of certain other features.

Only in *Tsaidamotherium* the cast of the foramen magnum, representing the medulla oblongata, is rhomboid in section; it is elongated due to lateral compression in *Plesiaddax*. The cerebellum too is distinctly moulded only in *Tsaidamotherium*; but the cast of the fossa subarcuata = flocculus cerebelli forms a smooth projection in the impression of the periotic bone also in the other specimens. Directly below it, a prominence with a rough surface is the cast of the internal acoustic meatus, representing the exit of the VIIIth nerves. The basal nerve-exits have already been determined in BOHLIN's basal views, e. g. of the *Tsaidamotherium* skull 1935 b, fig. 1: XII at the caudal border of the otic impression cannot be separated in the cast from the posterior lacerate foramen (IX—XI) —; V_3 = foramen ovale in front of the otic capsule; V_2 in the broken anterior border of the fragment was marked foramen rotundum. No separate foramen rotundum, however, is recognizable in the casts comprising the complete basicranium, nor does BOHLIN, in fact, name the corresponding incision so in *Urmiatherium* (1935 a, fig. 6): the foramen rotundum is confluent with — i. e. is the posterior end of — the foramen lacerum anterius s. sphenorbitale for V_1, III, IV and VI. The optic nerves (II) are hardly indicated in the *Plesiaddax* casts, but are prominent stems in *Urmiatherium*.

The different form of the fossa pituitaria is more striking in the longitudinal sections of the skulls of *Plesiaddax* (BOHLIN 1935 a, fig. 47), of *Urmiatherium* (fig. 9 a), and of *Ovibos* (fig. 9 c) than in the hypophysis casts. Actually, the form of the hypophysis does not seem to be a feature of neurological significance; but the question of size cannot be ignored by the palaeoneurologist, as comparisons show that difference of size may play a significant rôle (EDINGER 1929, p. 67—70). The following

approximate measurements were taken from casts and drawings. Lengths: *Urm.* 18 mm; *Ples.* I 17, III 17; *Tsaid.* 15 — breadths: *Ples.* I 12, *Tsaid.* 10 — depths: *Urm.* 9; *Ples.* fig. 39: 12, III 11; *Tsaid.* 8. The relation to brain size was apparently similar in all three genera.

No fissures are impressed on the base of the piriform lobe in the Upsala *Ovibos* cast, none with a distinct course in *Tsaid.* left side, *Ples.* II left side, nor in *Ples.* III: one straight longitudinal impression is found in *Ples.* I. On the other hand, the piriform lobe in *Urm.* (fig. 4 b) is so good a reproduction of that of the *Ovibos* brain that it is actually described in RETZIUS' words on *Ovibos*: »Am Lobus hippocampi sieht man .... einen gut entwickelten, rundlichen, erhabenen Gyrus lunaris und nach aussen davon einen deutlichen Gyrus ambiens mit einem halbringförmigen Sulcus semiannularis zwischen sich und dem Gyrus lunaris sowie nach hinten davon, an der Oberfläche des Lobus zwei parallel verlaufende, durch einen Sulcus sagittalis getrennte Windungen, den Gyrus sagittalis medialis und den Gyrus sagittalis lateralis» (p. 104, see fig. 4 b). The surface of the right piriform lobe in *Tsaidamotherium*, only the posterior portion of which is well reproduced in the cast, bears the same two gyri. But their separating sulcus sagittalis must have lodged a vessel; for the cast of its impression, with an upward bend towards the sylvian fissure, now projects between the two sagittal gyri (fig. 1 b: vas). This vessel was a tributary either of the vena rhinalis posterior or of the arteria cerebri media.

This shows once again that when distinct fissures are marked on the internal cast of an ungulate skull, they do actually reproduce cerebral sulci. In my belief, this is not only valid for the basal brain surface (this is apparently the case in all orders of mammals), but for the neencephalic fissures too as far as ungulates are concerned (though not throughout the mammalian stock as has been recently proved in primates by LE GROS CLARK and WEIDENREICH).

The specimens discussed in the present paper furnish further proof of this, 1) directly, 2) indirectly:

1) The Frankfurt (= New Haven) cast of the brain-cavity of *Ovibos* is an exact replica of the *Ovibos* brain figured by RETZIUS; it not only shows the sulci figured and named by RETZIUS in his diagram (pl. XXIII a, fig. 1), but also some shallow connections which can be seen in the photogravure (pl. XXIII b, fig. 1).

2) In harmony with the biotope which included its bearer, the fissuration of the *Tsaidamotherium* brain appears more primitive in the cast of the *Tsaid.* brain-cavity than the fissuration of the brain of its contemporaries *Plesiaddax* and *Urmiatherium.*

The only part of the neocortex preserved in *Tsaidamotherium,* however, is the postsylvian — i. e. the portion which, in ontogeny and in

phylogenetical specialisation and increase of body-size, retains the primitive longitudinal fissuration the longest. Praesylvically, the fissuration of the *Tsaidamotherium* cortex may have been more complex — its postsylvian portion certainly shows only practically straight, sagittal sulci, and none of the »wulstigen Windungen» of the musk-ox brain (RETZIUS, p. 99). In *Urmiatherium* and *Plesiaddax,* on the other hand, tortuous gyri are present all over the brain. Whoever can visualize the poor *Ples.*- and *Urm.*-casts complete and perfect will see before his mind's eye a sort of sheep brain, i. e. a small ovibovine brain; whereas the *Tsaid.*-cast with its simple straight sulci, though it is larger than the corresponding portion of the sheep's brain, recalls stages VII and VIII of ANTHONY & GRZYBOWSKY's ontogeny of the *Ovis*-neopallium, and stages VI and VII in their ontogeny of the *Bos*-brain.

The dominant sulcus on the dorsal surface of the *Ovibos*-brain is the undulating and branchiating s. lateralis; it is a more or less undulating line in 3 of the 4 *Ples.*-hemispheres in which it could be traced, straight in *Ples.* III; its area is not reproduced in *Urm.*; it is absolutely straight in *Tsaid.* Its proximal parallel the s. entolateralis is straight on the right side and angular on the left side of RETZIUS' *Ovibos*-brain; a relatively longer straight dash in *Tsaid.*; unfortunately included in the indistinct median area in the *Ples.*-, *Urm.*- and the only *Ovibos*-cast now at hand. The s. ectolateralis too is, in *Tsaid.,* a long furrow as straight and as parallel to the lateral sulcus as possible on the cerebral vault; it is a long sinuous line in *Ples.,* in *Urm.* and in *Ovis,* whereas in *Bos* and *Ovibos* it consists of several short branched pieces.

The suprasylvian arc in *Urm.* and *Ples.* clearly possesses the ovibovine number of branches; in *Tsaid.* only one shallow impression can be detected branching off at the top of its curve and bending back — it corresponds to the ramus superior sulci suprasylvii —. The different course of the s. obliquus (HOLL; posticus RETZIUS) may be seen in figs. 1—4. I may add that the s. obliquus in the series of sheep and oxen brains in the Museum of the Royal College of Surgeons of England exhibits an infinite variety of upward and downward arcs, zigzags, breaks and branches.

The s. obliquus divides the temporal lobe in the upper and lower gyri temporales. In *Ples.* probably the inferior temporal gyrus receded below the gyrus temporalis superior as in *Urm., Ovibos, Bos* and *Ovis,* and thus is invisible in top view of the brain. However, in *Tsaid.* the lower gyrus protrudes in a peculiar way; the brain is broadest at the level of the lower gyrus in this animal instead of at the upper as is generally the case.

The frontal lobes being in *Ovibos* almost as broad as the temporal lobes, RETZIUS states that the musk-ox brain »gewissermassen eine rectanguläre Form darbietet» (p. 99). The brains of *Ples.* and *Urm.* were

distinctly pear-shaped, i. e. the frontal lobes appear less developed in the pliocene *Ovibovinae,* even of the more advanced type, than they are in the living musk-ox. But although the frontal lobe is generally regarded as a seat of mental capacity we must, in view of the variety of frontal breadth in sheep brains, refrain from drawing conclusions.

Conclusions.

Although this paper deals exclusively with incomplete casts and casts taken from distorted brain-cavities, and although comparison of these fossil brains with sheep, oxen and musk-oxen brains serves once more to establish the insignificance of the course of individual sulci, it shows the phylogenetic significance to be attached to the general type of fissuration.

The fissuration of the brain cortex of *Urmiatherium* and *Plesiaddax* obviously resembles that of the ovine as well as, beyond this, the ovibovine brain, the richer ramification of the latter's sulci being the direct result of greater body-size (which in itself represents a higher degree of evolution).

In *Tsaidamotherium,* an animal hardly smaller than its contemporary near relatives *Urmiatherium* and *Plesiaddax* but belonging to a type of *Hipparion*-fauna with less progressive species, straight parallel fissures on the cerebral vault demonstrate a distinctly lower type of brain evolution; the brain of *Tsaidamotherium* resembles the embryonic sheep brain.

Bibliography.

ALLEN, J. A.: Ontogenetic and other Variations in Musk-Oxen. — Mem. Amer. Mus. Nat. Hist., I, 1913.

ANDREE, J.: Über diluviale Moschusochsen. — Abh. westfäl. Prov.-Mus. f. Naturk., IV, 1933.

ANTHONY, R. & DE GRZYBOWSKY, J.: Le Néopallium du Boeuf. Etude de son Développement et Interprétation de ses Plissements. — Journ. of Anatomy, *68,* 1934.

——: Le Néopallium du Mouton. Etude de son Développement et Interprétation de ses Plissements. — Journ. of Anatomy, *71,* 1937.

BOHLIN, B.: Cavicornier der *Hipparion*-Fauna Nord-Chinas. — Palaeont. Sinica (c), *9,* 1935 (a).

——: *Tsaidamotherium hedini* n. g. n. sp. — Geogr. Annaler, 1935 (b).

——: Eine tertiäre Säugetier-Fauna aus Tsaidam. — Palaeont. Sinica, *14,* 1937.

EDINGER, T.: Die fossilen Gehirne. — Berlin (J. Springer) 1929, and: Erg. Anat. Entwicklungsgesch., *28,* 1929.

RETZIUS, G.: Das Gehirn von *Ovibos moschatus.* — Biol. Unters., N. F. *9,* 1900.

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