MORPHOLOGY AND GROWTH OF THE *MASSOSPONDYLUS* BRAINCASE (DINOSAURIA PROSAUROPODA)

by

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ABSTRACT

The almost complete disarticulated braincase of a young *Massospondylus*, and the partial braincase of a very large individual in which the laterosphenoid bones are preserved, are described

INTRODUCTION

The braincase of the prosauropod *Plateosaurus* is well known (Galton 1984), while Galton (1985) has described the morphology of the brain based on several endocasts, and compared it with the brains of other dinosaurs from data reviewed by Hopson (1979).

The skull of the southern African prosauropod *Massospondylus* is reasonably well known (Gow, Raath & Kitching, this volume), but until recently insufficient braincase material has been available to warrant publication. Two quite superb new specimens are described and illustrated here. The first pertains to the skull of a young animal which is crushed and distorted, but in which the elements of the braincase were completely disarticulated post mortem and prior to fossilisation, thus providing unique material for study. The second specimen is the partially eroded and remarkably undistorted braincase of a very large individual, in which changes resulting from growth are evident, and which has well preserved orbitosphenoids, elements missing from the smaller specimen and poorly known in *Plateosaurus*.

The braincases of the two prosauropods *Plateosaurus* and *Massospondylus* of the late Triassic and early Jurassic respectively, are very similar in all essential details; superficial differences relate to the requirement for relatively more powerful muscles in the larger *Plateosaurus*. The braincase (and thus the brain) is essentially unmodified in the huge sauropods of the later Jurassic and Cretaceous (Janensch 1935). It is in fact plesiomorphic not only for Archosauria but arguably for the Class Reptilia. It is salutary to note that this conservative brain plan has served reptiles from the smallest to the largest.

MATERIAL AND METHODS

The badly crushed skull BP-1-5231 would have been under 10 cm in length, making it one of the smallest *Massospondylus* skulls known. The skull lay in water long enough for the braincase to fall apart before it was covered by sediment. The pink mudstone matrix contains a fair amount of calcium carbonate cement. The disarticulated elements of the braincase were compacted together in close juxtaposition to each other and to the rest of the skull, making preparation both tedious and difficult: several elements had to be extracted piecemeal and part of the palate had to be sacrificed in order to free the parasphenoid. Most of the work was done with needles, and once individual elements were free final preparation was done with 2% acetic acid. The material comprises: basioccipital, supraoccipital, paired fused opisthotics plus exoccipitals, paired prootics and laterosphenoids and the para/basisphenoid.

The braincase BP-1-6276A represents an exceptionally large individual and appears undistorted: it displays the prootics, laterosphenoids, orbitosphenoids and dermal roofing elements particularly well. Preparation simply required removal of a deeply weathered encrusting haematite layer by means of a pneumatic engraving tool.

DESCRIPTION

The specimens are illustrated by means of stereophotographs and explanatory sketches. Descriptive notes follow the sequence adopted by Galton (1984, 1985).

Basioccipital, Figures 1 A, B

The illustrations are self explanatory. An interesting feature of this and some of the other elements is the presence of small vascular foramina which are not seen in mature bones.

Para/basisphenoid, Figures 2 A, B; 3A, B

From the illustrations it is clearly seen how basioccipital abuts against basisphenoid, while lateral wings of parasphenoid underlie basioccipital in the region of the basal tubera. The basipterygoid processes have clearly demarcated roughened ends where the pterygoids attached. The basisphenoid has articular facets with deeply concave margins for reception of the prootics. Galton (1985) describes the internal carotids as entering the sella turcica through a common foramen in *Plateosaurus*. Such is not the case in the small specimen illustrated here, but this condition could change with age and is in any event a trivial point. Prominent vascular foramina on the posterior ventral surface of this bone are apparently absent in mature specimens. The parasphenoid rostrum is u-shaped in section with a deep dorsal gutter (in which matrix has been left as the walls are delicate). In the large, apparently undistorted specimen (fig. 3a) the walls actually meet and roof a short section in the infundibular region.

Orbitosphenoid, Figures 3 A, B; 4 A, B

Orbitosphenoids have not been located in the jumbled small specimen, but they are present and undistorted in the large specimen; they are in fact the best prosauropod orbitosphenoids available. These bones show that the cerebral region of the brain was more attenuated anteriorly than is the case in *Plateosaurus* as indicated by the endocranial casts (Galton 1985).

There are three points of contact with laterosphenoid: i) posteriorly immediately above the latter's suture with the pila antotica; ii) medially fine outgrowths from each element make contact (above and behind this point the laterosphenoid edge has a comb-like appearance, suggesting that membranous tissue could have attached here); iii) anteriorly the orbitosphenoids are united in the midline and meet the laterosphenoids laterally.

The orbitosphenoids enclose a large foramen which must have transmitted the optic nerves (II). Anterior to this and close to the midline is a pair of small foramina from which the internal carotid arteries would have emerged. Posterolateral foramina between orbitosphenoid and laterosphenoid would have transmitted the oculomotor nerve (III), while the large foramen anterior to this would have been for the trochlear nerve (IV) and likely also for the supratemporal vein draining forwards into the orbital sinus.

Laterosphenoid, Figure 3 A, B; 4A, B

The large articulated specimen is a great help in understanding the laterosphenoid. This bone has an extensive anterolateral contact with the postorbital, while most of its dorsal surface lies in direct contact with the parietal. A groove with a delicate lateral wall marks the course of cranial nerve VI. In the small specimen contact with the prootic was weak and there is no evidence of the overlapping contact with prootic which in mature skulls separates the foramen for the vena cerebralis media from the trigeminal foramen, nor has contact been established between laterosphenoid and pila antotica as is the case in the adult. Tucked behind the edge which meets prootic is a broad vertical groove for the vena cerebralis media.

Prootic, Figures 3 A, B; 4 A, B; 6 A, B

There is no sign of any medial contact between the prootics of the small specimen, but as far as one can see it appears that in the adults the prootics are linked by a transverse bridge sutured to the dorsum sellae. Where prootic rests on basisphenoid a deep lateral pit reflects the corresponding condition in the latter bone. The facial nerve (VII) emanates from below the crista prootica and is immediately followed ventrally by another, sharper, ridge which could be termed a crista subfacialis. A small vascular foramen (not present in adults) pierces this ridge at its posterior extremity. Dorsally a clearly defined groove in the prootic is continuous with both the channel in the supraoccipital which transmitted the vena capitis dorsalis and the groove on the medial surface of the laterosphenoid which transmitted the vena cerebralis media, thus neatly corroborating the evidence from the endocasts of *Plateosaurus* , which show the meeting of these veins at this point (and incidentally indicating that the brain filled the endocranium).

In the adult prosauropod the vena cerebralis media exits the braincase via a foramen entirely separate from the trigeminal foramen. The bridge between these foramina is formed by a backgrowth of laterosphenoid overlapping onto the lateral surface of prootic. In the juvenile this extension had not yet ossified, but the prootic already had a roughened contact area.

In medial view the anterior ampullary recess is clearly seen, with above it a small depression which is part of the floccular recess. Posteriorly the bone drops away, leaving only a thin sheet which overlaps the opisthotic laterally. The anterior vertical semicircular canal contains matrix, but its extremities are clearly defined and its course is marked by swelling of the prootic. A previously unrecorded feature of this bone is the small auditory branch of the facial nerve (VII) which branches off midway along the course of VII through the prootic. The prootic does not make contact with the parietal.

In *Plateosaurus* the prootic presents a robust, flattened area of attachment for the protractor pterygoidei muscle (Galton 1984). No doubt this muscle was similarly attached in *Massospondylus* but this is not at all obvious even in the adult.

Exoccipital and Opisthotic, Figures 7 A, B

These elements are almost indistinguishably fused. They are separated by the metotic fissure, so that contact with basioccipital behind this feature is by exoccipital only, while in front of the metotic fissure the crista interfenestralis of the opisthotic sutures with basioccipital. Foramina in the exoccipital transmit two branches of the XIIth nerve. Dorsally a process of exoccipital sutures with supraoccipital, though extensive supraoccipital borders the foramen magnum between the exoccipital processes. A triangular projection of exoccipital runs one third of the length of the paroccipital process on its occipital surface.

On the surface facing the metotic fissure the exoccipital is stepped, thus presaging the condition in adult prosauropods where the foramen lacertericum for cranial nerves IX to XI is separated by bone from the jugular foramen below (in the photographs the gap is bridged by adhesive). The crista interfenestralis is distorted out of position. Internally the posterior ampullary recess is well displayed, with the foramen for the posterior semicircular canal above it in the contact area for the supraoccipital.

Supraoccipital, Figures 4 A, B; 6 A, B.

The supraoccipital in the small specimen is a little damaged on the right side. Contact with opisthotic is poorly defined because this is a region of active growth. Several useful features are displayed. Most remarkable is the sharp turn which the vena capitis dorsalis makes within the supraoccipital before continuing along the mesio-dorsal surface of prootic to join the vena cerebralis media. The thickened lateral portions of the bone contain semi-circular canals of the inner ear (not fully prepared as the bone is very spongy and friable). Medially these thickened areas bear depressions which form part of the floccular recess. This depression and the venous tract allow the prootic to be accurately positioned. Posteriorly where supraoccipital borders the foramen magnum there are facets on either side which received processes from the exoccipitals. As these animals grew, pits developed on the occipital surface of the supraoccipital where neck muscles attached.

NON-ENDOCHONDRAL BONES ASSOCIATED WITH THE BRAINCASE

Parietal, Figures 3 A, B; 4 A, B

The parietals of the small specimen are too badly flattened and damaged to be of much use. The large specimen confirms prootic is excluded from contact with parietal. The parietals are broad anteriorly where they overlie laterosphenoids and meet postorbitals.

Postorbital, Figure 4 A, B

The postorbitals are firmly slotted into grooves in the frontals and also suture with parietals and laterosphenoids. The braincase and skull roof thus constitute a single rigid unit.

Epipterygoid, Figure 3 A, B

The epipterygoid and its relationships still need to be studied. At this stage there is no evidence that the epipterygoid made contact with the braincase, suggesting that the pterygoids and palatines may have had some shock-absorbing capacity. Material is now required which will allow detailed study of the palate.

DISCUSSION

Prosauropods and sauropods have a rigid, well ossified, plesiomorphic braincase. It can be safely inferred that the brain itself underwent little change in this lineage. Brain size as a function of body size (EQ or "encephalization quotient") was in the reptilian range (Hopson 1980). One must agree with Hopson that the brain served these animals adequately and that it is difficult to regard them as the physiological equals of theropods and pterosaurs, let alone of birds and mammals.

ACKNOWLEDGEMENT

These initially rather unprepossessing specimens were collected by, you guessed it, James Kitching.

LIST OF ABBREVIATIONS

Bsph	basisphenoid
Ept	epipterygoid
Exoc	exoccipital
F	frontal
i.c.	internal carotid
Lsph	laterosphenoid
Obs	orbitosphenoid
Op	opisthotic
P	parietal
Po	postorbital
Pro	prootic
Psph	parasphenoid
So	supraoccipital
st	stapes
v.c.m.	vena cerebralis media

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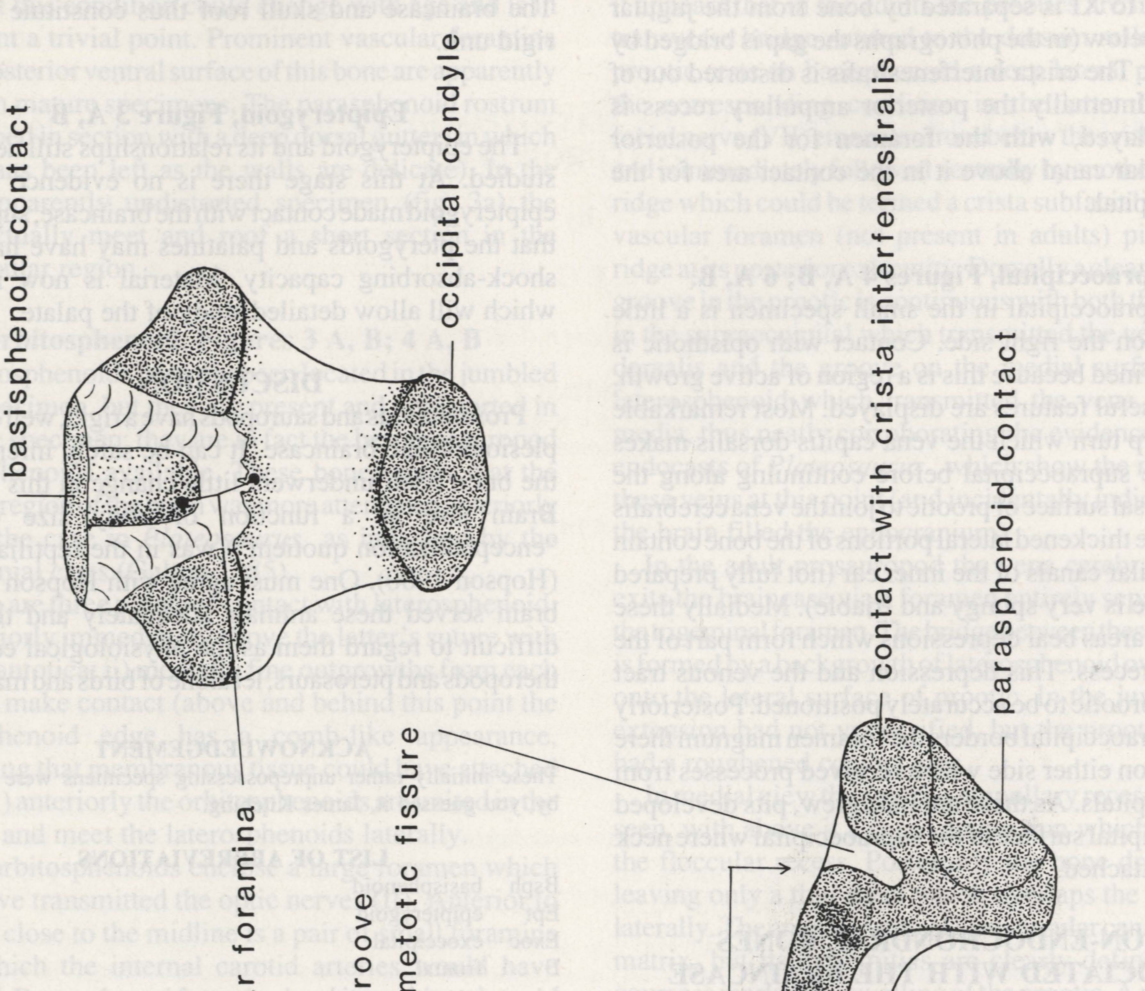
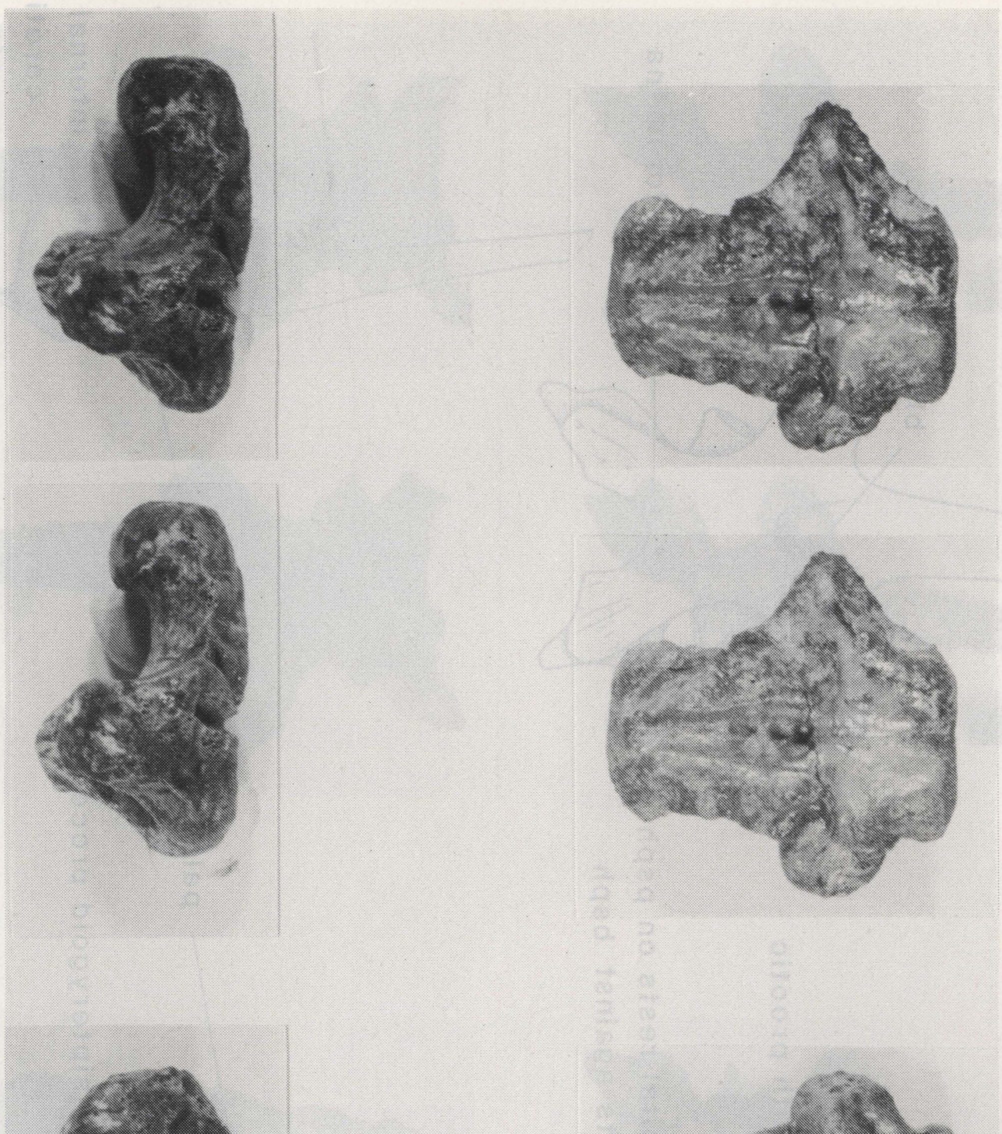


Figure 1 A. BP-1-5321 Basioccipital dorsal, ventral and lateral views. The vascular slot seen in dorsal view was found subsequent to preparation of the photographs.
B. Basioccipital as in 1a but including the anterior view.
Scale = 1 cm



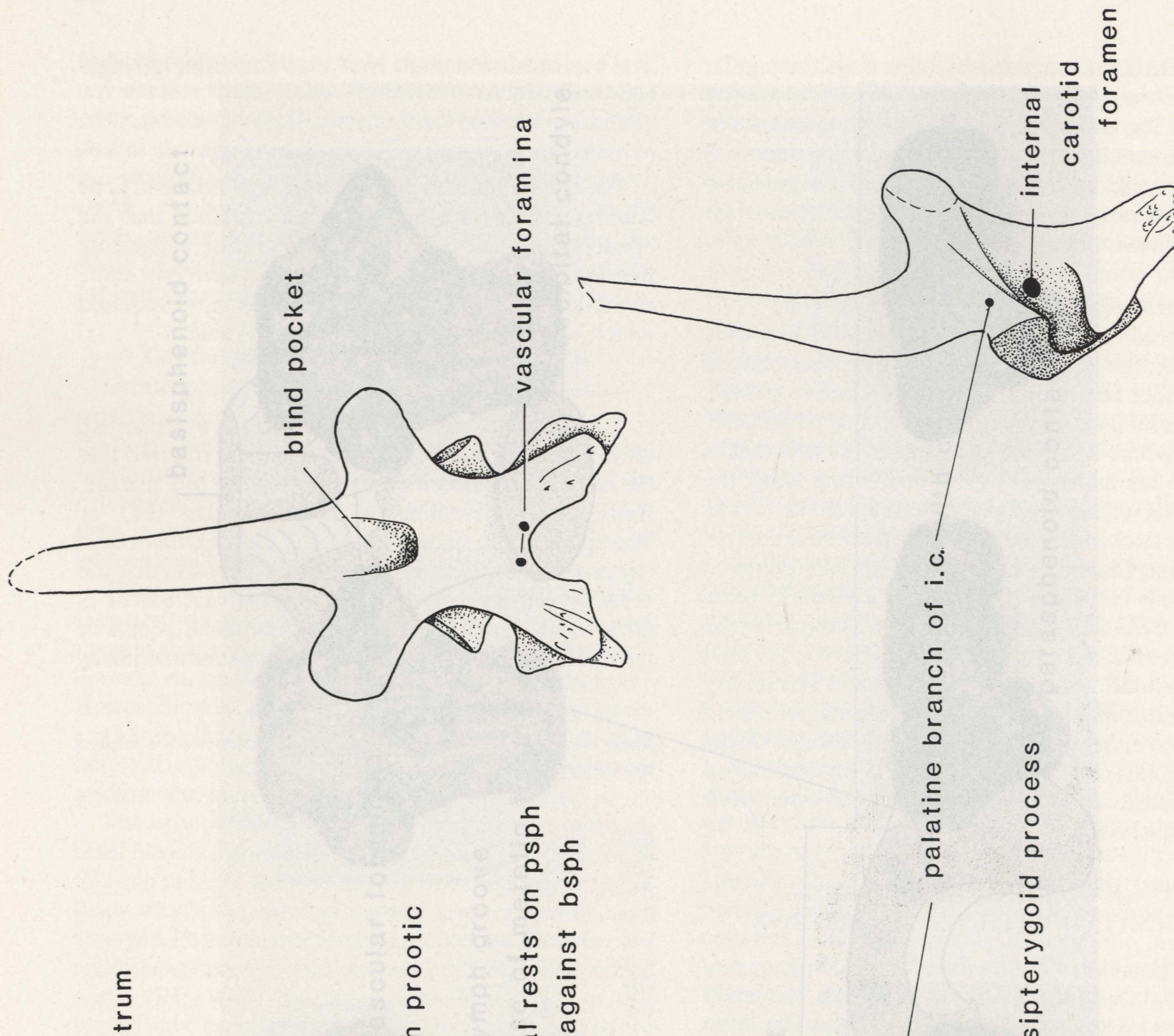
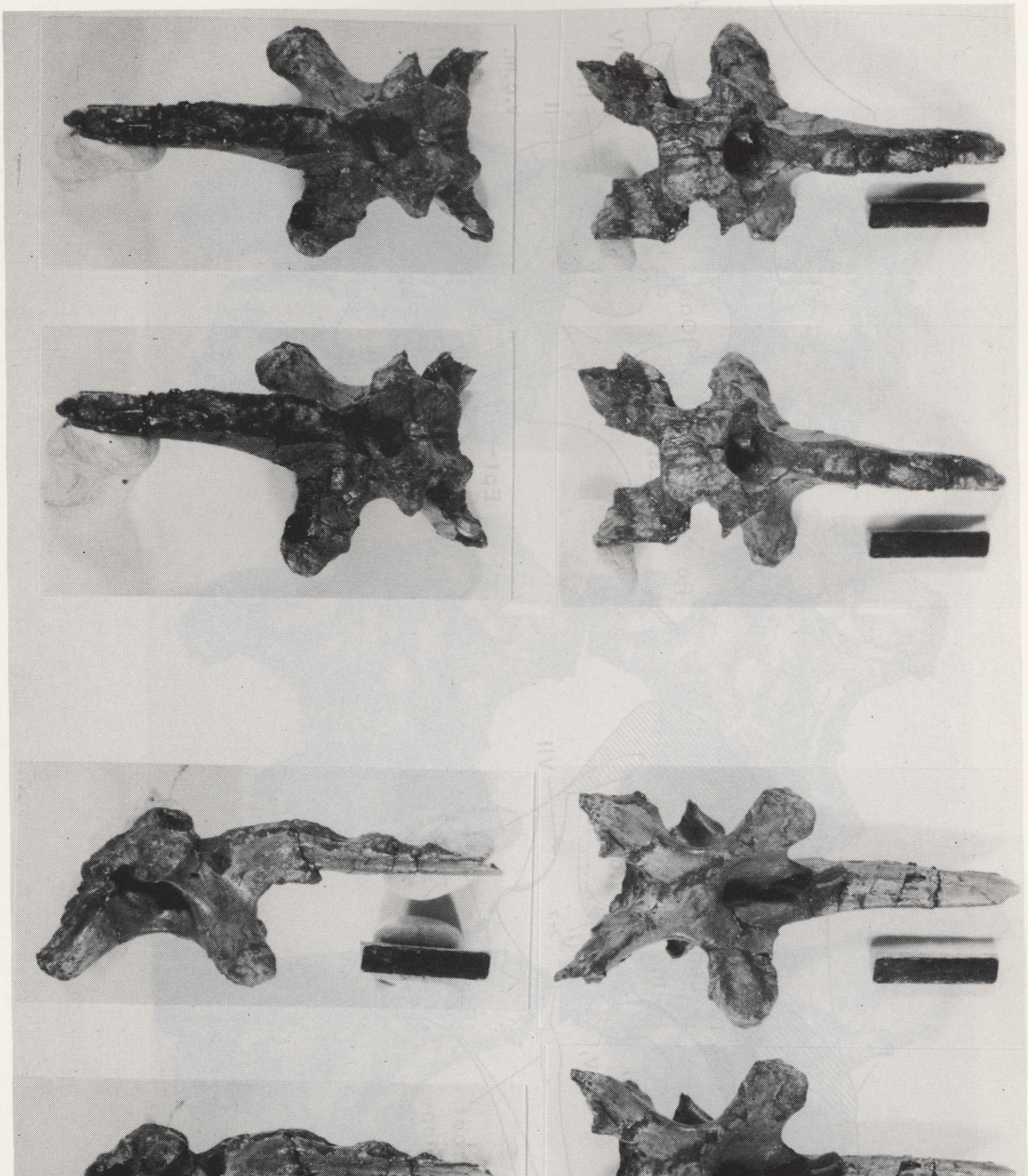


Figure 2 A. BP-1-5231 Para/basisphenoid. Dorsal, ventral, anterior oblique and lateral views.
B. Para/basisphenoid as in 2 a.
Scale = 1 cm



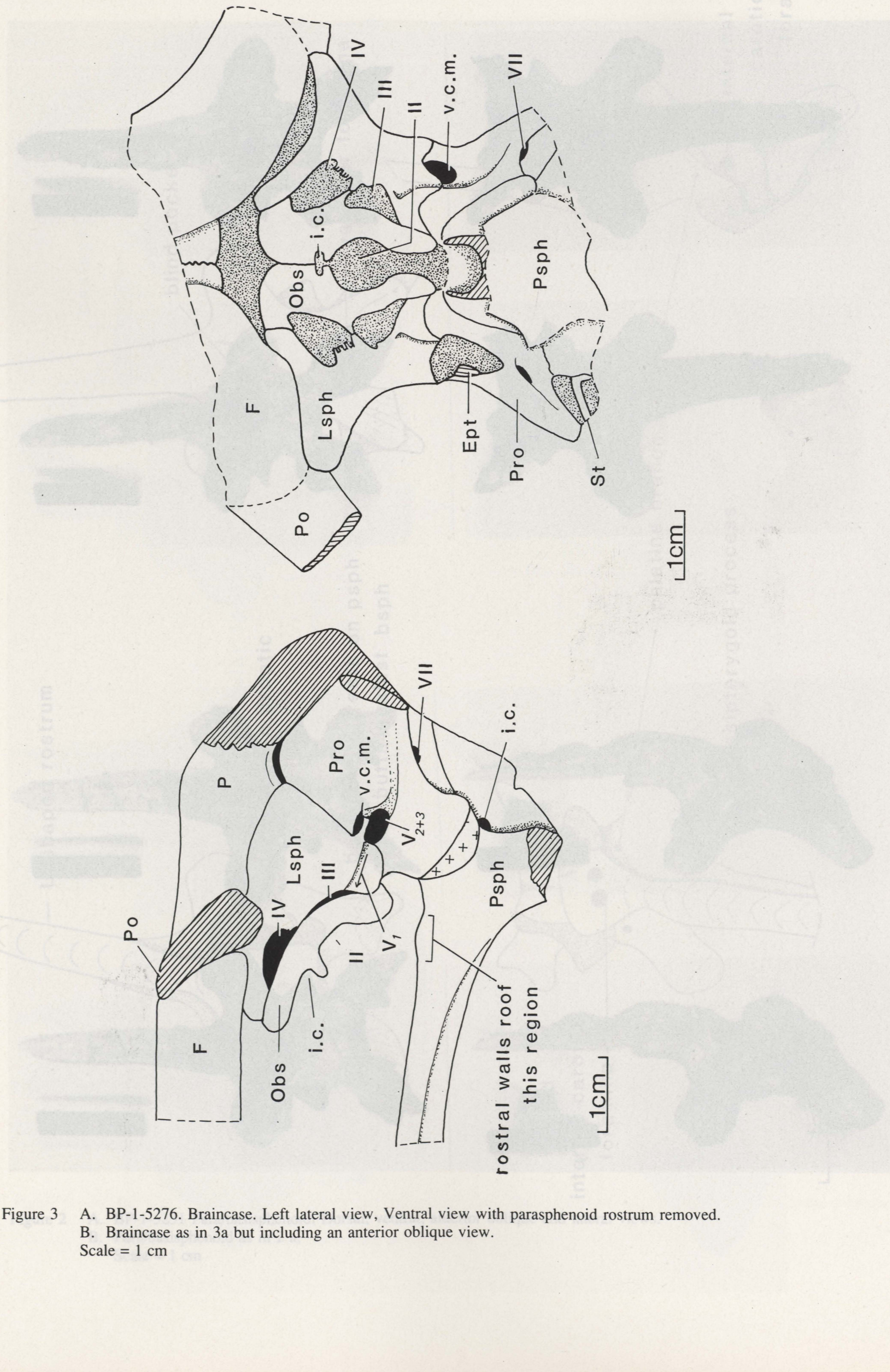
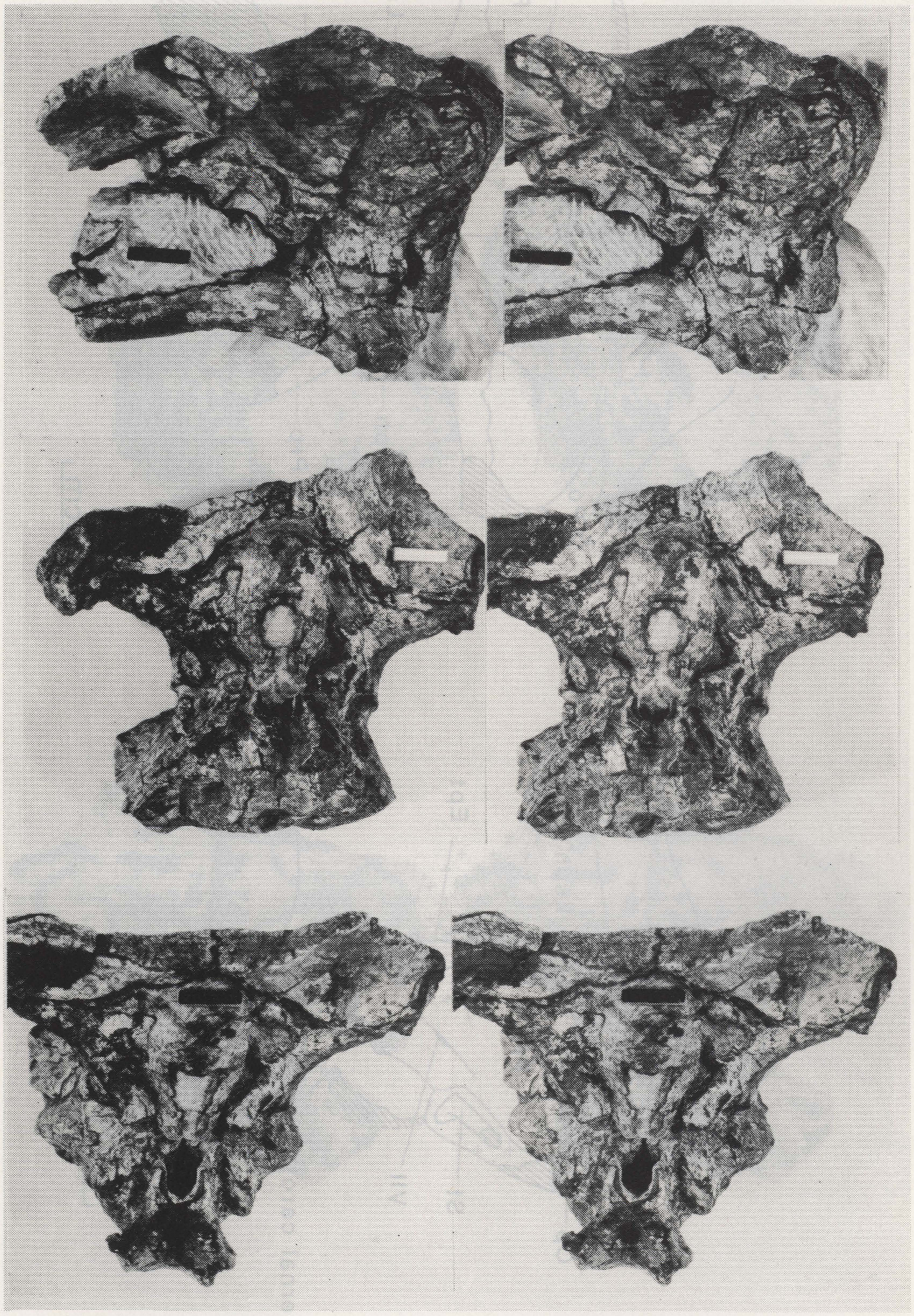


Figure 3 A. BP-1-5276. Braincase. Left lateral view, Ventral view with parasphenoid rostrum removed.
B. Braincase as in 3a but including an anterior oblique view.
Scale = 1 cm



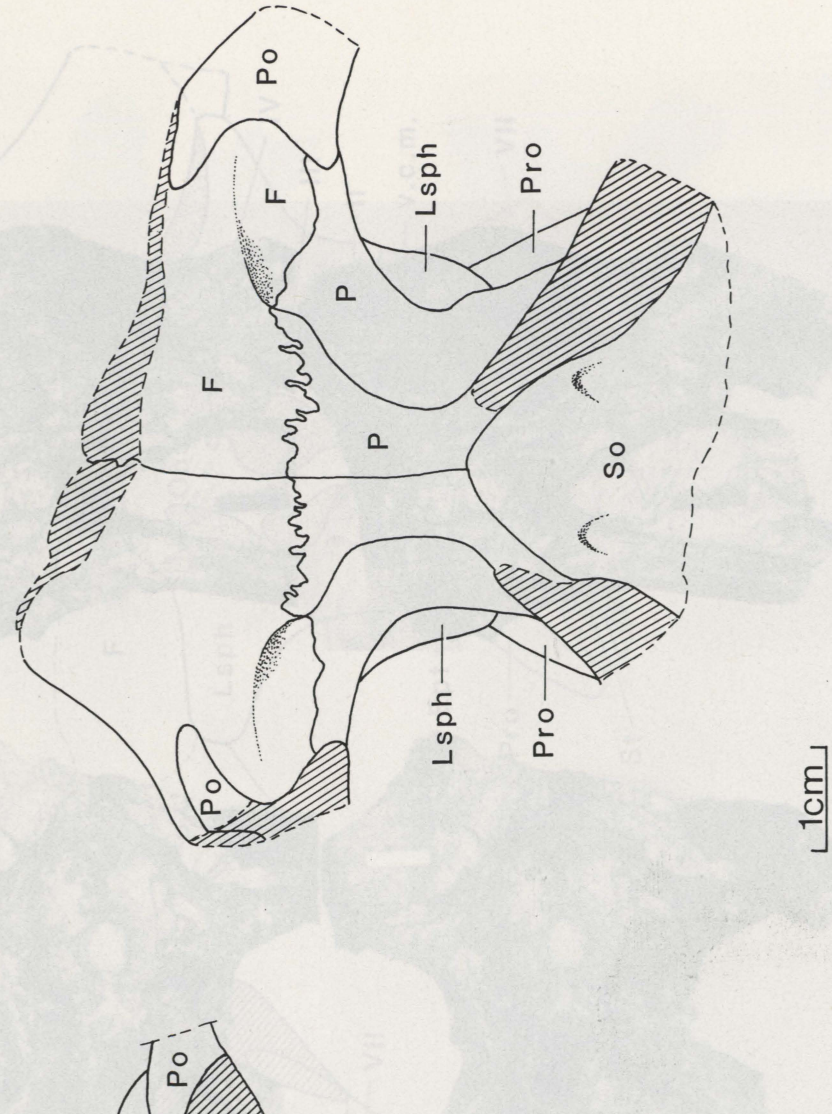
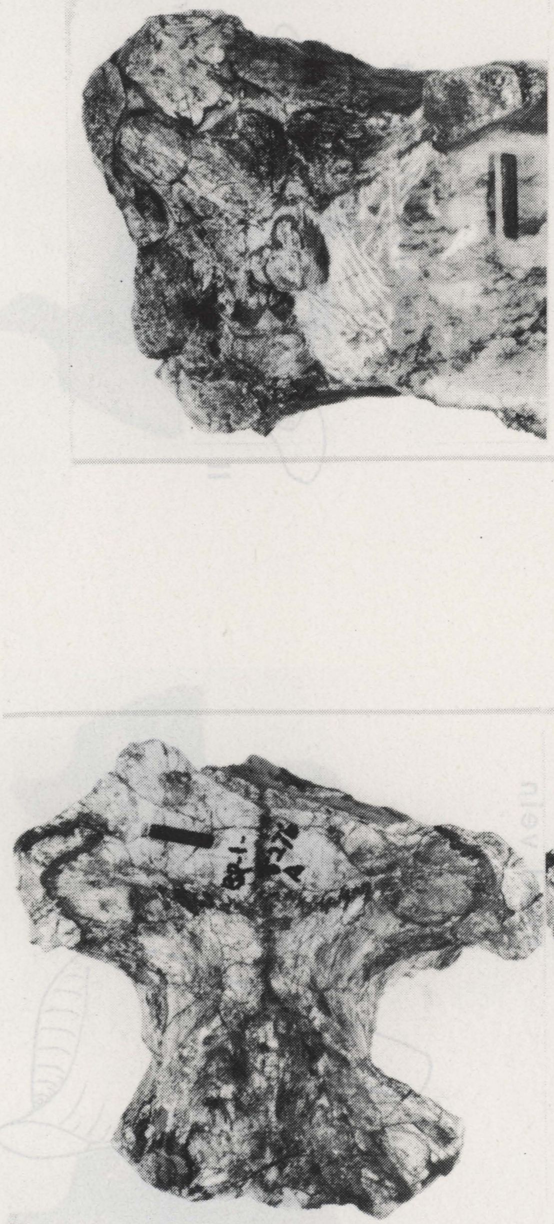


Figure 4 A. BP-1-5276 Braincase. Right lateral and dorsal views;
B. Braincase as in 4a
Scale = 1 cm



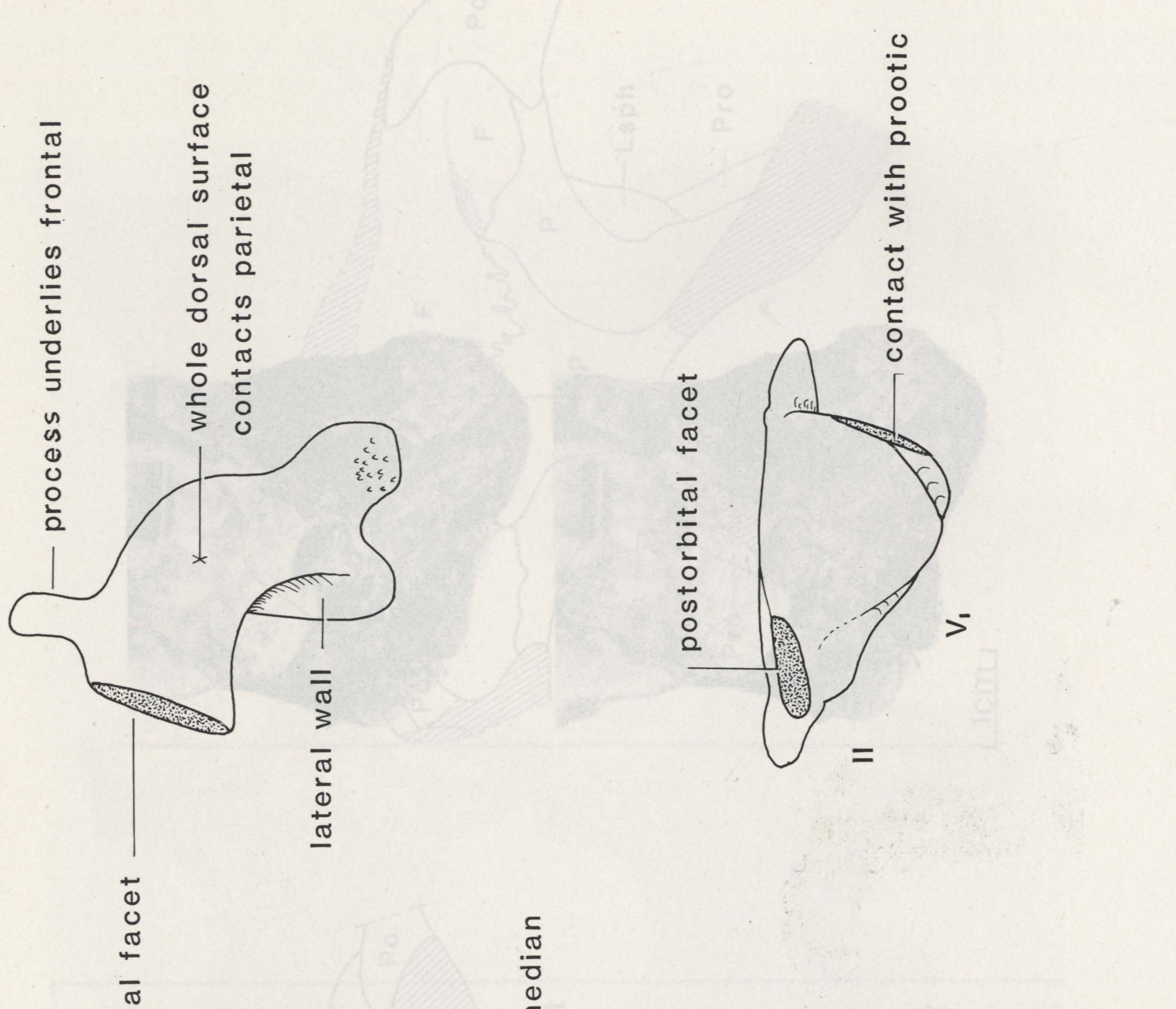


Figure 5 A. BP-1-5231. Laterosphenoid. Top left ventral; top right, dorsal; below left, median; below right, lateral;
B. Laterosphenoid as in 5 a.
Scale = 1 cm

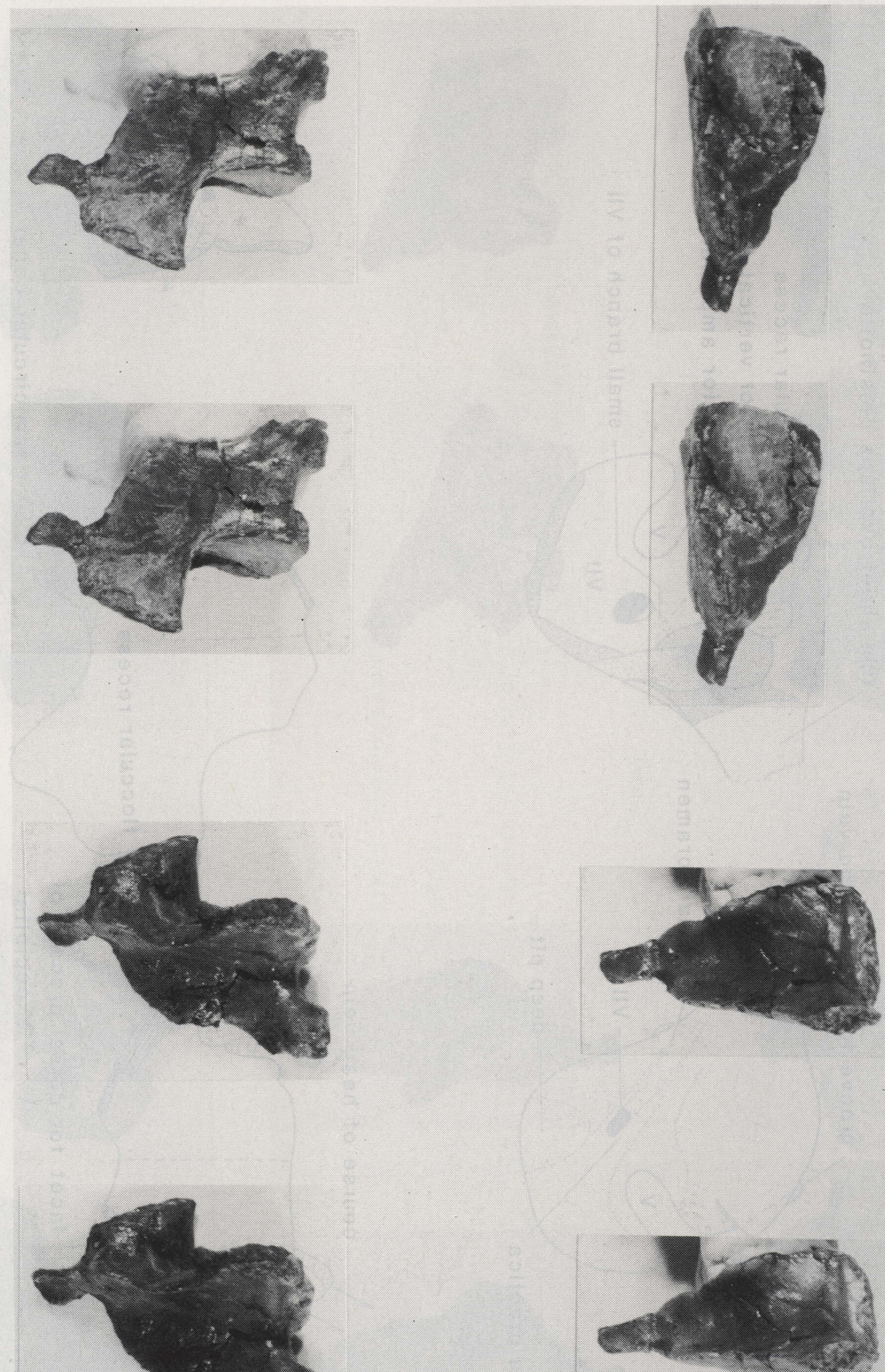


Figure [illegible] A. BP-1-5231 Above left prootic in median and lateral views Below supraoccipital in dorsal, [illegible] and lateral views.
B. Left prootic in lateral, medial and dorsal views. Supraoccipital in lateral, anterior and ventral views.
Scale = 1 cm

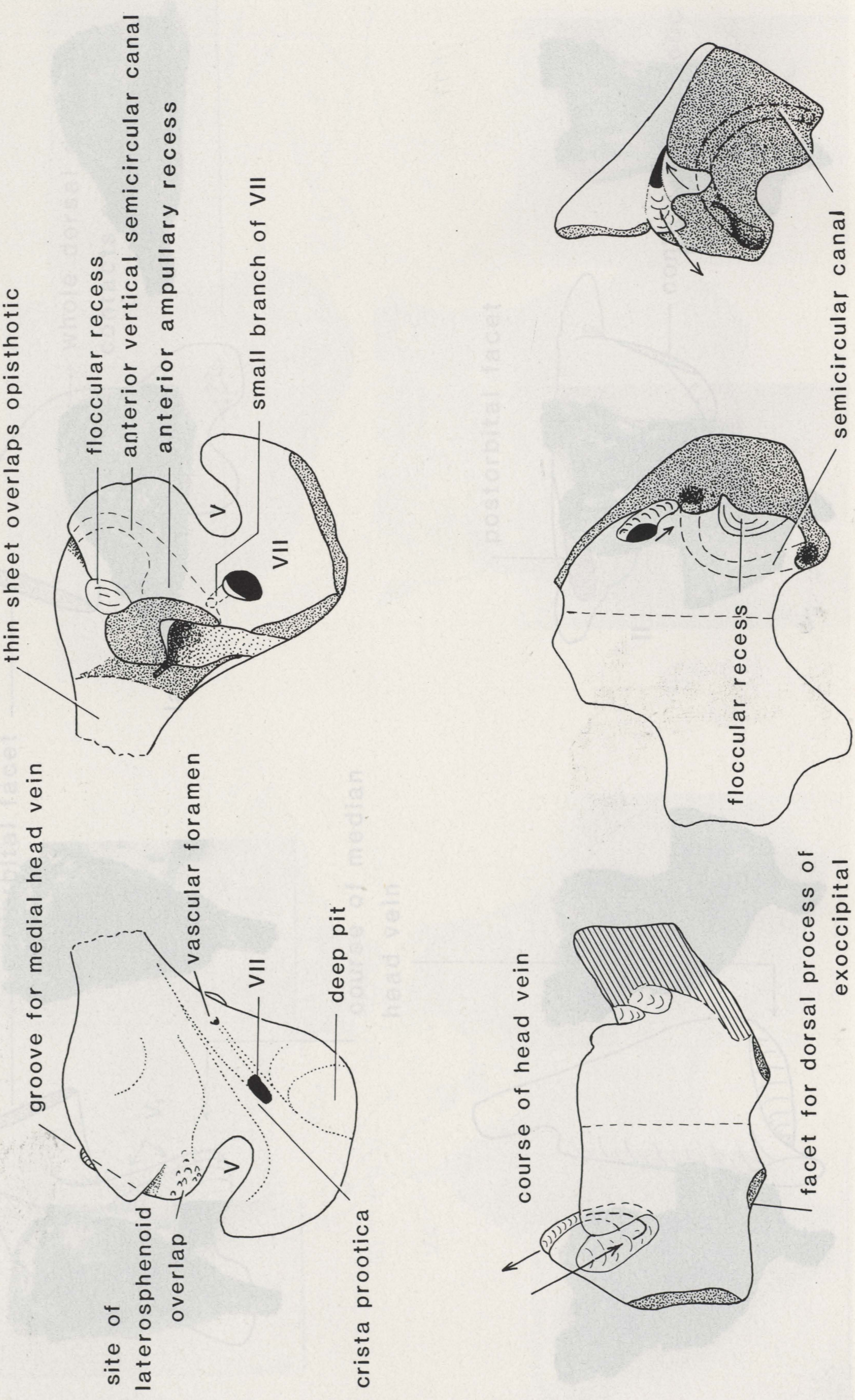
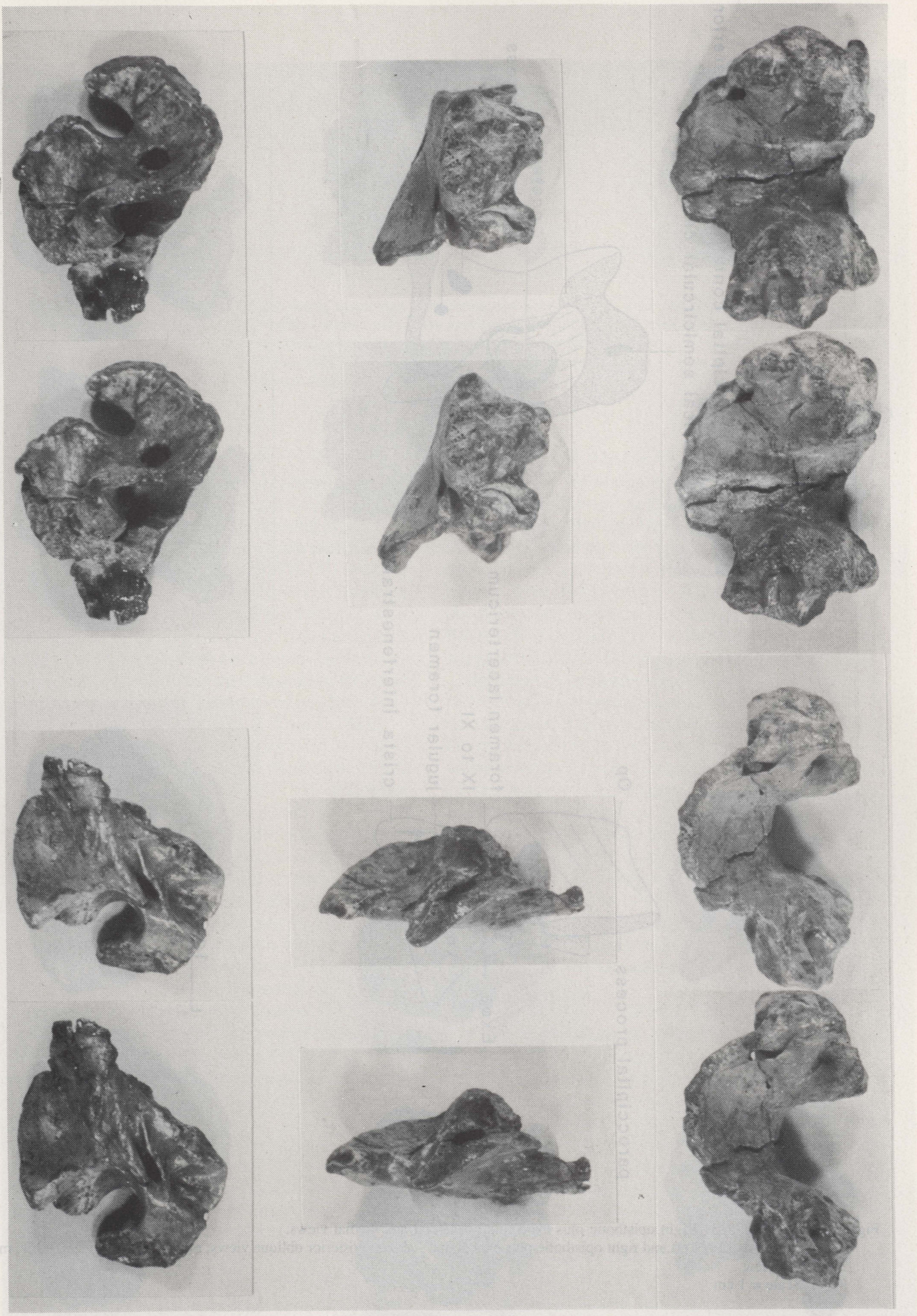


Figure 6 A. BP-1-5231 Above left prootic in median and lateral views Below supraoccipital in dorsal, ventral and lateral views.
B. Left prootic in lateral, medial and dorsal views. Supraoccipital in lateral, anterior and ventral views.
Scale = 1 cm



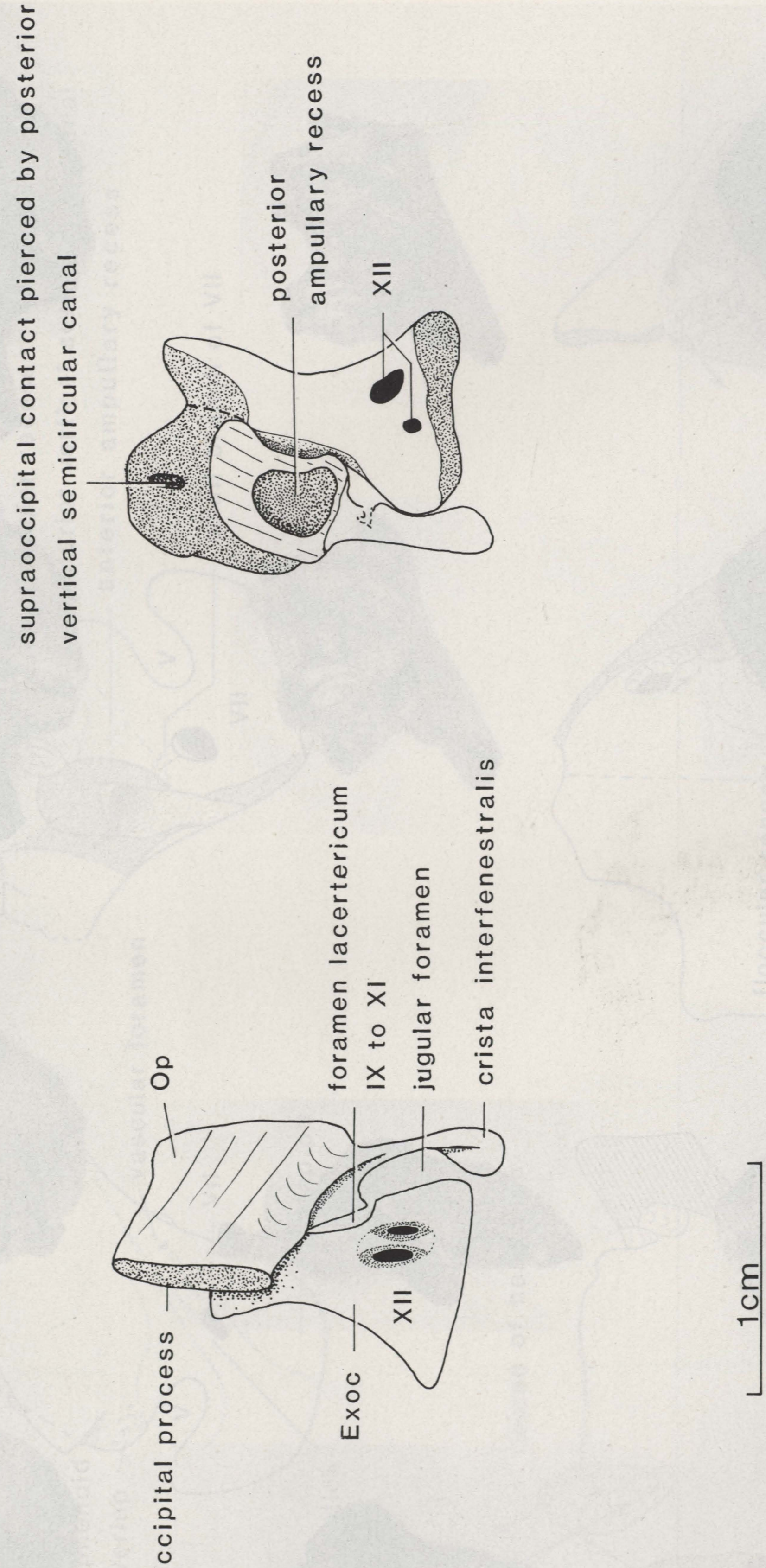


Figure 7 A. BP-1-5231 Right opisthotic plus exoccipital in lateral and medial views.
B. BP-1-5231 Left and right opisthotic plus exoccipital - above: posterior oblique views; middle: lateral view; below: medial view.
Scale = 1 cm