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A NEW SPECIMEN OF *PROMOSCHORHYNCHUS PLATYRHINUS* BRINK 1954 (MOSCHORHINIDAE) FROM THE *DAPTOCEPHALUS*-ZONE (UPPER PERMIAN) OF SOUTH AFRICA

by

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ABSTRACT

The morphology of the skull of *Promoschorhynchus platyrhinus* (Moschorhinidae) from the *Daptocephalus*-zone (Upper Permian) of South Africa) is described with special reference to the palate and posterior part of the skull. *Promoschorhynchus* is compared with *Moschorhinus* and considered to be a vaild genus mainly differing from *Moschorhinus* in retaining a longer snout, and in possessing a more primitive morphology of the palatal plates of the premaxillae and vomers.

Promoschorhynchus also differs from *Moschorhinus* in having developed a sharp *crista choanalis* and a fairly broad epipterygoid. The composition of the South African Moschorhinidae is briefly discussed and is considered temporarily as consisting of five genera: *Moschorhinus (? = Tigrisuchus). Cerdops, Promoschorhynchus* and *Hewittia. Tigrisuchus* and *Moschorhinus* are probably synonyms.

RÉSUMÉ

La morphologie du crâne de *Promoschorhynchus platyrhinus* (Moschorhinidae de la zone à *Daptocephalus* (Permien supérieur) d'Afrique du Sud) est étudiée en insistant sur la description du palais et de l'arrière crâne. *Promoschorhynchus* est comparé à *Moschorhinus* et considéré comme un genre valable différant essentiellement de *Moschorhinus* par la retention d'un plus long museau et d' une morphologie plus primitive des plaques palatales des premaxillaires et vomers. *Promoschorhynchus* diffère également de *Moschorhinus* par le développement d'une *crista choanalis* aiguë et d'un assez large épiptérygoide. La composition des Moschorhinidae sudafricains est discutée brièvement et est temporairement considérée comme constituée de cinq genres: *Moschorhinus (?=Tigrisuchus), Cerdops, Promoschorhynchus* et *Hewittia. Tigrisuchus* et *Moschorhinus* sont probablement synonymes.

ZUSAMMENFASSUNG

Die Morphologie des Schädels von *Promoschorhynchus platyrhinus* (Moschorhinidae aus der *Daptocephalus* Zone (Oberes Perm) von Südafrika) ist beschrieben mit besonderer Berücksichtigung des Gaumens und des hinteren Schädelteiles. *Promoschorhynchus* wird mit *Moschorhinus* verglichen, und für eine selbständige Gattung befunden. Sie ist hauptsächlich unterschieden von *Moschorhinus* durch die Beibehattung der längeren Schnautze, und der mehr primitiven Morphologie der Gaumenplatten der Prämaxillaren und der vomeren. *Promoschorhynchus* ist von *Moschorhinus* auch darin unterschieden dass sie eine scharfe *crista choanalis* entwickelt hat. Die Zusammensetzung der südafrikanischen Moschorhinidae ist kurz behandelt und vorläufig als aus funf Gattungen bestehend erachtet: *Moschorhinus, (? = Tigrisuchus), Cerdops, Promoschorhynchus* und *Hewittia. Tigrisuchus* und *Moschorhinus* sin sehr wahrscheinlich synonym.

INTRODUCTION

Promoschorhynchus platyrhinus is based on a snout (B.P.I. No. F.484/M.192) described by Brink (1954, pp. 43—45, Fig. 2). A new skull and lower jaw, almost complete, save for the weathered skull roof, and only slightly distorted (R.C. No. 116) has permitted a more complete study of this genus. One other specimen, represented by a snout, can also be included in this genus, so that our knowledge of *Promoschorhynchus* is limited to three specimens.

I *Material:*

A. *Holotype:* B.P.I. No. F.484/M.192: a snout including part of the interorbital region, but lacking the orbital margins; the lower jaw is missing.
Collection: Bernard Price Institute for Palaeontological Research, Johannesburg.
Locality: Wilgerbosch, New Bethesda (collector: J. W. Kitching).
Horizon: Former *Cistecephalus* zone (*s.l.*) (Upper Permian). More precisely the *Daptocephalus* zone, cf. Kitching (personal communication, 13/11/1973).

B. *Other Specimens:*

1. R.C. No. 116: an almost complete skull with lower jaw; the entire dorsal surface of the skull and dorso-lateral portions of the occiput have been weathered away.
Collection: Rubidge collection, Wellwood, Graaff-Reinet.

Locality: Wellwood, Graaff-Reinet (collector: Hans Wessels).
Horizon: Daptocephalus zone.

2. G.S.P., K.C. No. R.85: a snout, which on the basis of external characters (the palate is not completely available) can be regarded as representing a probable *Promoschorhynchus*.
Collection: Geological Survey, Pretoria, Keyser collection.
Locality: Ferndale, Graaff-Reinet (collector: André Keyser).
Horizon: Cistecephalus zone (*s.l.*), more precisely the *Daptocephalus* zone, cf. Keyser (personal communication, 21/11/1973).

II *Diagnosis:*

Promoschorhynchus is a moschorhinid which can be distinguished from *Moschorhinus* by the following features: (1) a more slender snout, more elongated in both the precanine and postcanine areas; (2) the nasals constricted at mid-length; (3) a broader epipterygoid with a posterior apophysis more ventrally located; (4) a clearer distinction between the mastoid and the quadrate processes of the opisthotic which are separated by a deep groove; (5) a premaxilla more widely expanded on the palate, especially at the mid-ventral line; (6) a less pronounced anterior expansion of the vomer both in length and breadth; (7) a sharp *crista choanalis,* which passes anteriorly to the upper canines and is farther ventral to the anterior plate of the vomer than in *Moschorhinus;* (8) a wider posterior opening of the post-temporal fossa; (9) the greater development of intermediate and mastoid processes of the squamosal; the former covers the postero-dorsal process of the opisthotic in anterior view and the latter covers a large part of the mastoid process of the opisthotic in occipital view; (10) a greater participation of the supra-occipital in the margin of the foramen magnum. The dentary of *Promoschorhynchus* differs from that of *Moschorhinus* in the following characters: (1) the relatively slender bone is not markedly constricted behind the canine; (2) the part of the dentary participating in the formation of the symphysis is separated from the horizontal ramus by a much less pronounced mentum angulation, and the dentary is less thickened at this level; (3) the ascending ramus is relatively longer and the gonial angle is smaller. The dental formula of *Promoschorhynchus* is $\frac{5}{4}$ I, $\frac{1pC,\ 1C}{1C}$, $\frac{5-6}{6-?}$ PC; it differs from that of *Moschorhinus* in the slightly greater number of postcanines.

DESCRIPTION

The skull of *Promoschorhynchus platyrhinus* (R.C. No. 116) is of medium size with a strongly built snout which is relatively longer and less massive than that of *Moschorhinus*. The dorsal sur-

TABLE 1
The chief measurements (in mm) are:

	B.P.I. No. F.484/M.192	R.C. No. 116	G.S.P., K.C. No. R.85
1. Total length of the skull (reconstructed)	—	135 approx.	—
2. Maximum width (reconstructed)	—	100 approx.	—
3. Distance between the anterior border of the premaxilla and the anterior orbital border (reconstructed)	—	66 approx.	—
4. Breadth of the snout at the level of its maximal constriction (reconstructed)	40 approx.	39 approx.	31 approx.
5. Height of the snout at the same level (reconstructed)	30 approx.	—	25 approx.
6. Total length of the maxillary dentition	26 (right)	28 (right), 26 (left)	25 (right) approx.
7. Total length of the postcanine tooth-row	16 (right)	15,5 (right), 13,5 (left)	16 (right) approx.
8. Length of the anterior part of the palate, on the middle-line, between the anterior edge of the first incisor alveolar border and the posterior edge of the medial part of the transverse processes	—	76	—
9. Length between this point of the transverse processes and the posterior limit of the tubercula spheno-occipitalia	—	36	—
10. Length, on the middle-line, of the palatal plate of the premaxilla	14	—	—
11. Length of the anterior plate of the vomers, from the premaxillo-vomerine suture to its narrowest part (near the posterior end of the choanal opening) in the middle-line	25	25	—
12. Breadth of the vomer at the premaxillo-vomerine suture	13,5	13,5	—
13. Total length of the dentary, from dorsal point of the symphysis anterior to the incisors to the posterior angle of the coronoid process	—	107	—
14. Length of the horizontal ramus of the dentary from the base of the symphysis to the goniac angle	—	55	—
15. Length of the ascending ramus from the goniac angle to the posterior angle of the coronoid process	—	41	—

face of the skull is weathered; however the dorsal surface of the snout of the type specimen (B.P.I. No. F.484/M.192) is well preserved. The type specimen is used also for the description of the anterior part of the palate because this area in R.C. No. 116 is obscured by the presence of the lower jaw.

Note on Figures: The skull of R.C. No. 116 being little distorted, the drawings correspond to reconstructions, allowing for the asymmetry and the slight crushing of the posterior part of the skull. The palate of the type (B.P.I. No. F.484/M.192) has been represented in an earlier article (Mendrez, 1973, Fig. 7). The dorsal surface of the snout of R.C. No. 116 is reconstructed after the type.

I. SKULL

A. Dermal Bones

1. *Dorsal surface* (Fig. 1 and Pl. I. A)

In the type specimen (B.P.I. No. F.484/M.192) premaxillae, septomaxillae, maxillae, nasals and a small part of the prefrontal and frontal are preserved.

The premaxillae (*Pmx*), of which the nasal processes are missing, are little exposed in anterior and lateral view. They are covered by the septomaxilla (*Smx*) and the maxilla (*Mx*). The latter extends anteriorly to the level of the fourth incisor.

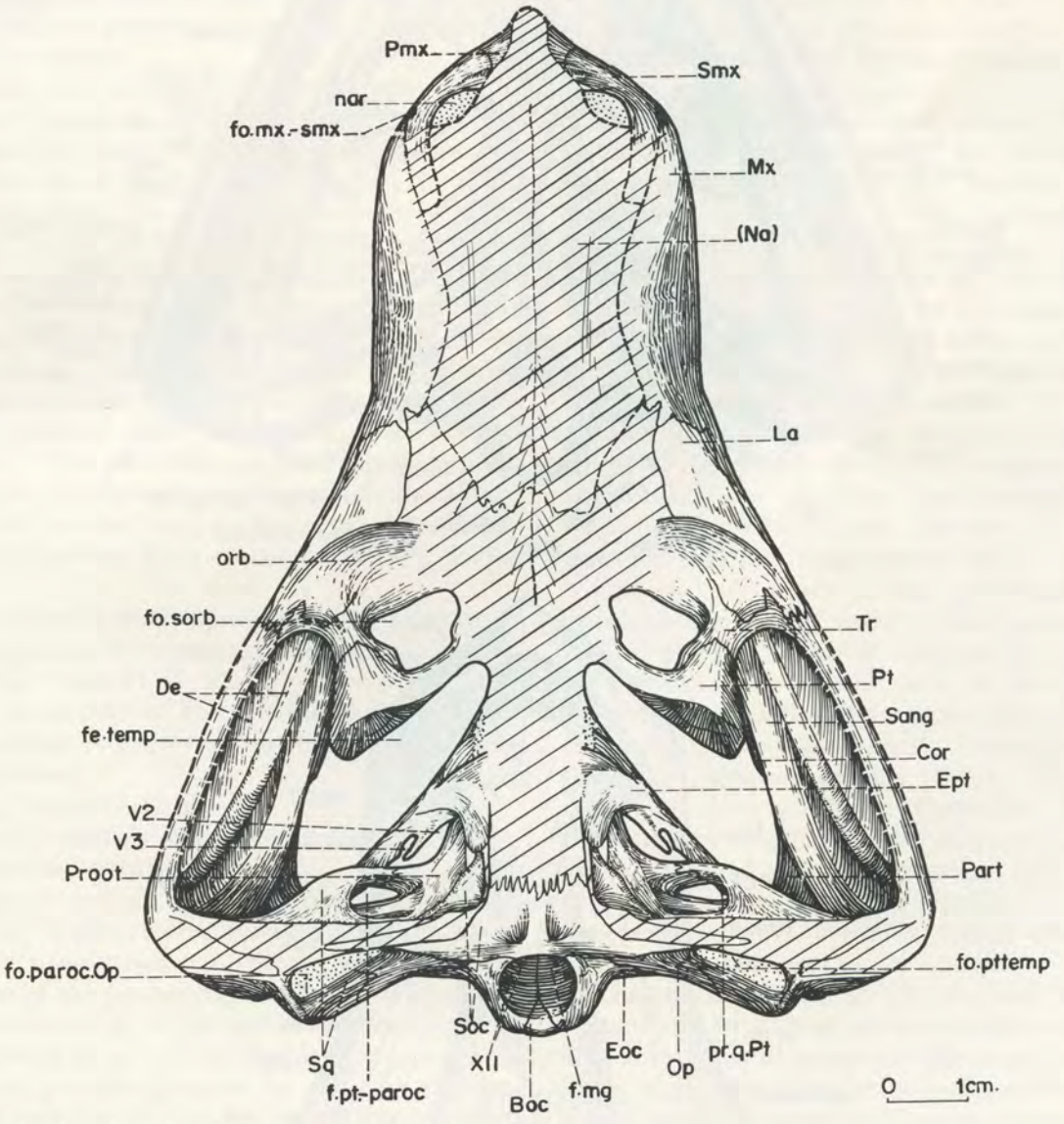
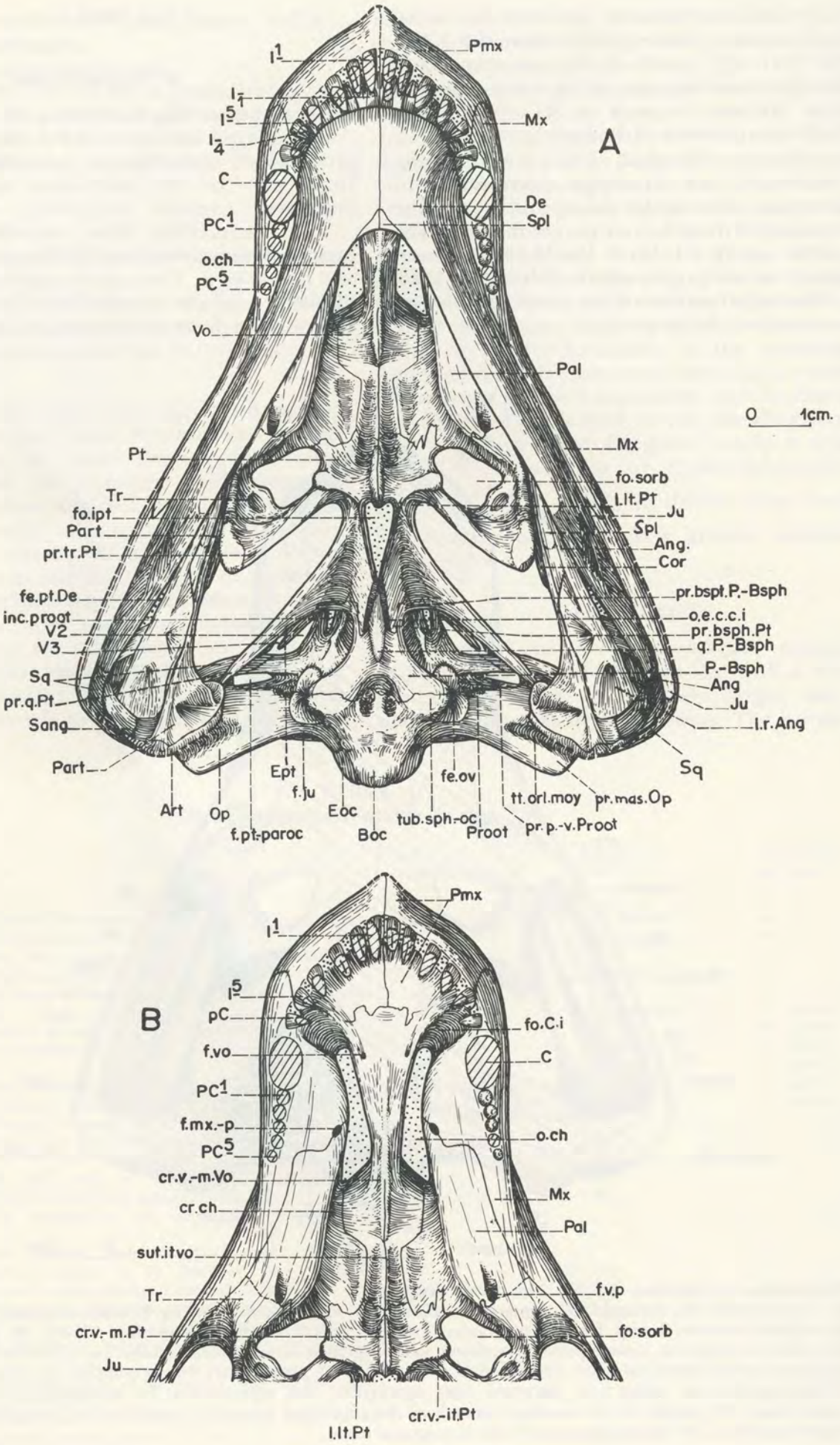


Fig. 1 *Promoschorhynchus platyrhinus*. RC. No. 116; dorsal view (x 1).
Boc, basioccipital; *Cor*, coronoid; *De*, dentary; *Eoc*, exoccipital; *Ept*, epipterygoid; *f.mg*, foramen magnum; *f.pt.-paroc*, pterygo-paroccipital foramen; *fe. temp*, fenestra temporalis; *fo.mx.-smx*, maxillo-septomaxillary fossa; *fo. paroc. Op*, paroccipital fossa of the opisthotic; *fo.pttemp*, posttemporal fossa; *fo,sorb*, suborbital fossa (or suborbital vacuity); La, lachrymal; *Mx*, maxilla; *(Na)*, impression of the nasal; *nar*, nare; *Op*, opisthotic; *orb*, orbit; *Part*, prearticular; *Pmx*, premaxilla; *pr.q.Pt*, quadrate process of the pterygoid; *Proot*, prootic; *Pt*, pterygoid; *Sang*, surangular; *Smx*, septomaxilla; *Soc*, supraoccipital; *Sq*, squamosal; *Tr*, transversum; *V2*, notch for the maxillary branch of the trigeminal nerve; *V3*, notch for the mandibular branch of the trigeminal nerve; *XII*, internal foramen for the hypoglossal nerve.


A
Pmx
I1
I1
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I4
C
PC1
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V2
V3
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Pal
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cr.v.-it.Pt

Fig. 2.

Fig. 2 *Promoschorhynchus platyrhinus*. RC. No. 116; *A:* complete ventral view with lower jaw *in situ* (x 1); *B:* palate, with lower jaw supposed to have been removed (x 1).
Ang, angular; *Art,* articular; *Boc,* basioccipital; *C,* canine; *Cor,* coronoid; *De,* dentary; *cr. ch, crista choanalis; cr.v.-it.Pt,* ventro-intermediate crest of the pterygoid; *cr.v.-m.Pt,* ventro-medial crest of the pterygoid; *cr.v.-m.Vo,* ventro-medial crest of the vomer; *Eoc,* exoccipital; *Ept,* epipterygoid; *f.ju,* jugular foramen; *f.mx.-p,* maxillo-palatine foramen; *f.pt.-paroc,* pterygo-paroccipital foramen; *f.v.p.,* foramen for the *vena palatina major; f.vo,* vomerine foramen; *fe.ov, fenestra ovalis; fe.pt.-De,* post-dentary fenestra; *fo.C.i,* fossa for the lower canine; *fo.ipt,* interpterygoid fossa; *fo.sorb,* suborbital fossa (or suborbital vacuity); I^1, first upper incisor; I_1, first lower incisor; I_4, fourth lower incisor; I^5, fifth upper incisor; *inc. proot, incisura prootica; Ju,* jugal; *l.lt.Pt,* lateral lamina of the pterygoid; *l.r.Ang,* reflected lamina of the angular; *Mx,* maxilla; *o.ch,* internal choanal opening; *o.e.c.c.i,* external opening of the canal of the internal carotid; *Op,* opisthotic; *P.-Bsph,* para-basisphenoid complex; *Pal,* palatine; *Part,* prearticular; PC^1, first upper postcanine; PC^5, fifth upper postcanine; *pC,* precanine; *Pmx,* premaxilla; *pr.bsph.Pt,* basisphenoid process of the pterygoid; *pr.bspt.P-Bsph,* basipterygoid process of the para-basisphenoid complex; *pr.mas.Op,* mastoid process of the opisthotic; *pr.q.Pt,* quadrate process of the pterygoid; *pr.tr.Pt,* transverse process of the pterygoid; *Proot,* prootic; *Pt,* pterygoid; *Sang,* surangular; *Spl,* splenial; *Sq,* squamosal; *sut.itvo,* intervomerine suture; *Tr,* transversum; *tt.orl.moy,* roof of the middle ear; *tub.sph.-oc, tuberculum spheno-occipitale; Vo,* vomer; *V2,* notch for the maxillary branch of the trigeminal nerve; V^3, notch for the mandibular branch of the trigeminal nerve.

The septomaxilla (*Smx*) is well developed and has a broad posterior process extending between the maxilla and the nasal.

The maxilla (*Mx*) is highest at a point opposite to the middle of the nasals. From this point the maxilla regularly slopes both forward and backward. Therefore, the nasals appear constricted in the middle. In *Moschorhinus* the maxilla reaches its maximum height at the level of the posterior end of the septomaxilla and this height remains constant to the level of the prefrontal, so that the nasals do not appear constricted. The snout of *Promoschorhynchus* is slightly constricted behind the canine; this is more noticeable in the upper part of the maxilla. This character has not been observed in *Moschorhinus*. The maxilla of *Promoschorhynchus* participates in the formatiom of the suborbital bar nearly as much as the jugal and extended probably as far as the posterior limit of the orbit (Fig. 3 and Pl. II. B).

In both genera, a mid-sagittal ridge is present in the posterior part of the nasal and the frontal.

2. *Occiput* (Fig. 4 and Pl. II. C).

Only the basal part of the occiput, belonging to the endocranium, is preserved in R.C. No. 116 and is described below.

3. *Cheek* (Fig. 3 and Pl. II. A—B)

The relatively narrow jugal (*Ju*) is represented by its anterior and suborbital portions.

Only a small part of the posterior area of the squamosal (*Sq*) is observable. Posteriorly (Fig. 3 and Pl. II. C) the squamosal contributes greatly to the lower margin of the post-temporal fossa. Within the temporal fenestra (Fig. 5) the antero-ventral process of the squamosal (*pr.a.-v.Sq*) is divided into two, the robust prootic process (*pr.proot.Sq*) and the slender epipterygoid process (*pr. ept.Sq*). A similar subdivision of the antero-ventral process has also been observed in *Moschorhinus* and in the Whaitsiidae.

The upper part of the quadratojugal (*Qj,* Fig. 2 and Pl. II. A—C) is well preserved and is broad. It is separated from the quadrate (*Q*) by the quadrate-quadratojugal foramen (*f.q.-qj*). The ventral part of the quadratojugal is weathered.

4. *Palate* (Fig. 2 A,B and Pl. I. B,C)

The palate of *Promoschorhynchus* is less specialized than that of *Moschorhinus,* but shows a sharper *crista choanalis* (*cr.ch*).

The relative length of the snout is reflected on the palate. In *Promoschorhynchus* the distance between the posterior edge of the medial part of the transverse processes of the pterygoid and the posterior limit of the *tubercula spheno-occipitalia* (Tab. 1, No. 9) equals only 47% of the length of the anterior part of the palate in the mid-line, between the anterior edge of the first incisor alveolar border and the posterior edge of the medial part of the transverse processes (Tab. 1, No. 8). This ratio is greater in *Moschorhinus* in which it varies from 61% to 68%. In *Moschorhinus,* the measurements have been taken on the four specimens in which the whole palate is available. The size of the specimen does not seem to influence this ratio.

The palatal plate of the premaxilla (*Pmx*) has approximately the same antero-posterior length both medially and laterally, whereas in *Moschorhinus* the lateral part of the plate is considerably longer than the medial part. Together with the maxilla, each premaxilla forms the roof of the fossa for the lower canine (*fo.C.i*). This fossa is not otherwise distinguishable from the long reniform choanal opening (*o.ch*). The sharp *crista choanalis* extends forward on the maxilla and reaches the anterior edge of the choanal opening. In *Moschorhinus* this crest is blunt and tapers to terminate at the level of the canine.

The vomers (*Vo.* Fig. 2B) are still well separated posteriorly by a clear intervomerine suture (*sut.itvo*). The anterior and posterior plates are situated at the same level dorsal to the *crista choanalis*. The anterior plate broadens anteriorly but to a lesser extent than in *Moscorhinus* and is oar-shaped rather than fan-shaped. The ventro-median crest (*cr.v.-m.Vo*) is very high and sharp. Two vomerine foramina (*f.vo*) are visible anteriorly.

The pterygoids (*Pt,* Fig. 2A) extend anteriorly to the level of the anterior border of the suborbital fossa (*fo.sorb*). They are remarkable because of the

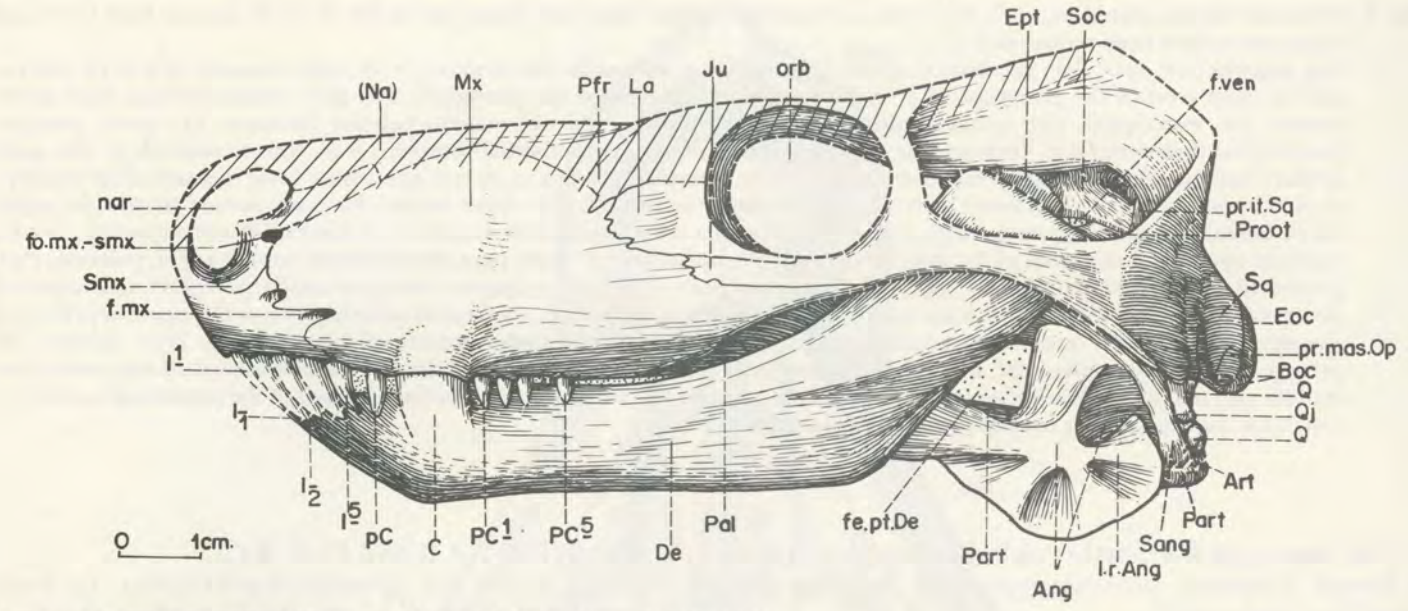

Fig. 3 *Promoschorhynchus platyrhinus.* RC. No. 116; left lateral view (x 1).
Ang, angular; *Art,* articular; *Boc,* basioccipital; *C,* canine; *De,* dentary; *Eoc,* exoccipital; *Ept,* epipterygoid; *f.mx,* maxillary foramen; *f.ven,* venous foramen; *fe.pt.-De,* post-dentary fenestra; *fo.mx.-smx,* maxillo-septomaxillary fossa; I^1, first upper incisor; I_1, first lower incisor, I_2, second lower incisor; I^5, fifth upper incisor; *Ju,* jugal; *l.r.Ang,* reflected lamina of the angular; *La,* lachrymal; *Mx,* maxilla; *(Na),* impression of the nasal; *nar,* nare; *orb,* orbit; *Pal,* palatine; *Part,* prearticular; *Pfr,* prefrontal; *pr.it.Sp,* intermediate process of the squamosal; *pr.mas.Op,* mastoid process of the opisthotic; PC^1, first upper postcanine; PC^5, fifth upper postcanine; *pC,* precanine; *Proot,* prootic; *Q,* quadrate; *Qj,* quadratojugal; *Sang,* surangular; *Smx,* septomaxilla; *Soc,* supraoccipital; *Sq,* squamosal.

prominence of the tuberosity at the posterior end of the ventro-intermediate crest of the pterygoid (*cr.v.-it.Pt*), and the very acute angle formed between the transverse (*pr.tr.Pt*) and the quadrate processes (*pr.-q.Pt*). The lateral lamina of the pterygoid (*l.lt.Pt*) is very small. The posterior edge of the transverse process seems to be in continuity with the edge of the quadrate process, while the edge of the tuberosity of the ventro-intermediate crest is continuous with the edge of the interpterygoid fossa (*fo.ipt*) (or "medial pterygoid crest" according to Barghusen's nomenclature (1968, pp. 6 and 41)). The lateral end of the concave transverse process is strongly swollen. The pterygoids of either side are closely approximated in front of the para-basisphenoid keel (*q.P.-Bsph*). The basisphenoid process (*pr.bsph.Pt*) extends anteriorly a little farther than the external opening of the internal carotid canal (*o.e.c.c.i.*). The lamina between the quadrate process and the basisphenoid process is strongly concave, bordered by the strong crest of the quadrate process.

The maxilla (*Mx.* Fig. 2B) is swollen medially to the canine (*C*) and is broadly extended medially to the postcanines (*PC*). In *Moschorhinus,* the contribution of the palatine (*Pal*) is much greater at the level of the postcanines. On the type of *Promoschorhynchus* (B.P.I. No. F. 484/M.192), this part of the maxilla is marked by shallow parallel grooves which correspond to the impressions of the lower postcanines ((*PCi*) in Mendrez, 1973, Fig. 7). In R.C. No. 116 there are six lower postcanines. In *Promoschorhynchus* the maxillo-palatine foramen (*f.mx.-p*) is situated more posteriorly than in *Moschorhinus.* Relative to the position of the anterior plate of the vomer, the *crista choanalis* is situated more ventrally than in *Moschorhinus.*

The maxilla carries one precanine, one canine and five postcanines.

The anterior and posterior parts of the palatine (*Pal*) are relatively narrow and the latter does not extend farther than the anterior border of the suborbital fossa.

The transversum (*Tr,* Fig. 2A,B) extends anteriorly a little farther than the anterior border of the suborbital fossa (*fo. sorb*). The crest of the transversum is separated from the suborbital vacuity by a short narrow and flat flange. The broader posterior area is marked by a strong dimple. Posteriorly the transversum does not extend far and its limit remains dorsal to the ventro-lateral swelling of the transverse process. In *Moschorhinus* the posterior limit of the transversum reaches the anterior limit of the swelling.

B. Endocranium

The morphology of the para-basisphenoid complex (*P.-Bsph,* Fig. 2) is typical of therocephalians. The basipterygoid process (*pr. bspt. P.-Bsph*) is incompletely covered by the pterygoid. The keel (*q.P.-Bsph*), partly broken, does not seem to have extended far ventrally. The tubercula spheno-occipitalia (*tub.sph.-oc*) are strong. The para-basisphenoid complex, together with the basioccipital (*Boc,* Fig. 7),

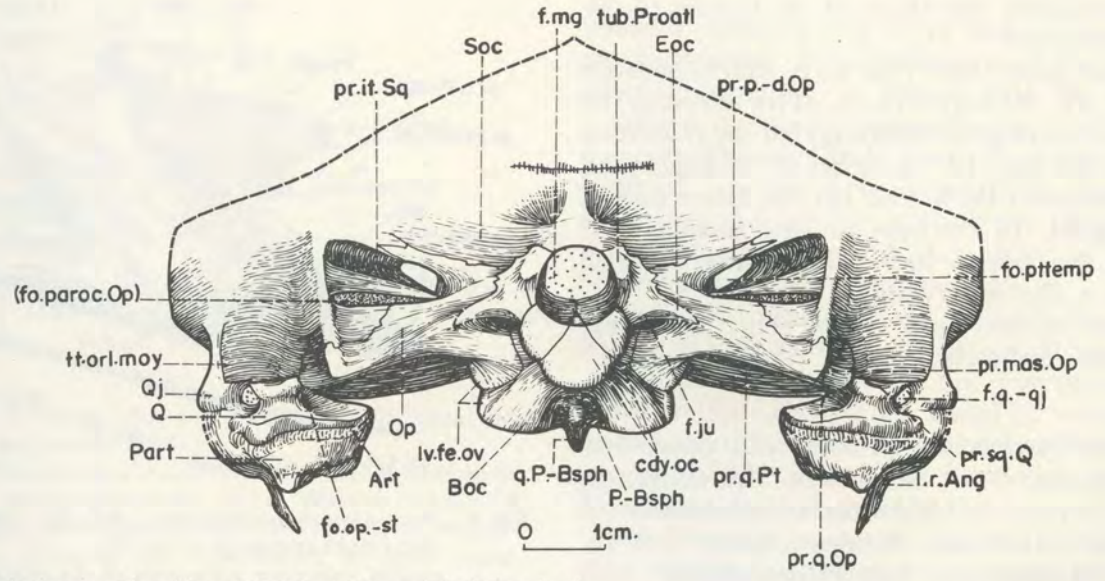

Fig. 4 *Promoschorhynchus platyrhinus.* RC. No. 116; occipital view (x 1).
Ang, angular; *Art,* articular; *Boc,* basioccipital; *cdy.oc,* occipital condyle; *Eoc,* exoccipital; *f.ju,* jugular foramen; *f.mg,* foramen; *(fo.paroc.Op),* paroccipital fossa of the opisthotic; *fo.pttemp,* posttemporal fossa; *lv.fe.ov,* 'lip' of the fenestra ovalis; *Op,* opisthotic; *Part,* prearticulr; *P.-Bsph,* para-basisphenoid complex; *pr.it.Sq,* intermediate process of the squamosal; *pr.mas.Op,* mastoid process of the opisthotic; *pr.p.-Op,* postero-dorsal process of the opisthotic; *pr.q.Op,* quadrate process of the opisthotic; *pr.q.Pt,* quadrate process of the pterygoid; *Q,* quadrate; *q.P.-Bsph,* keel of the para-basisphenoid complex; *Qj,* quadratojugal; *Soc,* supraoccipital; *tt.orl.moy,* roof of the middle ear; *tub.Proatl,* tuberosity for the articulation with the proatlas.

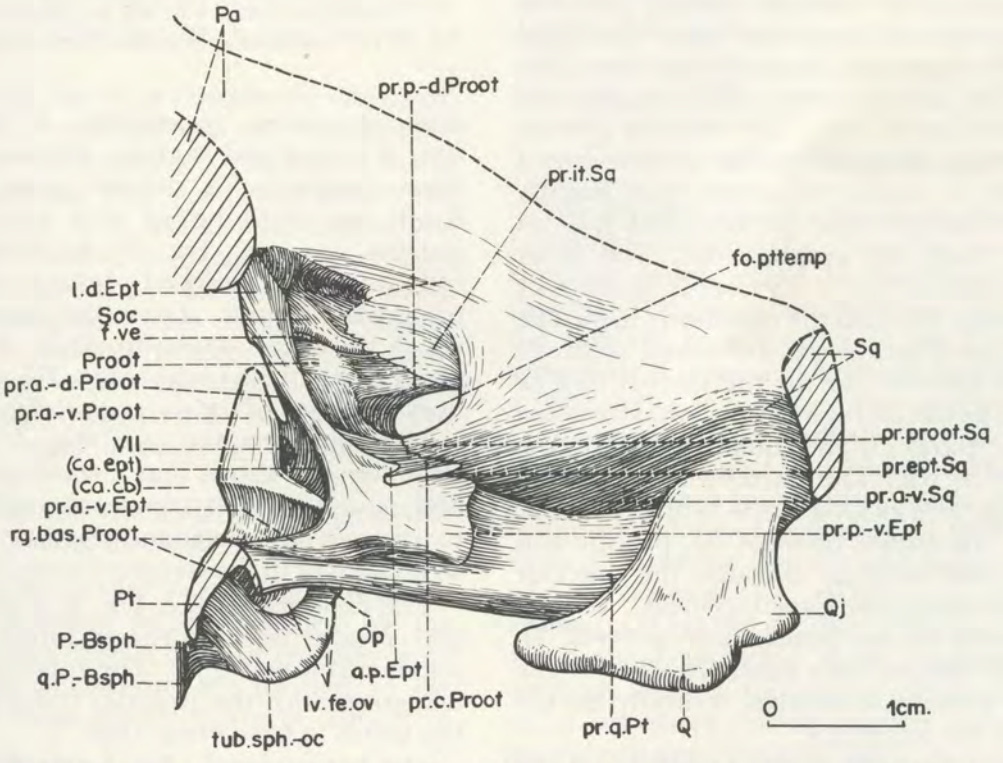

Fig. 5 *Promoschrohynchus platyrhinus.* RC. No. 116; Anterior view of the posterior wall of the left temporal fossa (x 5/3).
a.p.Ept, posterior apophysis of the epipterygoid; *(ca.cb),* brain cavity; *(ca.ept), cavum epiptericum; f.ven,* venous foramen; *fo.pttemp,* post-temporal fossa; *l.d.Ept,* dorsal lamina of the epipterygoid; *lv.fe.ov,* 'lip' of the *fenestra ovalis; Op,* opisthotic; *P.Nsph,* para-basisphenoid complex; *Pa,* parietal; *pr.a.-d.Proot,* antero-dorsal process of the prootic; *pr.a.-v.Ept,* antero-ventral process of the epipterygoid; *pr.a.-v.Proot,* antero-ventral process of the prootic; *pr.a.-v.Sq,* antero-ventral process of the squamosal; *pr.c.Proot,* central process of the prootic; *pr.ept.Sq,* epipterygoid process of the squamosal; *pr.it.Sq,* intermediate process of the squamosal; *pr.p.-d.Proot,* postero-dorsal process of the prootic; *pr.p.-v.Ept,* postero-ventral process of the epipterygoid; *pr.proot.Sq,* prootic process of the squamosal; *pr.q.Pt,* quadrate process of the pterygoid; *Proot,* prootic; *Pt,* pterygoid; *Q,* quadrate; *q.P.-Bsph,* keel of the para-basisphenoid complex; *Qj,* quadratojugal; *rg.bas.Proot,* basal area of the prootic; *Soc,* supraoccipital; *Sq,* squamosal; *tub.sph.-oc, tuberculum spheno, occipitale; VII,* foramen for the facial nerve.

form approximately one third of the border of the fenestra ovalis (*fe.ov*).

The epipterygoid (*Ept,* Fig. 6) is much broader than that of *Moschorhinus*. The posterior apophysis, separating the openings for the maxillary (*V2*) and mandibular (*V3*) branches of the trigeminal nerve, is positioned fairly low, on the lower half of the epipterygoid. In contrast, in *Moschorhinus* it is situated on the upper half. The postero-ventral process (*pr.p.-v.Ept*) is very high.

The cavum epiptericum (*ca.ept,* Fig. 5) is very broad in *Promoschorhynchus*.

The otic bones

In *Promoschorhynchus* the prootic and opisthotic are distinguishable from each other. This condition has been observed by Mendrez in a number of therocephalian families: Ictidosuchidae (1972a, p. 201), Whaitsiidae, Pristerognathidae and Moschorhinidae (1974). It is probably a general feature of the Therocephalians.

The prootic (*Proot,* Fig. 7) is fairly well preserved. It shows the general therocephalian morphological pattern (*Ptomalestes* excluded, which has an additional process) as far as this is known. The basal area of the prootic (*rg.bas*) is in contact with the para-basisphenoid complex (*P.-Bsph*) and forms a third of the border of the fenestra ovalis (*fe.ov*). The antero-ventral process (*pr.a.-v*) is strong with ventral and lateral faces separated by a sharp crest. The foramen for the facial nerve (*VII*) is situated posteriorly to the lateral face. The incisura prootic (*inc.proot*) is narrow posteriorly. The antero-dorsal process (*pr.a.-d*) is positioned above and slightly lateral to the antero-ventral process and has no sutural contact with the epipterygoid. The short postero-dorsal process (*pr.p.-d.Proot*) is in contact with the squamosal (*Sq*) and the opisthotic (*Op*). The long central process (*pr.c.Proot*), bordered ventrally and dorsally by grooves, forms the medial half of the bar anterior to the pterygo-paroccipital foramen (*f.pt.-paroc,* Figs. 1 and 2). The squamosal forms the lateral half of this bar. The latero-ventral process (*pr.p.-v.Proot,* Fig. 2) is as long as the central process. In dorsal view, the suture between the prootic and the opisthotic runs laterally through the anterior half of the post-temporal fossa (*fo.pttemp*). It then emerges anteriorly to the paroccipital process. In ventral view, the suture runs medially towards the fenestra ovalis where it continues ventrally on the dorsal border of the fenestra.

The opisthotic (*Op*) also forms one-third of the margin of the fenestra ovalis. Its dorsal process (*pr.p.-d.Op,* Fig. 4) is thin and elongated; it is completely covered anteriorly by the intermediate process of the squamosal (*pr.it.Sq,* Fig. 5) in contrast to the situation observed in *Moschorhinus* S.A.M. No. K. 118 (Mendrez, 1974, Figs. 6—7). The paroccipital process is very strong and is marked ventrally by a very deep and narrow groove (*tt.orl.may*) separating the quadrate process (*pr.q.Op*) from the

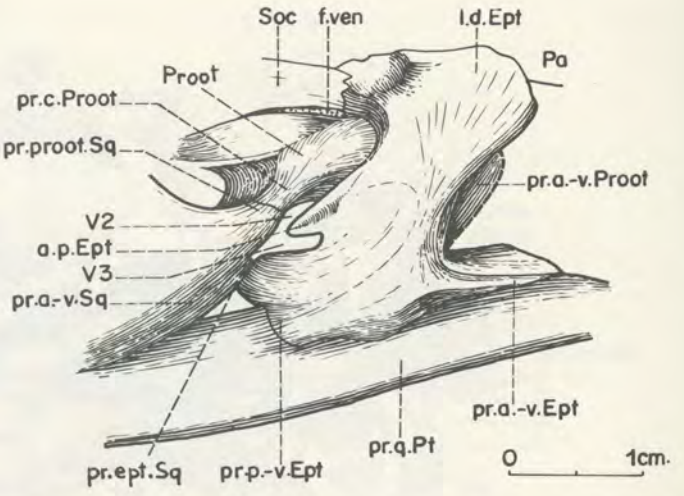

Fig. 6 *Promoschrohynchus platyrhinus.* RC. No. 116; lateral view of the right epipterygoid (x 1/3).
a.p.Ept, posterior apophysis of the epipterygoid; *f.ven,* venous foramen; *l.d.Ept,* dorsal lamina of the epipterygoid; *Pa,* parietal; *pr.a.-v.Ept,* antero-ventral process of the epipterygoid; *pr.a.-v.Proot,* antero-ventral process of the prootic; *pr.a.-v.Sq,* antero-ventral process of the squamosal; *pr.c.Proot,* central process of the prootic; *pr.ept.Sq,* epipterygoid process of the squamosal; *pr.p.-v.Ept,* postero-ventral process of the epipterygoid; *pr.proot.Sq,* prootic process of the squamosal; *pr.q.Pt,* quadrate process of the pterygoid; *Proot,* prootic; *Soc,* supraoccipital, *V2,* notch for the maxillary branch of the trigeminal nerve; *V3*, notch for the mandibular branch of the trigeminal nerve.

mastoid process (*pr.mas.Op*). In *Moschorhinus* this area is broad and shallow. The mastoid process of *Promoschorhynchus* is slender, even taking into account the crushing of that area. The quadrate process (*pr.q.Op,* Fig. 4) is more massive. The opisthotic is marked ventro-anteriorly by a triangular groove above the fenestra ovalis into which the stapes probably fitted. A long and broad paroccipital fossa (*fo.paroc.Op,* Fig. 4) is found on the dorsal surface of the paroccipital process.

The supraoccipital (*Soc,* Fig. 4) is damaged but what remains shows that it was tripartite, fairly high and broad. It participates broadly in the upper margins of the foramen magnum (*f.mg*). It is also well exposed in the temporal fossa (Figs. 1, 3 and 5).

The exoccipital (*Eoc,* Fig. 4) is tripartite. Its long and slender lateral process forms the roof of the jugular foramen (*f.ju*). The tuberculum for the articulation with the proatlas (*tub.Proatl*) is damaged but seems to have been large.

The basioccipital (*Boc*) forms slightly more than one third of the occipital condyle. In dorsal view it is visible posteriorly, but more anteriorly, at the level of the foramen magnum (*m.mg*), it is covered by the united exoccipitals. Two internal foramina for the hypoglossal nerve (*XII,* Fig. 1) open through the exoccipitals on each side. Ventrally, the basioccipital participates in the formation of the strong tuberculum spheno-occipitale (*tub.sph.-oc,* Fig. 2) together with the para-basisphenoid complex. Of the four

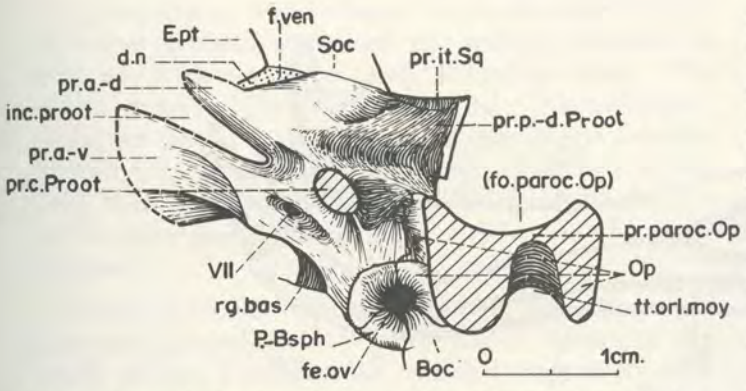

Fig. 7 *Promoschrohynchus platyrhinus.* RC. No. 116; lateral view of the left prootic (x 5/3).
Boc, basioccipital; *d.n.,* dorsal notch; *Ept,* epipterygoid; *f.ven,* venous foramen; *fe.ov, fenestra ovalis; (fo. paroc.Op),* paroccipital fossa of the opisthotic; *inc.proot, incisure prootica; Op,* opisthotic; *P.-Bsph,* parabasisphenoid complex; *pr.a.-d,* antero-dorsal process; *pr.a.-v,* antero-ventral process; *pr.c.Proot,* central process of the prootic; *pr.it.Sq,* intermediate process of the squamosal; *pr.p.-d.Proot,* postero-dorsal process of the prootic; *pr.paroc.Op,* paroccipital process of the opisthotic; *rg.bas,* basal area of the prootic; *Soc,* supraoccipital; *tt.orl.moy,* roof of the middle ear; *VII,* foramen for the facial nerve.

bones surrounding the fenestra ovalis, the basioccipital participates least in the formation of its margin.

The quadrate (Q, Fig. 4) is posteriorly damaged. It can be observed in occipital view and medial view. In addition, in dorsal view the left quadrate is visible because the squamosal has weathered away. The squamosal process (*pr.sq.Q*) has a short narrow and thick base which is visible in occipital view. More dorsally, it spreads laterally to form a flange which meets the quadratojugal. This flange is convex posteriorly. The opisthotic process appears fairly short, but the floor of the opisthotic-stapes fossa (*fo.op.-st*) is widely expanded medially. The quadrate-quadratojugal foramen (*f.q.-qj*) is broad.

C. Principal fossae and openings of the posterior part of the skull

The interpterygoid vacuity (*fo.ipt,* Fig. 2) is heart-shaped with its anterior margin divided by the bulging of the ventro-medial crest of the pterygoid (*cr.v.-m.Pt*). Its lateral margins are formed by the medial pterygoid crests which converge almost to meet posteriorly.

The fenestra ovalis (*fe.ov,* Fig. 7) is bordered by four bones (as said above): the prootic forms one third, the opisthotic forms one third and the parabasisphenoid complex, along with a minor contribution from the basioccipital, forms the remaining third of the border.

The posterior opening of the post-temporal fossa (*fo.pttemp,* Fig. 4) is broad and triangular-shaped; its border is formed by equal contributions from the squamosal and the opisthotic. The border of the anterior opening (Fig. 5) of this fossa is formed by the squamosal, the opisthotic and the prootic. The anterior opening is about half the size of the posterior one and is situated more medially, so that the two openings only partly face one another. In contrast, in the pristerognathid *Ptomalestes* the anterior opening is completely medial to the posterior opening and this latter is thus placed behind a sheet of the squamosal.

The paroccipital fossa (*fo.paroc.Op,* Fig. 4) is almost as long as the post-temporal fossa.

The anterior wall of the pterygo-paroccipital foramen (*f.pt.-paroc,* Figs. 1 and 2), which is formed by the central process of the prootic and the prootic process of the squamosal is narrow in its vertical dimension as in *Moschorhinus.*

The foramen magnum (Fig. 4) is bordered by the exoccipitals and the supraoccipital, which makes a greater contribution than in *Moschorhinus.*

The jugular foramen (Fig. 4) is bordered by two bones: the exoccipital and the opisthotic.

II. LOWER JAW (Figs. 3 and 8)

The lower jaw of *Promoschorhynchus* is characterized by a long dentary (*De*) of which the coronoid process extends above the level of the zygomatic arch. In addition, the postero-ventral corner of the coronoid process is separated by a short distance only from the squamosal.

A. Membrane bones

The dentary's horizontal ramus (Fig. 3) is relatively slender and does not show the dorso-ventral constriction which exists in *Moschorhinus* behind the canines. The coronoid process is thick. The part of the dentary participating in the formation of the symphysis is separated from the horizontal ramus by a very slight angulation. Posteriorly the horizontal ramus is separated from the ascending ramus by a wide goniac angle. The lateral surface of the coronoid process is marked by a slight groove anterior to the well-defined post-dentary fenestra (*fe.pt.-De*). Even if distortion is taken into account, the dentary of *Moschorhinus* differs from that of *Promoschorhynchus:* the "mentum" area of *Moschorhinus* is much more massively developed; on both sides a thickening of the dentary bulges in a manner comparable to that of the gorgonopsians—though not so pronounced and not median. The ascending ramus is relatively shorter in *Moschorhinus* and is separated from the horizontal ramus by a greater angle. The ratio between the length of the ascending ramus (Tab. 1, No. 14) and that of the horizontal ramus (Tab. 1, No. 15) is approximately 60% in *Moschorhinus* (B.P.I. No. F.2788/M.378) and approximately 82% in *Promoschorhynchus* (R.C. No. 116). These ratios are only given as an indication, as lack of specimens precludes the study of variation in either genus.

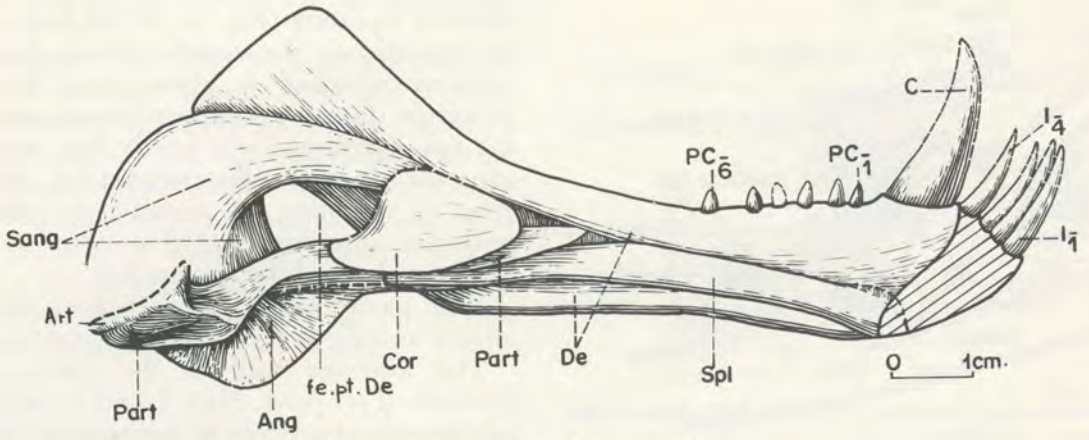

Fig. 8 *Promoschorhynchus platyrhinus*. RC. No. 116; medial view of the left mandible.
Ang, angular; *C*, canine; *Cor*, coronoid; *De*, dentary; *fe.pt.-De*, post-dentary fenestra; I_1, first lower incisor; I_4, fourth lower incisor; *Part*, prearticular; PC_1, first lower postcanine; PC_6, sixth lower postcanine; *Sang*, surangular, *Spl*, splenial.

The angular (*Ang*) and its reflected lamina have the typical therocephalian morphology with its pattern of bulges and grooves.

The splenial (*Spl*, Figs. 2A and 8) is an elongated bone participating in the formation of the lower part of the symphysis. Its posterior extent cannot be determined because it is broken slightly beyond the goniac angle.

The coronoid (*Cor*) is only partially visible in the specimen examined, but is elongated antero-posteriorly.

The surangular (*Sang*) is also only partly visible but its morphology appears to conform with the general therocephalian pattern.

The prearticular (*Part*) is characterized by the height and the sharpness of the buttress linking its vertical lamina to its ventral plate which covers the articular.

B. Cartilage bone

The area corresponding to the articular is too damaged to show any details.

III. DENTITION

The upper dental formula is identical in the type specimen (B.P.I. No. F.484/M.192) and the more complete specimen of the Rubidge collection (R.C. No. 116): 5I, 1pC, 1C, 5PC. These two specimens are almost identical in size. The specimen in the Keyser collection (G.S.P., K.C. No. R.85) which here is considered as a probable *Promoschorhynchus* has the following dental formula: 1pC, 1C, 6PC. This specimen is slightly smaller than the other two, so the number of postcanines may be reduced during growth, without affecting the length of the post-canine row (Tab. 1, No. 7).

The lower dental formula is 4I, 1C, 6PC. The greater number of postcanines in the lower jaw than in the maxilla is a very common feature amongst the therocephalians.

Very little can be said about the teeth because they are damaged. Both upper and lower incisors show labial facets extending half of their length from the tip. The fifth upper incisor is smaller than the others, but still larger than the precanine which in turn is bigger than the postcanines.

The postcanines seem to be simple cones. The single upper canines, as preserved, are large. The mesio-distal diameter of each canine is slightly larger than the labio-buccal diameter.

IV. DISCUSSION

Brink (1954, pp. 43—45, Fig. 2) when creating the genus *Promoschorhynchus* noted two points of resemblance with *Moschorhinus:* a mid-sagittal ridge on the nasal and frontal and the dimensions of the external nares. He noted one point of dissimilarity: the different proportions of the snout. He also considered that *Promoschorhynchus* agrees with *Moschorhynchus* in its general proportions and in the dimensions of the external nares. In addition, he concludes that *Promoschorhynchus* had no lower postcanine but possessed a palate "as far developed as in *Whaitsia*". He (p. 58) also concluded that *Promoschorhynchus* "evolved from *Moschorhinus*" and that "*Whaitsia* branched from *Promoschorhynchus* fairly early and *Moschorhynchus* much later". All the genera quoted above were included in the Whaitsiidae by Haughton and Brink (1954, pp. 147—151) and Watson and Romer (1956, p. 70).

In 1958 (p. 38—39), Brink divided the former family into Whaisiidae proper and Moschorhinidae. He then observed that "the aberrant *Whaitsia pricei*" may turn out to be a *Moschorhynchus* and this genus, with *Promoschorhynchus,* could then be included in the Moschorhinidae. He included *Notaelurops* in *Notosollasia,* doubting the existence of any difference between this latter and *Whaitsia.*

Concerning the South African Whaitsiids, Kitching (1972, thesis, p. 69) states that: "the marked similarity in the skull morphology, irrespective of minor individual variations, has led the author and others to conclude that the genera

Aneugomphius, Notosollasia and *Moschorhynchus* represent growth stages of the genus *Whaitsia,* as well as *Whaitsia pricei* and *Whaitsia major.* The other genera *Theriognathus* and *"Notaelurops"* based on single badly preserved specimens are also included in *Whaitsia.* It has been observed in the field that *"Notosollasia"* and *Whaitsia* normally occur in close association in the field or in the same horizon[11].

Mendrez (1973b, in press and 1974) recognizes only one valid genus for the Whaitsiidae of Tanzania and South Africa: *Theriognathus,* which has priority over *Whaitsia* and which, after further preparation, shows all the essential characteristics of *Whaitsia* for that part of the specimen which is preserved. *Theriognathus* is considered then as including *Hyenasuchus* as well as *Alopecopsis, Aneugomphius, Moschorhynchus, Notoaelurops, Notosollasia* and *Whaitsia* (including *W. pricei*). The differences between the Whaitsiidae and the Moschorhinidae have been emphasized.

In the Moschorhinidae, Kitching (1972, thesis, p. 70) does not accept the validity of the genus *"Promoschorhynchus platyrhinus,* based on a distorted snout . . . " and coming " . . . from the same horizon and exposure on the slopes of Compassberg that had previously yielded two specimens of the genus *Moschorhinus".* He concludes that "additional preparation to *Promoschorhynchus platyrhinus, Moschorhinus warreni* and *Cerdops burgheri* has revealed that these specimens are juvenile stages of *Moschorhinus kitchingi"* as well (possibly) as *Hewittia.*

It has been shown by Mendrez (1973, Fig. 7, in press) that the palate of the type specimen of *Promoschorhynchus* is very different from that described by Brink but is close to that of *Moschorhinus* though clearly distinguishable. The palate of the second specimen quoted by Mendrez (id, Fig. 8) agrees with that of the type. Further study of the latter specimen gives additional points of comparison between *Moschorhinus* and *Promoschorhynchus* and leads to the conclusion that they are different genera.

Mendrez (1974) has discussed also the composition of the South African Moschorhinidae, subfamily Moschorhininae which can be summarized as follows:

Moschorhinus is almost certainly synonymous with *Tigrisuchus. Tigrisuchus* is represented by the anterior half of the snout and shows a structure identical to that of *Moschorhinus;* however, the precanine formula is uncertain.

Cerdops is apparently very closely related to *Moschorhinus,* but is more lightly built if one compares specimens of the same size belonging to these two genera. The snout is much less massive and the suborbital bar and the postorbital and zygomatic arches are more slender. the precanine formula is shorter. What is available of the palate compares favourably with that of *Moschorhinus,* but the part of it anterior to the canines is obstructed by the lower jaw.

Hewittia has been compared to *Moschorhinus* on the bais of Brink's dentition (1958, pp. 37—38, Figs. 14—15) in Mendrez (1974) who concludes that it is better to leave it as a separate genus since the type specimen is now lost.

CONCLUSION

At present, the South African Moschorhinidae include five genera of which one is very doubtful: *Tigrisuchus* which is probably a synonym of *Moschorhinus;* if this can be proved *Tigrisuchus* has priority. Of the four other genera, *Promoschorhynchus* appears to be the most different from *Moschorhinus;* on the one hand, it has a relatively longer snout, a larger palatal plate of the premaxillae and a narrower anterior plate of the vomer, but, on the other hand, it is more advanced in having a broader epipterygoid and a sharper *crista choanalis.*

ACKNOWLEDGEMENTS

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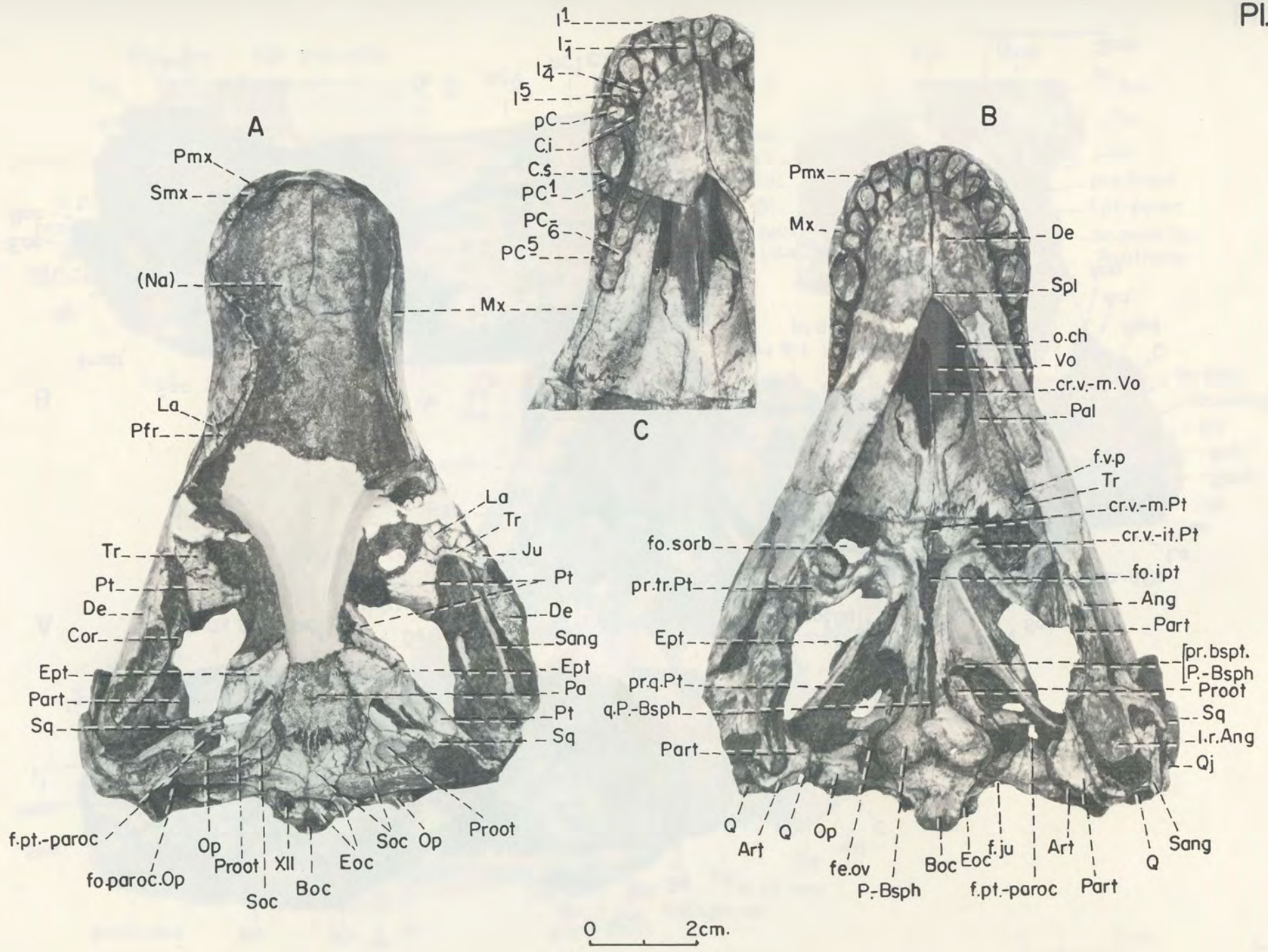
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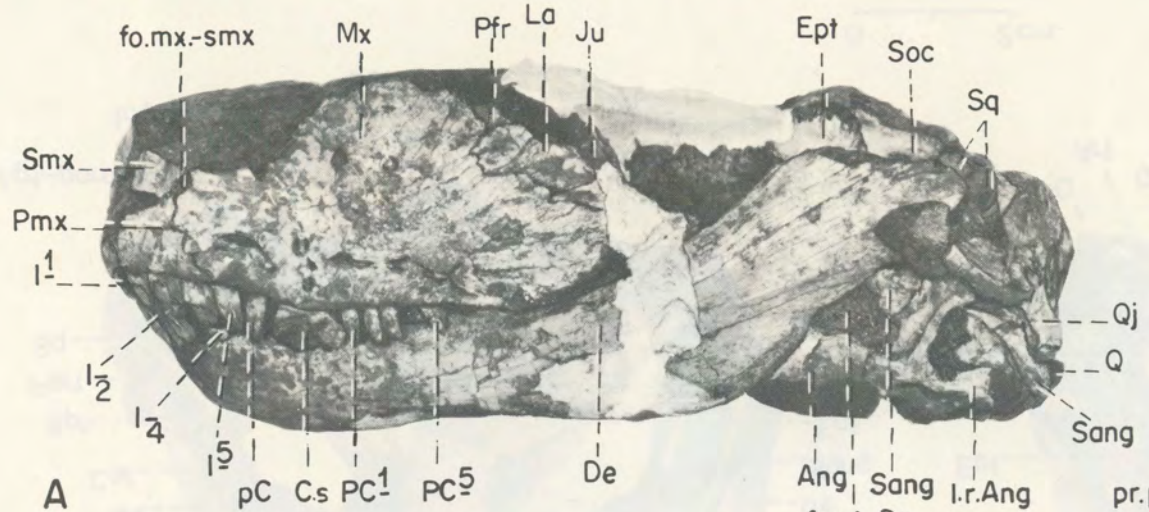
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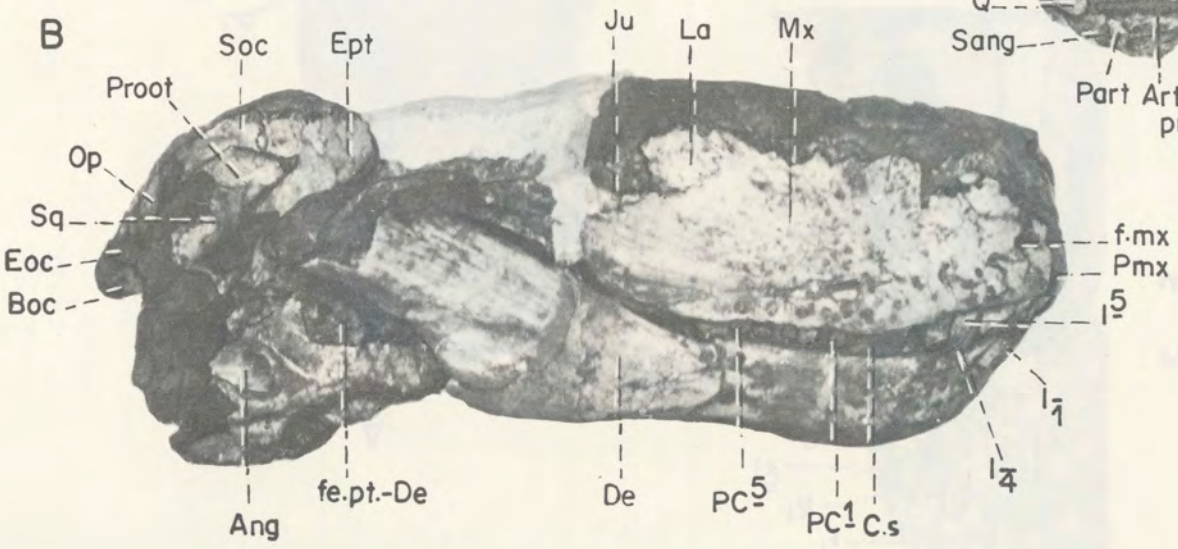
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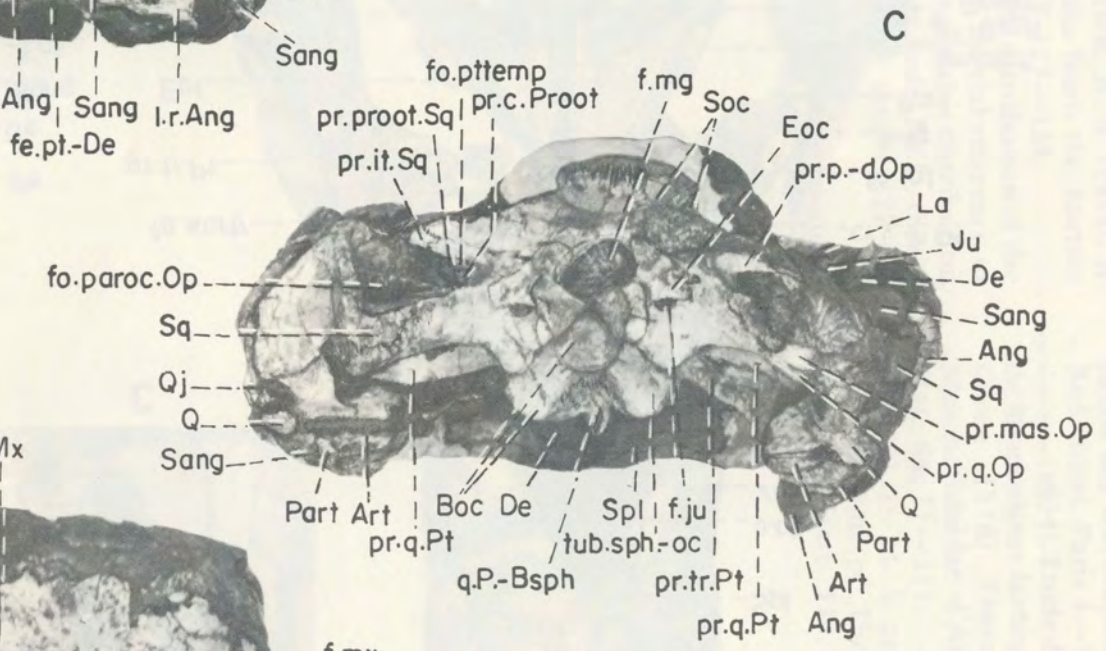
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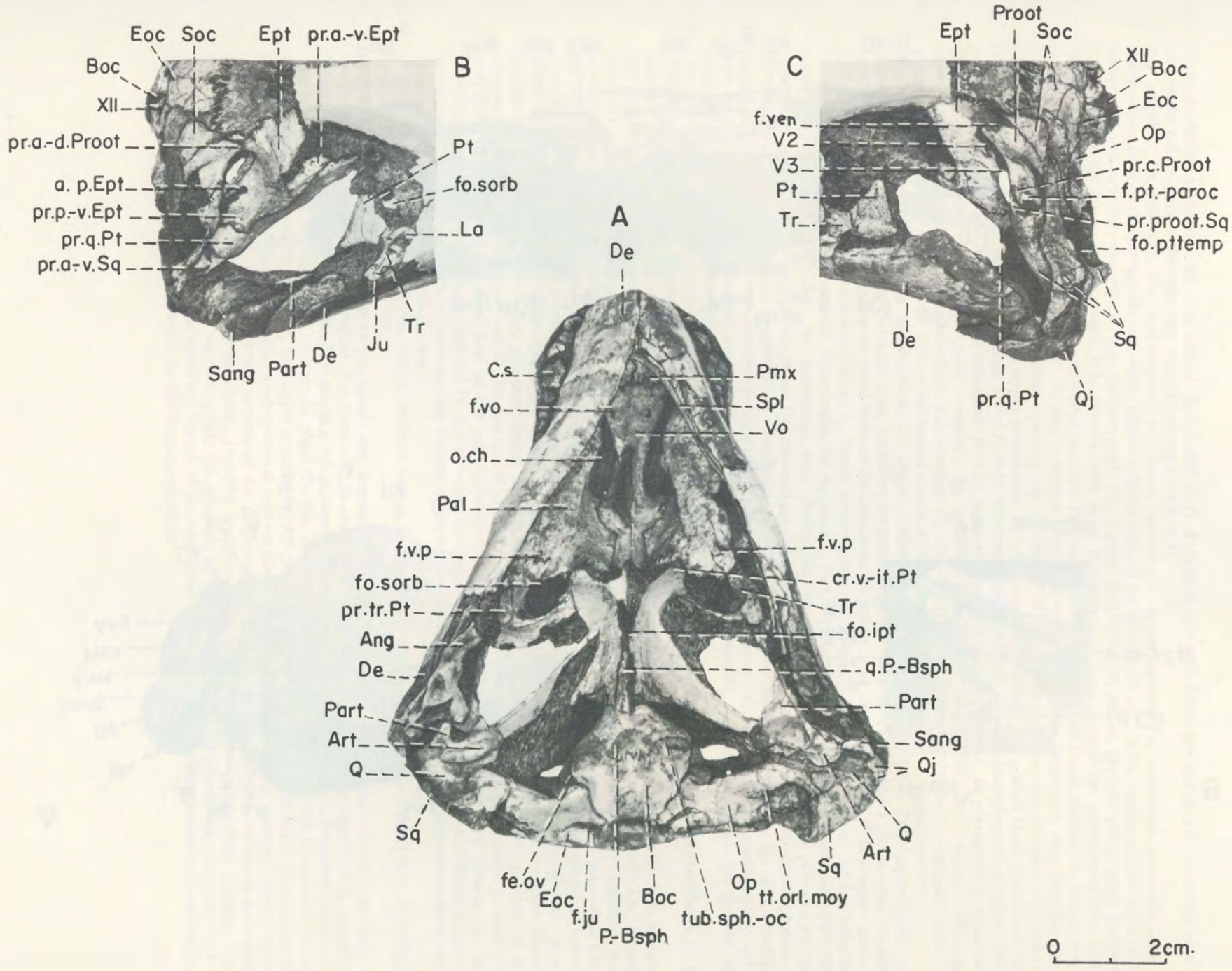
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pr.c.Proot
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Pl. IV

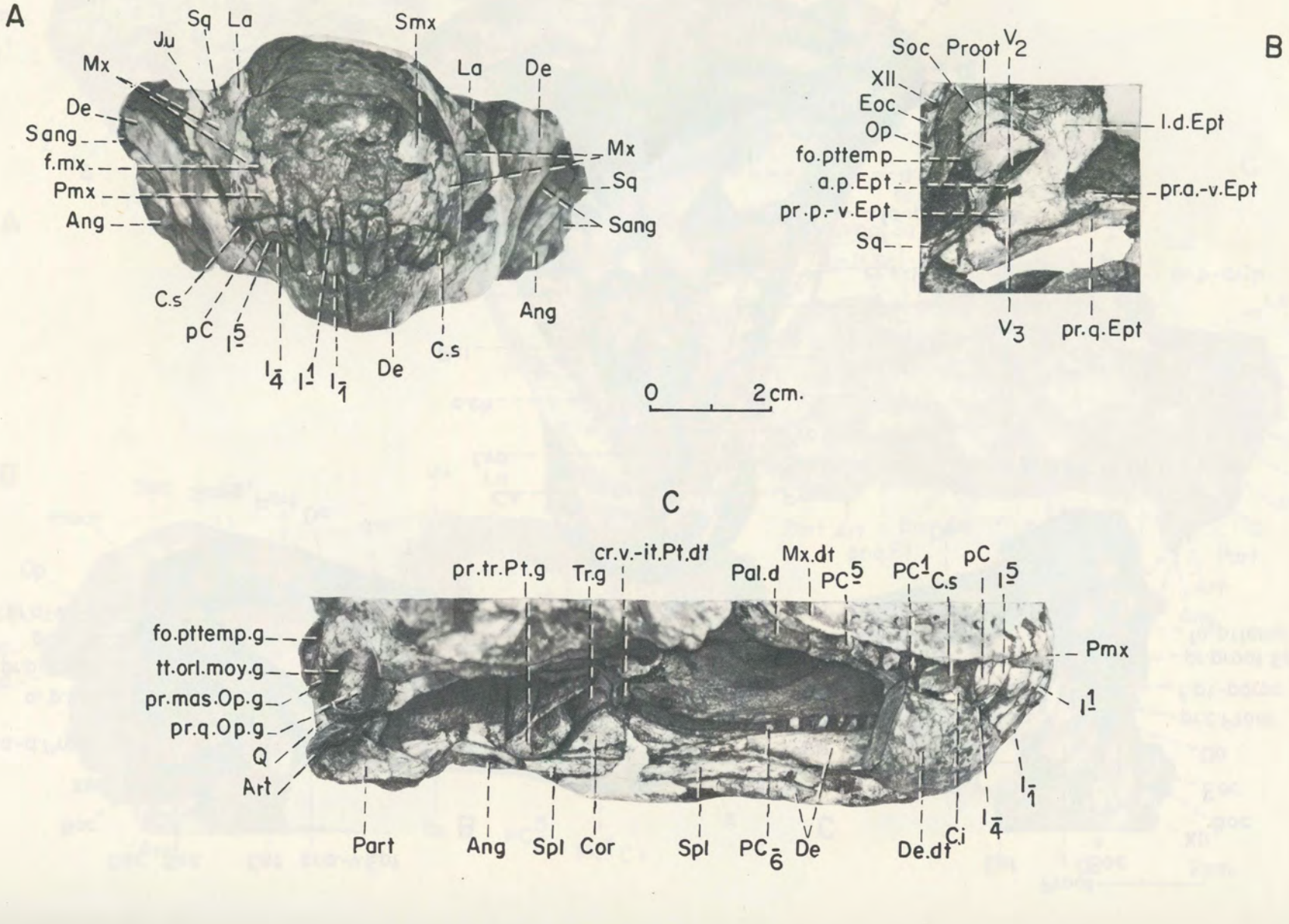
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Plate I *Promoschorhynchus platyrhinus*. RC. No. 116; *A*: dorsal view (x 1); *B:* ventral view with lower jaw in situ (x1); *C:* ventral view of part of the palate, part of the right jaw removed along a crack (x 1).
Ang, angular; *Art*, articular; *Boc*, basioccipital; *C.i.*, lower canine; *C.s*, upper canine; *Cor*, coronoid; *cr.v.-it.Pt*, ventro-intermediate crest of the pterygoid; *cr.v.-m.Pt*, ventro-median crest of the pterygoid; *cr.v.-m.Vo*, ventro-median crest of the vomer; *De*, dentary; *Eoc*, exoccipital; *Ept*, epipterygoid; *f.ju*, jugular foramen; *f.pt.-paraoc*, pterygo-paroccipital foramen; *f.v.p.*, foramen for the *vena platina major; fe.ov, fenestra ovalis; fo.ipt*, interpterygoid fossa; *fo.paroc.Op*, paroccipital fossa of the opisthotic; *fo.sorb*, suborbital fossa (or suborbital vacuity); I^1, first upper incisor; I_1, first lower incisor; I_4, fourth lower incisor; I^5, fifth upper incisor; *Ju*, jugal; *l.r.Ang*, reflected lamina of the angular; *La*, lachrymal; *Mx*, maxilla; *(Na)*, impression of the nasal; *o.ch*, internal choanae opening; *Op*, opisthotic; *P.-Bsph*, para-basisphenoid complex; *Pa*, parietal; *Pal*, palatein; *Part*, prearticular; PC^1, first upper postcanine; PC^5, fifth upper postcanine; PC_6, sixth lower postcanine; *pC*, precanine; *Pfr*, prefrontal; *Pmx*, premaxilla; *p.bspt.P.-Bsph*, basipterygoid process of the para-basisphenoid complex; *Proot*, prootic; *pr.q.Pt*, quadrate process of the pterygoid; *pr.tr.Pt*, transverse process of the pterygoid; *Pt*, pterygoid; *Q*, quadrate; *q.P.-Bsph*, keel of the para-basisphenoid complex; *Qj*, quadrato-jugal; *Sang*, surangular; *Smx*, septomaxilla; *Soc*, supraoccipital; *Spl*, splenial; *Sq*, squamosal; *Tr*, transversum; *Vo*, vomer; *XII*, internal foramen for the hypoglossal nerve.

Plate II *Promoschorhynchus platyrhinus*. RC. No. 116; *A;* left lateral view (x 1); *B:* right lateral view (x 1); *C:* occipital view (X 1).
Ang. angular; *Art*, articular; *Boc*, basioccipital; *C.s*, upper canine; *De*, dentary; *Eoc*, exoccipital; *Ept*, epipterygoid; *f.ju*, jugular foramen; *f.mg*, foramen magnum; *f.mx*, maxillary foramen; *fe.pt.-De*, post-dentary fenestra; *fo.mx.-smx*, maxillo-septomaxillary fossa; *fo.paroc.Op*, paroccipital fossa of the opisthotic; *fo.pttemp*, post-temporal fossa; I^1, first upper incisor; I_1, first lower incisor; I_2, second lower incisor; I_4, fourth lower incisor; I^5, fifth upper incisor; *Ju*, jugal; *l.r.Ang*, reflected lamina of the angular; *La*, lachyrymal; *Mx*, maxilla; *Op*, opisthotic; *Part*, prearticular; PC^1, first upper postcanine; PC^5, fifth upper postcanine; *pC*, precanine; *Pfr*, prefrontal; *Pmx*, premaxilla; *pr.c.Proot*, central process of the prootic; *pr.it.Sq*, intermediate process of the squamosal; *pr.mas.Op*, mastoid process of the opisthotic; *pr.p.-d.Op*, postero-dorsal process of the opisthotic; *pr.proot.Sq*, prootic process of the squamosal; *pr.q.Op*, quadrate process of the opisthotic; 6pr.q.Pt, quadrate process of the pterygoid, *pr.tr.Pt*, transverse process of the pterygoid; *Proot*, prootic; *Q*, quadrate; *Qj*, quadratojugal; *q.P.-Bsph*, keel of the para-basisphenoid complex; *Sang*, surangular; *Smx*, septomaxilla; *Soc*, supraoccipital; *Spl*, spenial; *Sq*, squamosal; *tub.sph.-oc, tuberculum spheno-occipitale*.

Plate III *Promoschorhynchus platyrhinus*. RC. No. 116; *A:* ventral view, the skull being slightly tilted to show the premaxillae (x 1); *B:* dorso-lateral view of the right temporal fossa (x 1); *C:* dorso-lateral view of the left temporal fossa (x 1).
a.p.Ept, posterior apophysis of the epipterygoid; *Ang*, angular; *Art*, articular; *Boc*, basioccipital; *cr.v.-it.Pt*, ventro-intermediate crest of the pterygoid; *C.s*, upper canine; *De*, dentary; *Eoc*, exoccipital; *Ept*, epipterygoid; *f.ju*, jugular foramen; *f.pt.-paroc*, pterygoparoccipital foramen; *f.v.p.*, foramen for the *vena* palatina major; *f.ven*, venous foramen; *f.vo*, vomerine foramen; *fe.ov, fenestra ovalis; fo.ipt*, interpterygoid fossa; *fo.pttemp*, posttemporal fossa; *fo.sorb*, suboribtal fossa (or suborbital vacuity); *Ju*, jugal; *La*, lachrymal; *o.ch*, internal choanae opening; *Op*, opisthotic; *P.-Bsph*, parabasisphenoid complex; *Pal*, palatine; *Part*, prearticular; *Pmx*, premaxilla; *pr.a.-d.Proot*, antero-dorsal process of the prootic; *pr.a.-v.Ept*, antero-ventral process of the epipterygoid; *pr.a.-v.Sq*, antero-ventral process of the squamosal; *pr.c.Proot*, central process of the prootic; *pr.p.-v.Ept*, postero-ventral process of the epipterygoid; *pr.proot.Sq*, prootic process of the squamosal; *pr.q.Pt*, quadrate process of the pterygoidl *pr.tr.Pt*, transverse process of the pterygoid; *Proot*, prootic; *Pt*, pterygoid; *Q*, quadrate; *q.P.-Bsph*, keel of the para-basisphenoid complex; *Qj*, quadratojugal; *Sang*, surangular; *Soc*, supraoccipital; *Spl*, splenial; *Sq*, squamosal **Tr**, transversum; *tt.orl.moy*, roof of the middle ear; *tub.sph.-oc, tuberculum spheno-occipitale; Vo*, vomer; *V2*, notch of the maxillary branch of the trigeminal nerve; *V3*, notch for the trigeminal nerve; *XII*, internal foramen of the hypoglossal nerve.

Plate IV *Promoschorhynchus platyrhinus*. RC. No. 116; *A:* anterior view (x 1); *B:* laterial view of the right epipterygoid (x 1); *C:* medical view of the left lower jaw.
a.p.Ept, posterior apophysis of the epipterygoid; *Ang*, angular; *C.s*, upper canine; *C.i*, lower canine; *cr.v.-it.Pt.dt*, ventro-intermediate crest of the right pterygoid; *Cor*, coracoid; *De*, dentary; *De.dt*, right dentary; *Eoc*, exoccipital; *f.mx*, maxillary foramen; *fo.pttemp*, post-temporal fossa; *fo.pttemp.g*, left posttemporal fossa; I^1, first upper incisor; I_1, first lower incisor; I_4, fourth lower incisor; I^5, fifth upper incisor; *Ju*, jugal; *l.d.Ept*, dorsal lamina of the epipterygoid; *Op*, opisthotic; *Pad.dt*, right palatine; *Part*, prearticular; PC^1, first upper postcanine; PC^5, fifth upper postcanine; PC_6, sixth lower postcanine; *pC*, precanine; *Pmx*, premaxilla; *pre.a.-v.Ept*, antero-ventral process of the epipterygoid; *pr.mas.Op.g*, mastoid process of the left opisthotic; *pr.p.-v.Ept*, postero-ventral process of the epipterygoid; *pr.q.Ept*, quadrate process of the epipterygoid; *pr.q.Op.g*, quadrate process of the left opisthotic; *pr.tr.Pt.g*, transverse process of the left pterygoid; *Proot*, prootic; *Sang*, surangular; *Smx*, septomaxilla; *Soc*, supraoccipital; *Spl*, splenial; *Sq*, squamosal; *Tr.g*, left transversum; *tt.orl.moy*, roof of the left middle ear; *V2*, notch for the maxillary branch of the trigeminal nerve: *V3*, notch for the mandibular branch of the trigeminal nerve; *XII*, internal foramen for the hypoglosal nerve.