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ON THE SCALOPOSAURID SKULL OF *OLIVIERIA PARRINGTONI*, BRINK WITH A NOTE ON THE ORIGIN OF HAIR

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Olivieria parringtoni was described by Brink in 1965 as a new genus and species. It stands closest, among the scaloposaurids, to *Ictidosuchops intermedius* (Broom). In general shape and size, their skulls are virtually indistinguishable from one another, but *Olivieria* comes from the top of the *Lystrosaurus*-zone (early Triassic) while the type-locality of *I. intermedius* is the *Cistecephalus*-zone (Upper Permian). Differences in dentition and differences in detailed skull moulding had argued for the creation of the new genus.

The writer undertook an examination of the type specimen of *Olivieria* because it seemed well suited to a study of the sensory nerve supply of the muzzle. Ever since Watson (1931) suggested that one might gauge the sensitivity, suppleness and therefore the possible hairiness of the muzzle by studying the size, numbers and position of the sensory nerve foramina in the fossil skull, it has seemed likely to point, albeit indirectly, to the origin of hair in the pre-mammalian stem. Such an abundance of nerves supplying the muzzle in scaloposaurid and bauriamorph reptiles would hardly be needed for scaly and inelastic cheeks. More probably, as Brink (1956) has emphasized, a mammalian type of tactile hair with soft cheeks had already come into being in these animals.

Proof for the existence of hair in these fossil animals is lacking entirely, yet there are several points favouring this idea. Firstly, the scaloposaurid-bauriamorph line is thought to be close to the mammalian stem where hair growth could be expected. Secondly, evidence from the structure and function of the eye in living mammals makes it likely that mammals are descended from a nocturnal reptilian stem with dark-adapted eyes (Walls, 1942). In such animals, sensitive tactile hairs would make up for poor vision at night. Thirdly, if the animal was adapted to life at night, the need to remain active and warm in the cold would be favoured by an insulating hairy coat. Such a dependence on touch, warmth in cold surroundings and a dominance of sound over sight would represent the preliminary ecological niche required for ground-living reptiles to emerge in due course as mammals.

The original description of *Olivieria* was based on an external preparation of the skull, principally of the left side. It seemed desirable to clean the right side and extend the preparation into areas hitherto conjectural or unknown. Camera lucida drawings of these new views are presented here (Figs. 1–5),

comprising the snout, orbit, temporal fossa, occiput and the ventral surface as far as preparation was possible without disarticulating the lower jaw. The two maxillae were also investigated for their foraminal patterns, and these have been illustrated (Figs. 6–7). To facilitate comparison and avoid duplication, the writer would advise reference to Crompton's (1955) text on *I. intermedius* as a guide to these illustrations. Crompton's lettering has also been adopted. The probable course of the trigeminal branches from the base of the epipterygoid, through the lacrymal and out through the sidewall of the snout can be deduced by conjecture from the foramina.

Comment

As no full description is necessary, only certain points of opinion will be noted.

(i) Brink's text and drawings (Figs. 49 and 50) are at variance. Five upper incisors are described and four are illustrated. The correct number is four according to my examination (Fig. 1).

(ii) The snout is shaped like the prow of a boat (Fig. 6) and is not rounded as restorations might suggest. The shape of the front ends of the nasals is not therefore a significant or dependable character because of ready damage to this region.

(iii) With one "incisor" less, there is one more canine in the maxilla—four on the left and possibly even five on the right (Figs. 6–7). There are three postcanines in both maxillae, as Brink described.

(iv) In *Olivieria* the incisors are bigger and fewer and occupy twice the space as compared with *I. intermedius*. The main canine is also a little longer and situated farther back along the alveolar margin. This produces a broader and bolder front half of the mouth, associated with an insignificant post-canine portion. In *I. intermedius* the teeth are smaller, more numerous, more evenly functional and are arranged on an alveolar margin with more nearly parallel sides along the palate.

(v) With this separation of the mouth in *Olivieria* into a more stumpy, butt-like front portion and a virtually non-biting back portion behind the main canine, one finds the internal nares flaring widely and coming level with the buccal cavity near the main canine. In *I. intermedius* this levelling takes place behind the last postcanine.

(vi) The alveolar arcade of the maxilla and premaxilla forms a U-shaped curve about 87 mm. long, measured from the posterior end of the alveolar fold on either side round the outer borders of the teeth. On Crompton's figures the same distance in *I. intermedius* is a little more—say 90 mm. The available tooth space is therefore about the same, the final dental formula being determined by tooth size, and by the maxillary tooth which becomes the main canine.

(vii) Along with this heavier front part of the mouth, the temporal and occipital muscles were clearly much stronger than in *I. intermedius*. Thus, the

parietals, squamosals, as well as their occipital counterparts, are sharply crested (Fig. 4). This difference leads to some re-shaping of the details in the upper half of the skull without altering either gross external measurements or the ventral surface of the skull as compared with *I. intermedius*. In the lower jaw, the dentary also becomes straighter, but not longer (80 mm.).

(viii) To interpret the bony structure in terms of biting function, one may investigate the way in which the tooth rows are stabilised across the skull in relation to the jaw joint. On the ventral surface, the bony support of the upper jaws from the jaw joint is arranged across the skull in a simple X-shaped pattern. If one draws a line from the jaw joint on one side to the posterior end of the alveolar margin of the maxilla of the opposite side, this line lies neatly along the quadrate ramus of the pterygoid, crosses the midline at the interpterygoid vacuity where, in this specimen, the pterygoid is heavily keeled anteriorly, and passes up the palatine to the hind end of the maxilla in the mouth. Except for the presence of a pterygoid keel, these relationships are the same in *Olivieria* and *I. intermedius*. Fig. 5 shows these points in part.

(ix) On the dorsum of the skull, the two limbs of the X-pattern are not the simple intersecting straight lines as described above. With the cresting of the parietals, this bone appears pinched together just above the epipterygoids and behind the pineal, at a point where the epipterygoid summits are only 10 mm. across (Fig. 4). From this area, where the limbs of the X appear to be fastened together as with a short tie-rod, the posterior limbs of the X curve out to the quadrates along the bony parietal and squamosal plates. The front limbs of the X, and the associated bony ridges on the skull roof, are clearly directed towards the root of the main canine.

(x) It would appear as if all other differences in skull form are subservient to this strengthening of the jaws as compared with *I. intermedius*. The top of the epipterygoid and the pineal foramen would be squeezed or pulled farther forward and the upper orbital margins would be outwardly displaced by increasing participation of the strengthened frontals. The prootic would have its anterior end turned more sharply medially by the posterior buttressing of the skull. These rotations, strengthenings and adjustments would lead to a relative constriction behind the canines, a virtual enlargement of the cavum epiptericum, a shift of the internal nares and a broadening in the form of the commencing secondary palate, a ready forward shift of the postorbital bar and a possible exclusion of the supraoccipital from the temporal fossa.

(xi) From Crompton's account of *I. intermedius*, it is clear that the connection between the X-shaped central skull structure and the back and base of the skull may not be united by closed sutures. The significance of this kinetism or looseness in structure, even in the components of the X itself, has been related to three things: ability to take bigger bites, ability to absorb shock during biting, ability for the bones to give way to an expanding brain. As will be noted below in the case of the hair, an evolutionary trend may well be established because of a group of minor advantages accruing simultaneously. A study of *Olivieria* shows

a combination of more powerful biting, a cramped brain space, a reduction in kinetism and a more reptilian palate. *I. intermedius* shows a less powerful bite, a more mammalian palate, a less cramped brain and more kinetism. It seems therefore as if kinetism, or failure of certain sutures to unite, may be a combined feature related more to a weaker dentition and greater brain growth—an evolutionary compromise resembling paedomorphism, and not the result of more violent eating habits alone. Violent eating would lead, *per se*, to loss of kinetism.

(xii) If the above interpretation of the skull structure in *Olivieria* is accepted, then this specimen must be regarded as a late form of *Ictidosuchops intermedius* in which a carnivorous habit was accentuated, associated with stabilization of the skull and loss of kinetism, and constriction of the cranial cavity.

Significance Of The Foramina For The Origin Of Hair

In *Olivieria parringtoni* there are to be found on each maxilla a large number of foramina which diverge and branch out over the outer surface of the bone. They appear to radiate from an imaginary central point which can be placed quite readily in the region of the main canine root. In the bone below the incisors of the dentary, the outer surface is likewise perforated by a number of foramina.

The only structures likely to have lain in the grooves on the maxilla are branches of the maxillary division of the trigeminal nerve. Among the alternative possibilities, arteries and veins to this area come from the external carotid and jugular systems, and would not enter or leave the cheek through the bone. Compound glands supplying the mouth or nose would, if they were the cause of the grooving, show a converging pattern of ducts from the acini and not a divergence from their acinar ends, as would have to be the case here if glands lay in the grooves. As causes of the grooving, none of these alternatives seems likely.

In mammals, the greatest part of the infra-orbital branch of the maxillary division of the trigeminal nerve usually reaches the cheek from the interior of the maxilla through the infra-orbital foramen. This foramen is situated not far from the canine root, and thereafter the nerves break up into a plexus in the tissues of the cheek. In the same way the mental branch of the inferior dental nerve reaches the chin by a single foramen. In the mammal-like reptile under discussion, one cannot help supposing that an earlier arrangement is present, wherein the nerve branches break up *inside* the bone to start with, and they reach the outside through a host of separate openings. A later mammalian development would comprise a transfer of the nerve plexus to the external surface of the bone, thus consolidating and confining the foramina to a few strategic points of more constant position.

Since the cheeks and chin are the sites in mammals of tactile vibrissae belonging to the infra-orbital, jugal, labial, angular and sub-mental groups supplied by the second and third divisions of the trigeminal nerve, one is justified in thinking that these mammal-like reptiles possessed sensory organs of similar importance in this area. It seems to matter little in principle whether these

sensory organs were activated by hairs or by some amplifying receptor which was converted eventually into a true hair. The difference depends on one important consideration only—how far did the amplifying receptor project? Tactile spots which exist in modern reptiles, and lie between the scales, require a touch stimulus which is applied directly on to the body surface. For an animal moving at night such a system would be highly unsatisfactory, since manoeuvrability and speed depend on having evidence of a safe span on all sides.

Although mammalian hair, once present, has been put in different species to numerous new uses, principally defensive or communicative in one way or another, the question as to whether hair was initially tactile or thermoregulatory in origin seems somewhat artificial. With the growth of hairs from the body surface the sensory enhancement and thermal resistance would both develop at the same time. Subsequent differentiation in texture and length would favour the one or the other function by further selection.

Palaeontology offers little help on the origin of body hair, although Broili (1941) has brought forward some evidence for its presence in extinct flying reptiles. The facts reviewed here, however, make it seem possible that hair arose in reptiles perhaps as far back as the Upper Permian, and that tactile vibrissae may have been one of the earliest types of hair to become differentiated. Their very early appearance in the skin of mammalian embryos may not merely be a sign of their greater complexity of development, but could point to their establishment far back in phylogeny.

Summary

In a study of the scaloposaurid skull of *Olivieria parringtoni*, it was concluded that it was a late relative of *Ictidosuchops intermedius* with a stronger carnivorous habit, but with little to separate them in other respects. Indirect evidence for the presence of hair in these mammal-like reptiles is discussed in the light of palaeontological and other evidence.

Acknowledgments

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EXPLANATIONS OF TEXT FIGURES

Fig. 1 —*Olivieria parringtoni*. View of snout showing foramina in the dentary.

Fig. 2 —View of right half of occiput. Skull tilted to show part of ventral surface. Intervening stapes and hyoid apparatus removed.

Fig. 3 —View of right orbital region seen from above.

Fig. 4 —View of right temporal fossa, seen obliquely from tle dorsolateral aspect with the jugal arch removed.

Fig. 5 —Ventral view of skull. The jugal arch is removed, and the anterior point of the preparation goes forward to a point where the vomer and maxilla are 1-2 mm. apart.

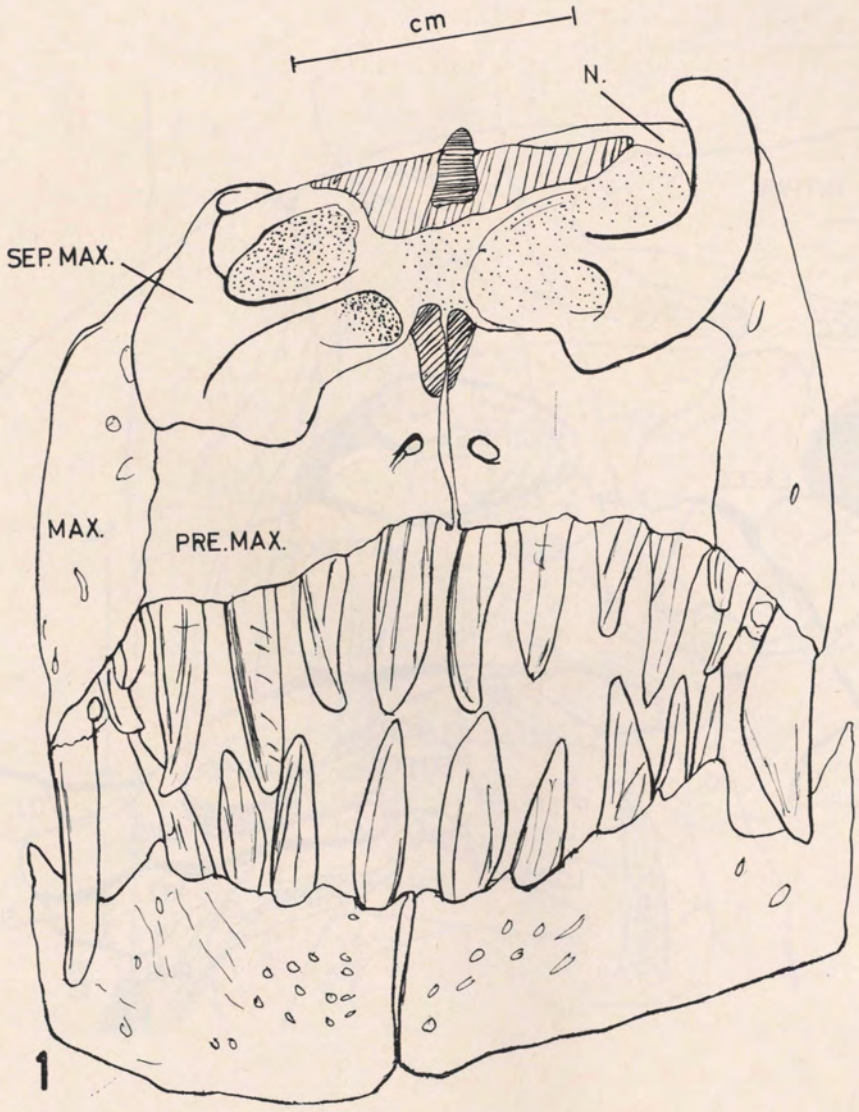
Figs. 6-7 —Lateral views of the right and left maxillae respectively. The alveolar portion of the maxilla extends about 8 mm. behind the last post canine.

KEY TO LETTERING OF FIGURES

A.D.P.	Anterior dorsal process of the periotic.
ANG.	Angular.
ART.	Articular.
A.V.P.	Anterior ventral process of the periotic.
BO.	Basioccipital.
BP. PROC.	Basipterygoid process.
BS.	Basisphenoid.
CAV. EPI.	Cavum epiptericum.
COR. PROC.	Coronoid process.
EPI.	Epipterygoid.
EX. OCC.	Exoccipital.
F.	Frontal.
I.C.	Internal carotid foramina.
INT. VAC.	Interpterygoid vacuity.
INT. PAR.	Interparietal.
J.	Jugal.
JC.	Jugular canal.
LAC.	Lacrymal.
LAC. FOR.	Lacrymal foramen.
LO. RG.	Longitudinal ridge.
MAST. PROC.	Mastoid process (paroccipital).
MAX.	Maxilla.
M.P. SQ.	Mastoid process (squamosal).
N.	Nasal.
P.	Parietal.
PAL.	Palatine.
PF.	Prefrontal.
PIN.	Pineal foramen.
PIT. FOS.	Pituitary fossa.
PO.	Postorbital.

Key to Lettering of Figures continued

POST. FOSS.	Post-temporal fossa.
P.P.	Paroccipital process.
P.P.E.	Pterygoid process of epipterygoid.
PRE. ART.	Prearticular.
PRE. MAX.	Premaxilla.
PRO.	Prootic.
PS.	Parasphenoid.
PTER.	Pterygoid.
PT. PROC.	Pterygoid process of the quadrate.
QJ.	Quadratojugal.
Q.R.P.	Quadrate ramus of the pterygoid.
QUAD.	Quadrate.
QUAD. PROC.	Quadrate process of the paroccipital.
SCL. PL.	Sclerotic plates.
SEP. MAX.	Septomaxillary.
SPL.	Splenial.
SQ.	Squamosal.
SQ. PROC. 1, 2 and 3	First, second and third processes of the squamosal.
ST.	Stapes.
ST. PROC.	Stapedial process.
SUP. OCC.	Supraoccipital.
SUR. ANG.	Surangular.
S.V.	Suborbital vacuity.
TAB.	Tabular.
TRAV.	Transversum.
V.	Vomer.
V 2 and 3	Notch in epipterygoid for 2nd and 3rd divisions of the trigeminal nerve.
VII	Foramen for facial nerve.
XII	Hypoglossal nerve foramen.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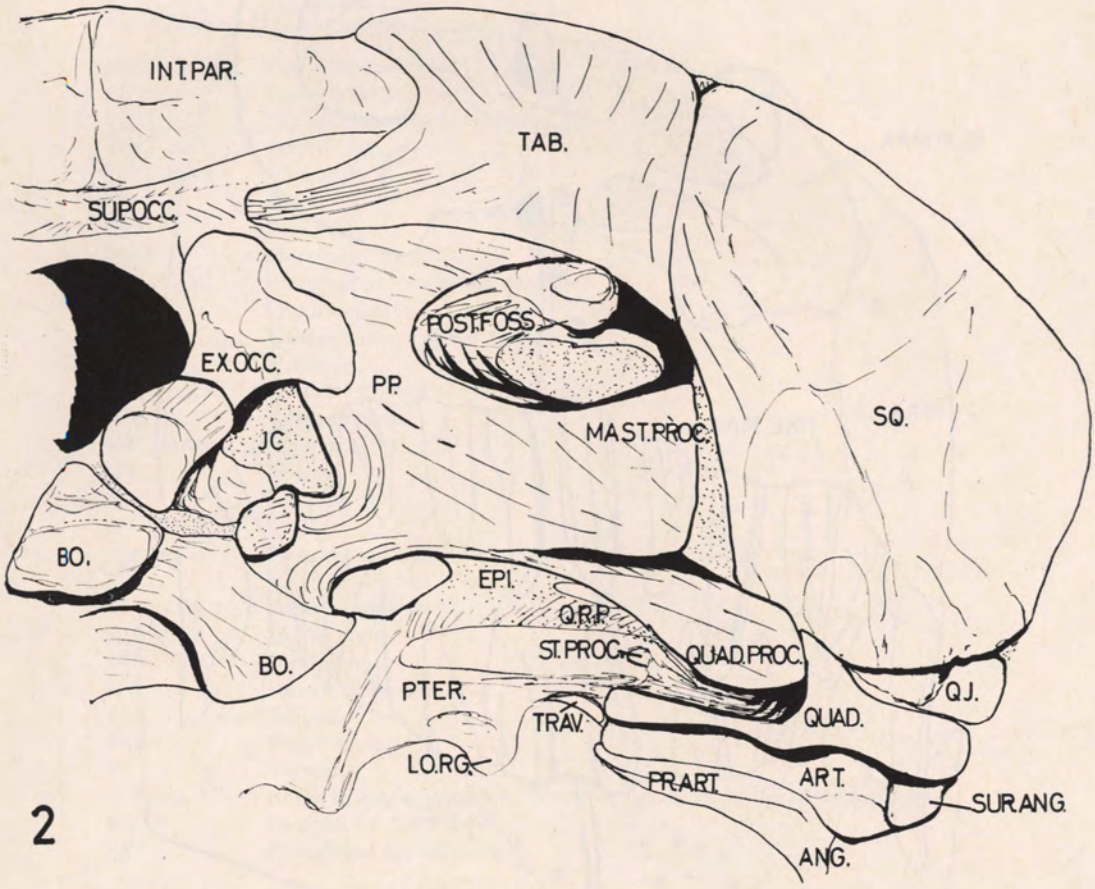
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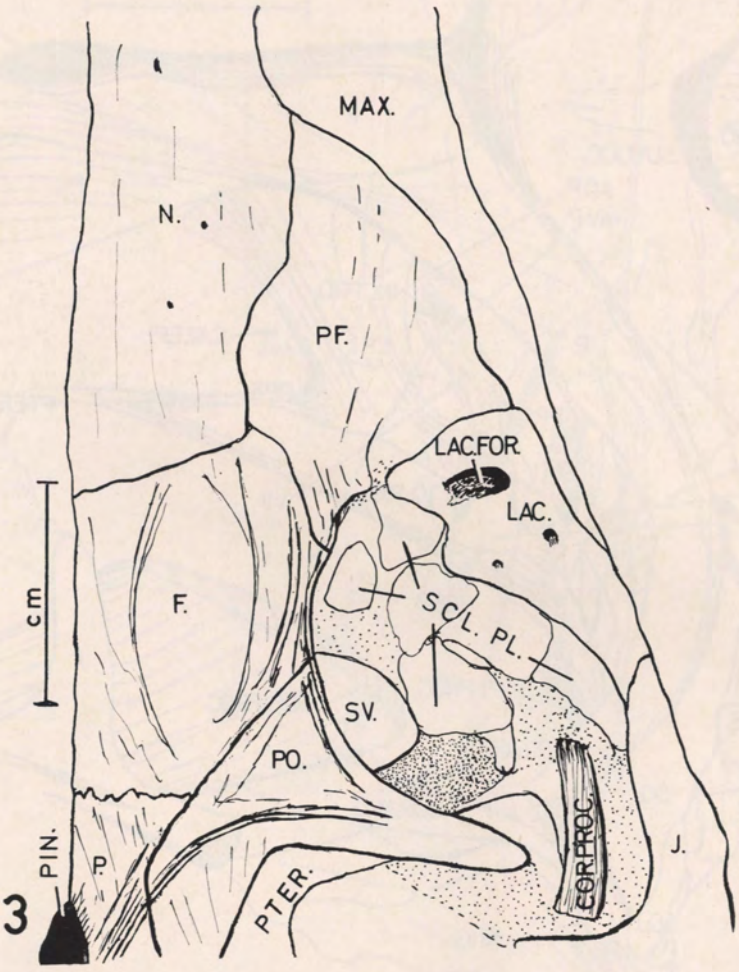
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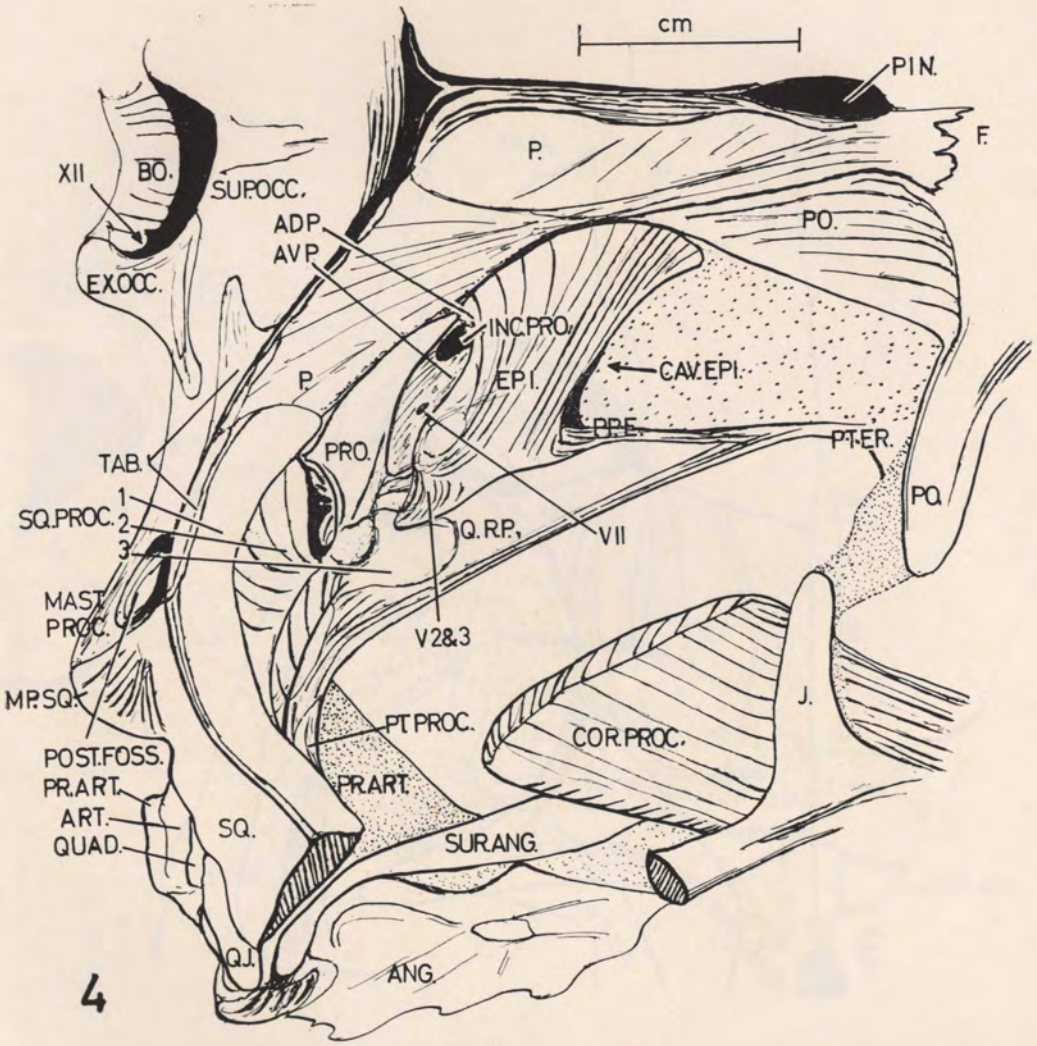
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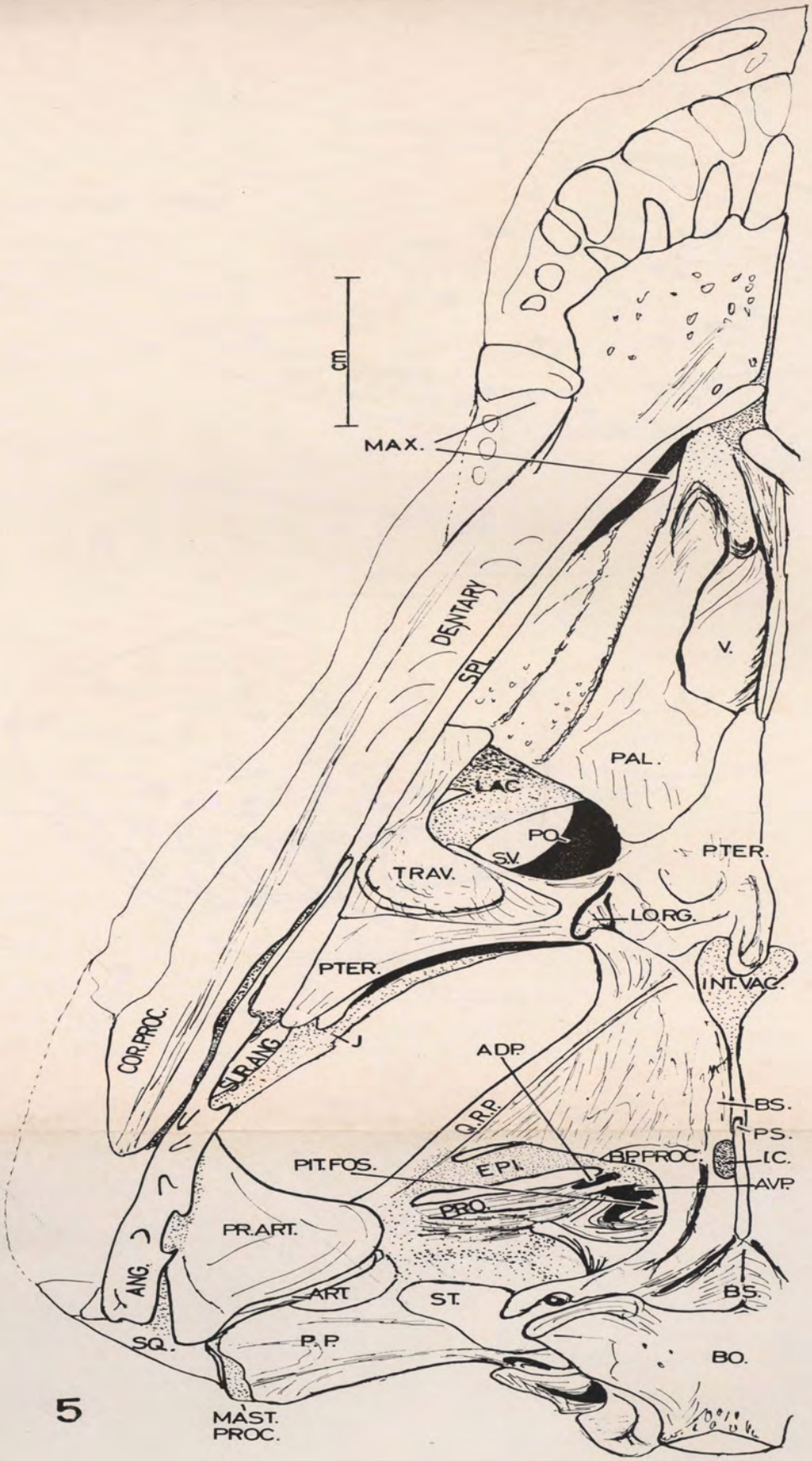
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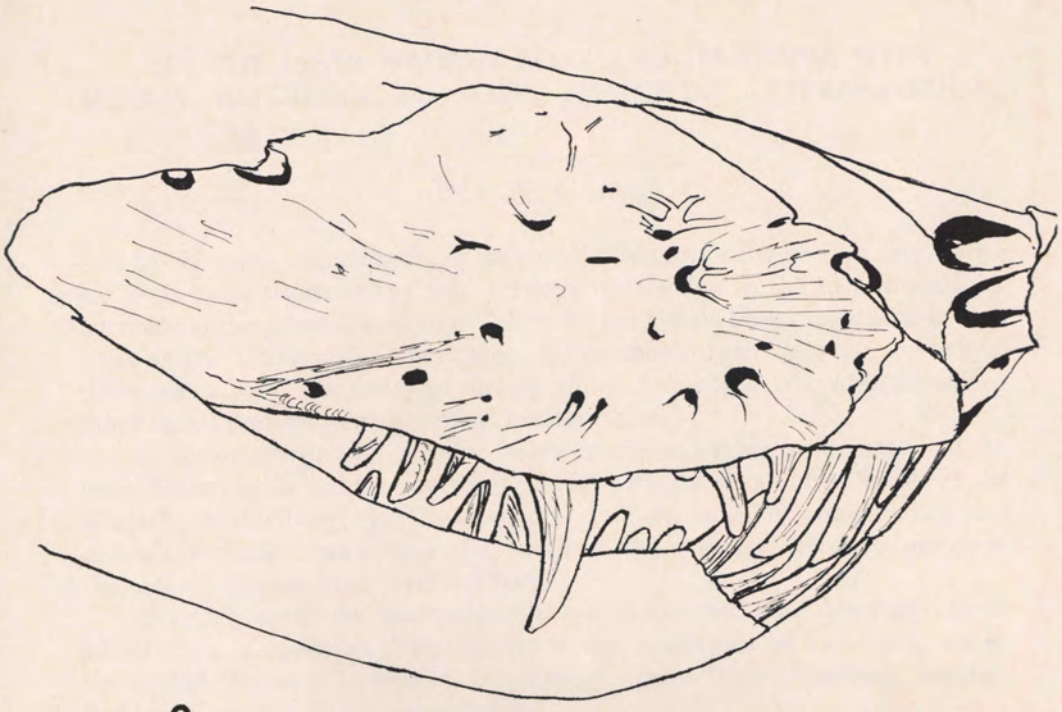

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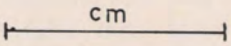
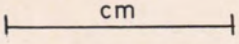
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