DEVELOPMENT OF THE SKULL IN CATFISHES
PART V. DEVELOPMENT OF SKULL IN *HETEROPNEUSTES FOSSILIS* (BLOCH)

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ABSTRACT

Five stages in the development of the skull and the adult skull have been described by using modern nomenclature as adopted by de Beer (1937).

The origin of some of the disputed bones of the siluroid skull has been traced and discussed in the paper. The maxillae and premaxillae are seen to develop fairly early during the development i.e., 8 mm. and 12 mm. larvae respectively. The ethmoid bone which arises as a perichondral ossification of the lamina precerebralis of the chondrocranium possesses membranous extensions but no separate membrane ossifications co-ossifying with it. The bone develops in the 29 mm. stage. The nasals which develop in the 33 mm. stage arise as membrane bones surrounding the anterior ends of the supraorbital sensory canals.

In the 19 mm. stage the parasphenoid and the frontals develop as membrane bones and the prootic, supraoccipital, basi-occipital and quadrate develop as perichondral ossifications. The supraoccipital bone which arises as a single centre of ossification from the tectum synoticum extends laterally and anteriorly. A parietal ossification is never noticed and the supraoccipital ossification extends to the region of the parietals.

The angular and dentary bones arise in the 19 mm. stage around Meckel's cartilage and no part of Meckel's cartilage is invaded by any ossification in any stage of development. Splenial bone is absent. In the 21 mm. stage the exoccipital, lateral ethmoids, sphenotics and pterotics with the supratemporal extension develop as perichondral ossifications. A posttemporal around the sensory canal is also seen to develop in this stage. The lateral ethmoids have ventral extensions which are connected with the orbitosphenoids. In the 33 mm. stage the pleurosphenoids, orbitosphenoids, hyomandibulae, metapterygoids and palatines are developed as perichondral ossifications. The other bones that develop in membrane in this stage are the prevomer, supraorbitals, nasals, opercles, preopercles and interopercles. The orbitosphenoids are seen to develop as paired perichondral ossifications in the 33 mm. stage and in the 49 mm. stage the two ossifications fuse to form a median bone. The intertemporal bones and suborbitals are seen to develop last in the series of the bones. The parietals, opisthotics, epiotics, symplectics, subopercles and basisphenoid bones are absent.

The lateral line system and the hyobranchial skeleton are described. In the branchial arches there are the second and third basibranchs. The pharyngobranchs of third and fourth arches are separate. The epibranchs of all the four arches are distinct. The hypobranches of third and fourth arches are represented by cartilage. The urohyal (parahyoid) is a large bone having a pair of long pointed lateral processes.

INTRODUCTION

In an earlier paper (Srinivasachar, 1957*b*) the development of chondrocranium has been completely described in *Heteropneustes* and in this paper an attempt has been made to describe the development of the osteocranium with a view to find out the origin of some of the disputed bones of the siluroid skull. Kindred (1919) has given a detailed account of the various bones of skull in *Amiurus*. Earlier McMurrich (1884) and Herrick (1901) have described the topographical relations of the cranial bones of the adult *Amiurus*. More recently Bhimachar (1933) has given an account of the morphology of the skull of certain Indian siluroids. David (1935, 1936) has described the skull of the African members of the siluroid families Calariidae and Bagridae and also has figured the dorsal aspect of the skull of

Saccobranchus fossilis. In all these cases it appears that the nomenclature of the bones is not in conformity with the development of the different bones. I have used in my description of the skull as far as possible the nomenclature adopted by de Beer (1937).

Material and Methods

The material presented in this paper consists of a number of developing stages and adults of *Heteropneustes* collected round about Bangalore and Trivandrum. Some of the early stages were reared in the laboratory. Alizarin transparencies were made for both the developing larvae and adults in order to study the centres of ossifications and also the topography of various bones of the skull. In certain cases slightly higher percentage of KOH was used in order to disarticulate the bones to study the individual bones in relation to the neighbouring ones. Differential staining of bones and cartilages was also used in some early stages to study the cartilage and membrane bones. The following stages have been studied in the development of skull in *Heteropneustes*.

Stage	Total-length	Head-length	Remarks
1.	19.0 mm.	3.5 mm.	Differential staining.
2.	21.0 mm.	4.0 mm.	Alizarin.
3.	29.0 mm.	5.0 mm.	Alizarin.
4.	33.0 mm.	5.5 mm.	Alizarin.
5.	49.0 mm.	9.0 mm.	Alizarin.
6.	Adult 210.0 mm.	33.0 mm.	Alizarin.

Adult skull of *Clarias batrachus* was also studied for the sake of comparison.

Observations

The adult skull of *Heteropneustes* is well ossified and compact, showing dorso-ventral compression. It also shows pitted appearance on the dorsal surface. The sutures separating the various bones are very clear and prominent. In the adult skull very little cartilage remains unossified and practically the cranium is free from cartilage. The large fontanelle noticed in the chondrocranium (Srinivasachar, 1957*b*) is almost completely closed except for a small anterior one between the frontals and a posterior one in the supraoccipital bone.

I shall now describe the skull in the following order.

A. *The cranium*
   1. Ethmoid region.
   2. Orbitotemporal region.
   3. Auditory region.
   4. Occipital region.

B. *The jaws and hyobranchial skeleton*
   1. Upper jaw.
   2. Lower jaw.
   3. Hyoid arch.
   4. Branchial arches.

A. *The cranium.*

1. *The ethmoid region :* The ethmoid region in the adult skull is formed by a median ethmoid bone and paired lateral ethmoids with dorsal nasals and ventral prevomer bones.

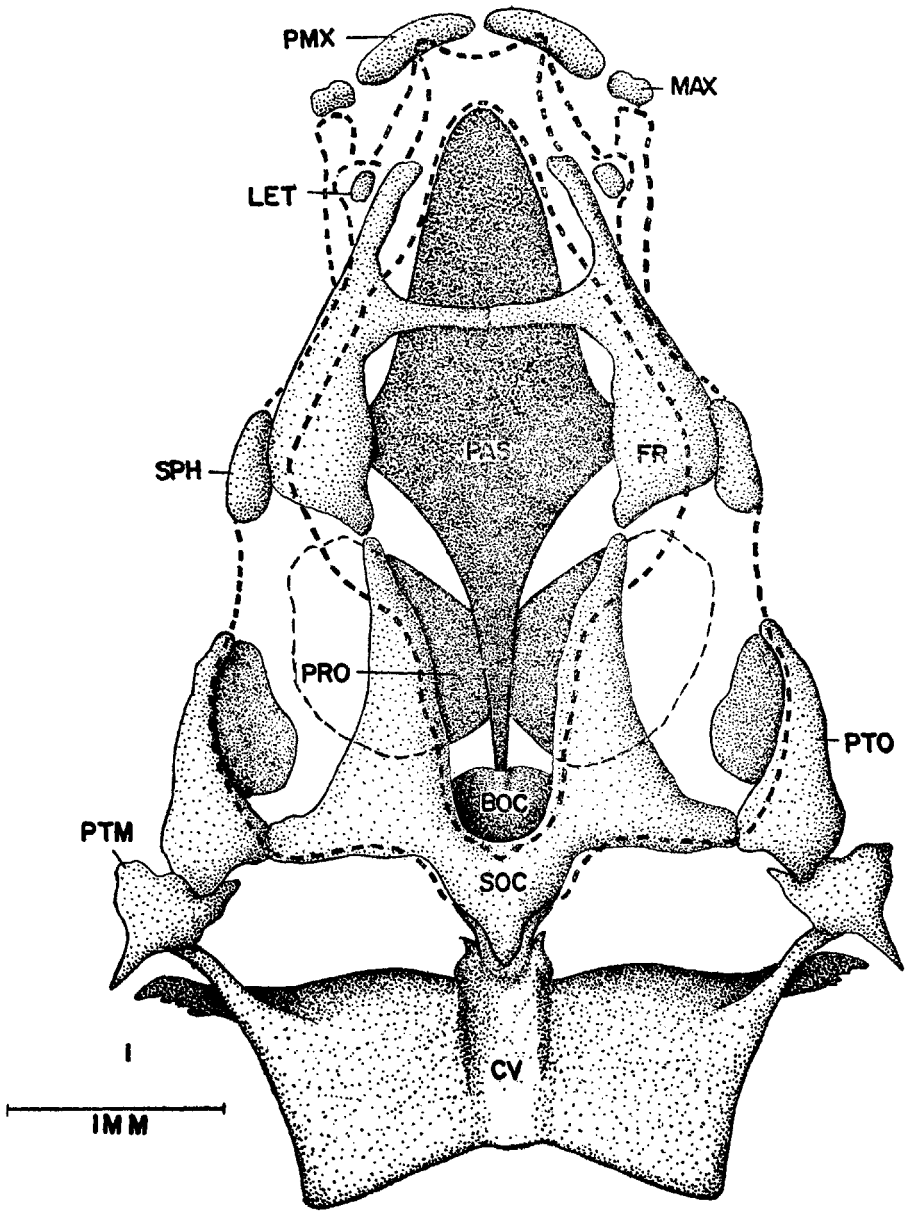
The ethmoid bone (Text-figs. 3, 4, 6, 7 and 9a, ETH) : The ethmoid bone forms the anterior terminal bone of the cranium. It is flat dorsally and anteriorly shows a pair of processes which can be recognised as the pre-ethmoid cornua. These cornua are quite evident in the chondrocranium (Srinivasachar, 1957*b*). The ethmoid ossification is seen as perichondral lamella of the lamina precerebralis in a chondrocranium of the 29 mm. stage and in the 33 mm. stage, the bone is almost completely ossified. I have not been able to see any separate membranous ossification associated with the perichondral ossification. Hence, I prefer to designate the bone as merely an ethmoid bone. This bone has been variously called by different authors without regard to the significance of the terminology used. Kindred (1919) described the bone as supraethmoid as done by Allis (1910) in Loricati. Anteriorly the ethmoid cornua extend over the premaxillae with which they are not connected. The ethmoid is connected by means of sutures laterally and ventrally with the lateral ethmoids and posteriorly with the frontals and it forms almost the anterior boundary of the anterior fontanelle.

The lateral ethmoids (Text-figs. 1, 3, 4, 6, 7 and 9a, LET) : The bone is developed in the region of the lamina orbitonasalis and the ossification is seen in the 21 mm. larva in the form of a small oval piece on the dorsal side of the lamina orbitonasalis. The bone therefore arises first as a perichondral ossification and in the adult skull each lateral ethmoid is a large bone having a prominent ventral process. It forms the posterior boundry for the nasal fossa. Dorsally the lateral ethmoid articulates with the ethmoid, mesially with the frontal and posteriorly with the supraorbital and frontal bones. The ventral process of the lateral ethmoid is connected by a piece of cartilage with the orbitosphenoid posteriorly and anteriorly with the ethmoid. Kindred (1919) described this bone as the ectethmoid in *Amiurus*. Both the olfactory nerve and superficialis branches of the trigeminal nerve pass through foramina in the lateral ethmoid ventrally.

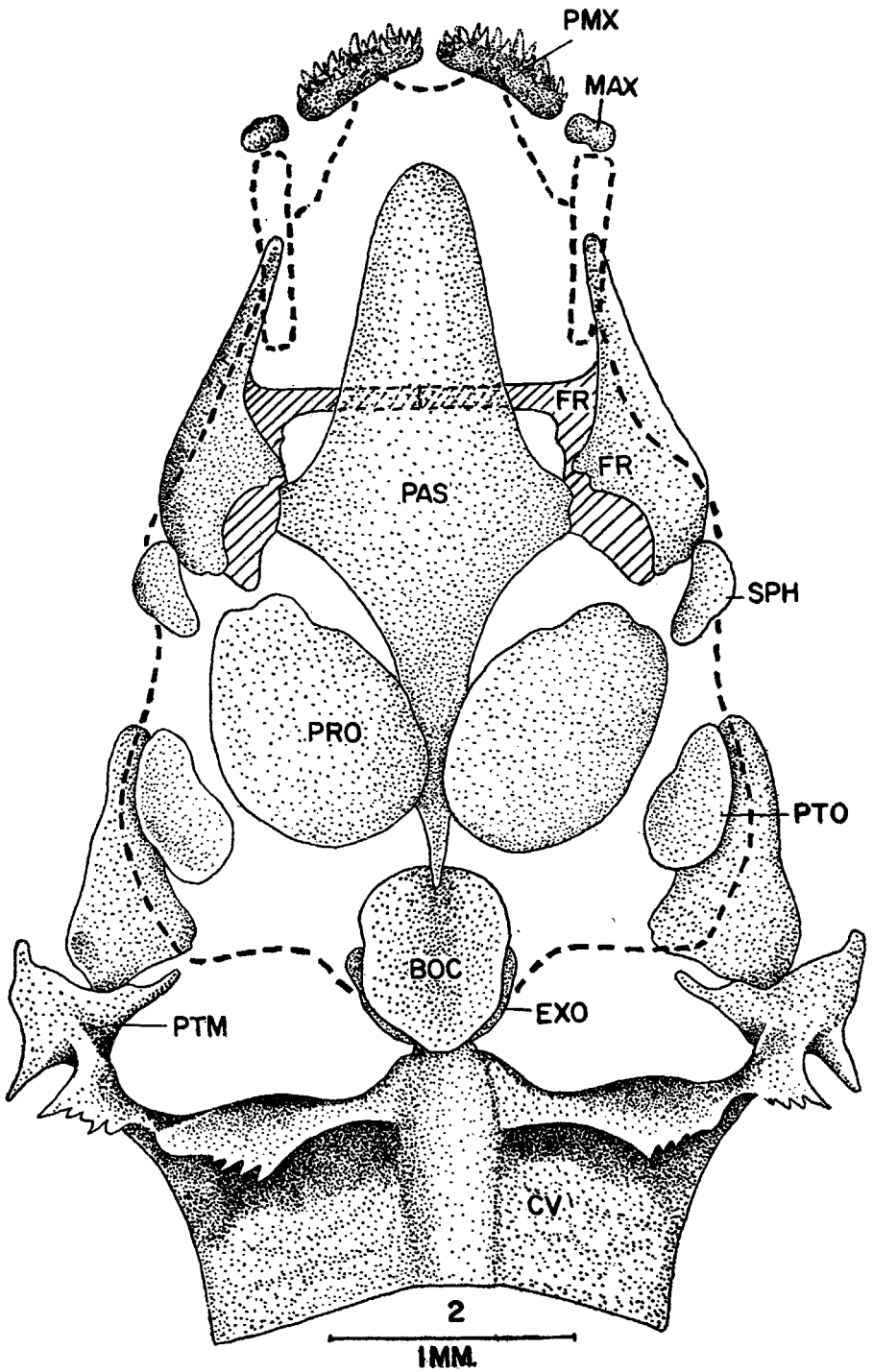
The nasals (Text-figs. 3, 4, and 6, NS) : These bones are developed on the dorsal side of the nasal fossae around the anterior end of the supraorbital sensory canal in the 33 mm. stage. Each nasal bone is in the form of a tube having anterior and posterior openings and forms a sort of incomplete roof for the nasal capsule. Dorsally the nasal bone is almost isolated from other bones but the sensory canal passes from the posterior tip of the bone through a piece of connective tissue into the frontal. The nasals of *Heteropneustes* resemble to a large extent those of Cyprinoids (Ramaswami, 1955). But nasals of the Characinidae (Sagemehl, 1885) are more like those in *Amia* (Segemehl, 1884) where the bone comes in contact with the ethmoid cartilage. In *Clarias* (George, 1954) the nasal is a flat bone fitting laterally into a groove in the ethmoid bone.

The prevomer (Text-figs. 4, 7 and 9a, PO) : The prevomer arises as an unpaired bone on the ventral surface of the anterior region of the skull. The bone is observed to develop in the 33 mm. stage behind the ventral extension of the ethmoid bone and in this stage the prevomerine teeth are still lacking. The median process of the prevomer in the above stage is very short. The teeth appear to develop in later stages independently of the bone. In the adult skull the prevomer is in the form of a T-shaped bone having a pair of prominent patches of teeth on the horizontal portion of the bone. The teeth are all of uniform shape and size. The vertical portion of the bone tapers posteriorly and fits into the anterior forked portion of the parasphenoid bone. Anteriorly the prevomer does not articulate with the premaxillaries.

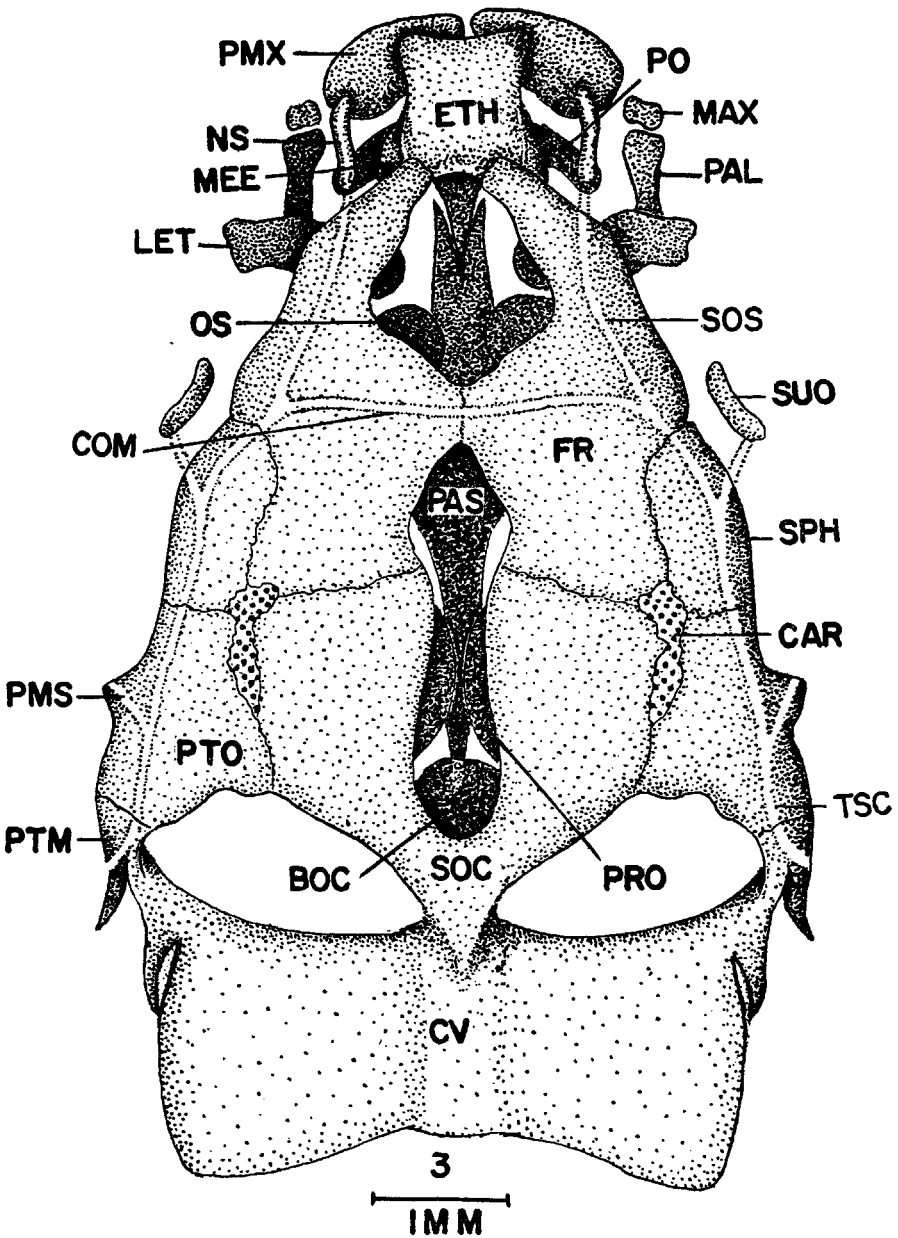
2. *The orbitotemporal region :* The region behind the orbit can be recognised as the sphenoid region. On the dorsal side there are a pair each of large frontals



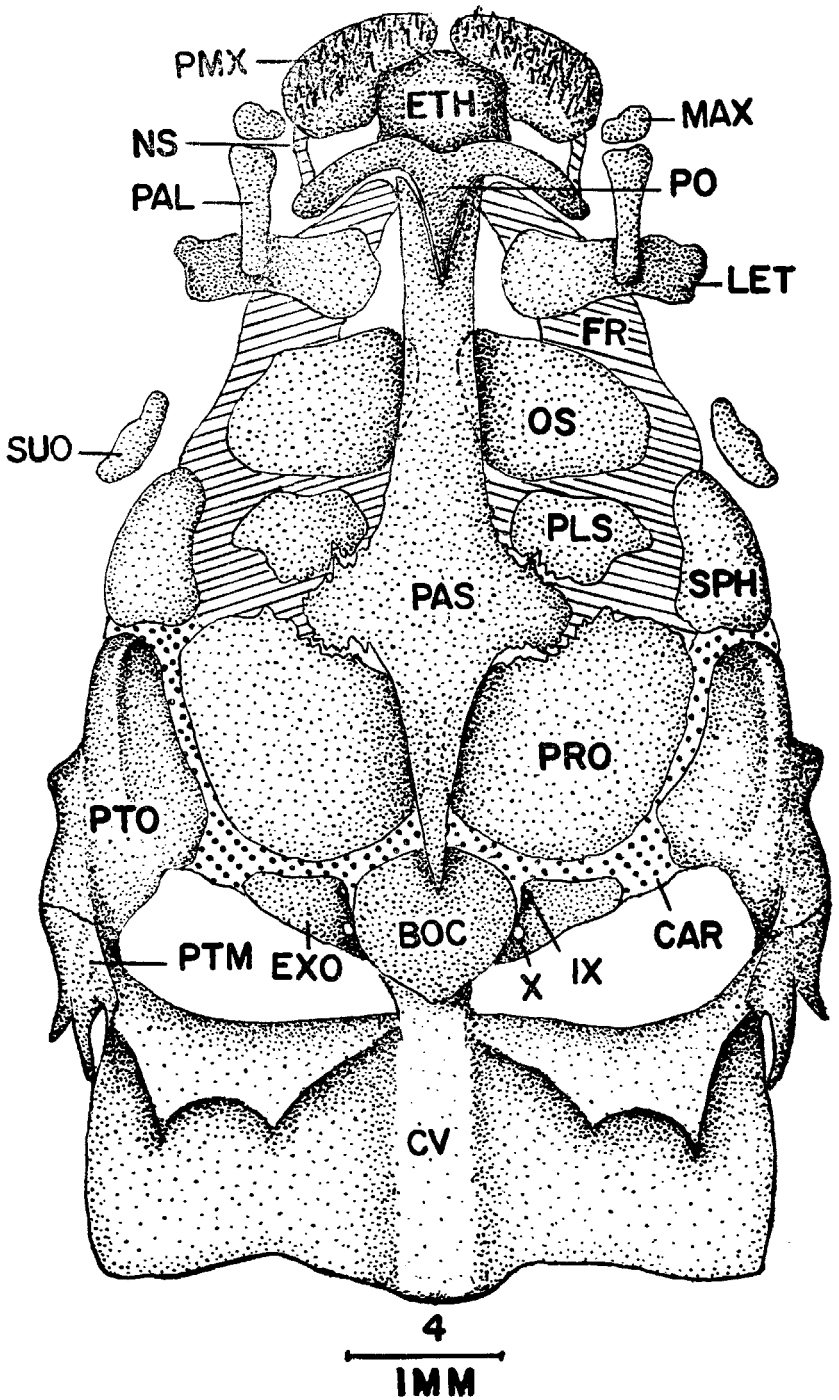
Text-fig. 1. Dorsal view of the skull of 21 mm. larva of *Heteropneustes fossilis* (Bloch). The outline of the chondrocranium has been shown by thick broken line.



Text-fig. 2. Ventral view of the same.



Text-fig. 3. Dorsal view of the skull of 33 mm. larva of *Heteropneustes fossilis* (Bloch).



Text-fig. 4. Ventral view of the same.

and supraorbitals with the sub-orbital series of bones and ventrally are present the parasphenoid, orbitosphenoids and pleurosphenoids.

The frontals (Text-figs. 1, 2, 3, 4, 6, 7 and 9a, FR) : The frontals are large bones arranged on either side of the mid-dorsal line of the skull. The frontal ossification is first seen in the 19 mm. larva forming a roof over the large fontanelle of the chondrocranium. The frontal ossifications in the 19 mm. and 21 mm. stages extend mesially in the form of tubular extension around the sensory canal at about the middle region of the chondrocranium and the ossifications are separated by a thin suture. Anteriorly the ossification extends to the level of the lamina orbitonasalis of the chondrocranium around the anterior extension of the supraorbital sensory canal. These ossifications are posteriorly separated from the ossification of the supraoccipital bone. In the 33 mm. stage the frontal ossification extends both anteriorly and posteriorly and the positions around the commissural sensory canal have also broadened thus dividing the dorsal fontanelle into an anterior broad and a posterior narrow fontanelle. The two frontal ossifications do not meet anteriorly in front of the anterior fontanelle at this stage. In the adult skulls the frontals are large flat bones with a small anterior fontanelle between them. Anteriorly they are connected suturally with the median and lateral ethmoids, laterally with the supraorbital and sphenotic bones and posteriorly with the pterotic and supraoccipital bones. Each frontal bone extends mesioventrally and is connected by sutures with the orbitosphenoid and pleurosphenoid of its side.

The parasphenoid (Text-figs. 1, 2, 3, 4, 7 and 9a, PAS) : This bone is a long flat bone extending on the ventral surface of the cranium. In the 19 and 21 mm. stages the parasphenoid ossification is seen ventral to the hypophysial fenestra of the chondrocranium. Anteriorly the ossification is round in shape and extends as far as the posterior end of the lamina precerebralis. In the middle region, the ossification extends as lateral processes and posteriorly tapers between the two prootic ossifications. In the 33 mm. larva the anterior end of the parasphenoid ossification shows a forked appearance and into this is fitted the posterior end of the prevomer. In the adult skull, the parasphenoid forms an almost ventral floor for the brain case and extends from the ethmoid to the posterior basioccipital bone. In the region of the optic foramen, the parasphenoid overlies the median portion of the orbitosphenoid bone. The middle portion of the parasphenoid possesses a pair of lateral pointed extensions which form the anterior boundary for the trigeminofacial foramen. The posterior end of the bone extends into the forked portion of the basioccipital bone.

The orbitosphenoid (Text-figs. 3, 4, 7 and 9a, OS) : It is an unpaired bone in the adult skull. However, it arises in the 33 mm. stage as paired perichondral ossifications in the preoptic roots of the orbital cartilages on either side of the anterior ends of the parasphenoid ossification. These paired ossifications are noticed behind the lateral ethmoids and in front of the optic foramen (Figs. 7, 9a, II). As development advances the perichondral ossification extends in the membrane across the anterior part of the hypophysial fenestra and fuses with the fellow of the opposite side to form a median bone dorsal to the parasphenoid bone. In the adult skull, the orbitosphenoid is a large bone attached ventrally by its median portion with the parasphenoid bone. The bone has laterally a pair of large processus which forms the side wall of the anterior part of the cranial cavity. Anteriorly these lateral portions of the orbitosphenoid are attached to the ventral extension of the lateral ethmoid, dorsally with the frontals and posteriorly with the pleurosphenoid bones.

A basisphenoid (suprasphenoid) bone is completely absent.

The pleurosphenoids (Text-figs. 4, 7 and 9a, PLS) : These are paired bones in the adult skull and in the 33 mm. stage the bones arise partly as perichondral ossification in the orbital cartilage and partly in the membrane of the side wall of the cranial cavity in front of the exit of the trigeminal nerve. Posteriorly these

ossifications are suturally connected with the lateral extensions of the parasphenoid bone. In the adult skull the pleurosphenoids are flat bones slightly bulged in the middle extending between the optic and trigeminal foramina. These bones form the side wall for the cranial cavity posterior to the orbitosphenoids. They are connected anteriorly with the orbitosphenoids, posteriorly with the lateral extensions of the parasphenoid and laterally with the sphenotic bones.

A myodome for insertion of the recti muscles is absent in *Heteropneustes* as in other siluroids.

The supraorbitals (Test-figs. 3, 4, 6 and 7, SUO): The bone arises for the first time in the 33 mm. stage in a membrane behind the orbit and anterior to the sphenotic ossification, surrounding the sensory canal branch given off from the supraorbital sensory canal. In the adult skull the supraorbital bone forms the dorsal boundary for the orbit and is connected by sutures anteriorly with the lateral ethmoid, laterally with the frontal and posteriorly with the sphenotic and intertemporal bones.

The suborbitals (Text-figs. 6, 7, AOR, LAC, SO1, SO2): This series consists of a chain of four bones forming the lower boundary of the orbit. None of them has appeared in the developing stages described. They appear to develop late in ontogeny around the suborbital sensory canal which continues from the supraorbital bone. The anterior of the four bones is a small oval piece lying in the connective tissue in the posterior part of the maxillary bone and could be designated as the antorbital (AOR) bone. Posterior to this antorbital bone is another one which is probably a lacrimal (LAC) in which the sensory canal ends, and the other two bones of the chain are large dorso-ventrally compressed ones and may be called the suborbitals (SO1 and SO2).

3. *The auditory region:* In the adult skull this region is formed by the prootics, sphenotics, pterotics and associated with these are the intertemporal bones. The latter bones are completely excluded from the auditory capsules.

The prootics: (Text-figs. 1, 2, 3, 4, 6, 7 and 9a, PRO): These bones are fairly large ones forming the floor and the lateral wall of the cranial cavity behind the pleurosphenoids and on either side of the median parasphenoid. The prootic bones arise as flat perichondral ossifications in the 19 mm. and 21 mm. stages in the anterior part of the parachordals and ventral portion of the otic capsules behind the hypophysial fenestra. Gradually in the 33 mm. larva the prootic ossifications extend inwards to meet the fellow of the opposite side dorsally to the posterior part of the parasphenoid bone. In the adult skull each prootic extends from the trigeminal (Text-figs. 7, 9a, V) to the glossopharyngeal foramina (IX). The bone has an irregular outline and is not pierced by any nerve or blood vessel. Anteriorly the prootic bone is connected by dovetails with the parasphenoid, laterally it is firmly connected with ventral extensions of the sphenotic and pterotic, and posteromesially with the exoccipital bones. Externally the bone is smooth and internally accommodates the otolith (Text-fig. 7, OT) which is visible through the bone.

The sphenotics (Text-figs. 3, 4, 6, 7 and 9a, SPH): These are situated in the postero-lateral region of the frontal bones. They appear comparatively to be small bones. In the 21 mm. stage the bones are seen as perichondral ossification in the region of the anterior semicircular canal of the auditory capsule. In the 33 mm. stage the ossification extends to the frontal anteriorly, to the pterotic posteriorly and to the prootics ventrally. In the adult skull the sphenotic shows a ventral extension forming a sort of anterior boundary for the auditory capsule. The facial foramen (Text-figs. 7, 9a, VII) is noticed between the ventral extension of the sphenotic and prootic bones.

The pterotics (Text-figs. 3, 4, 6, 7 and 9a, PTO): These bones are situated on either side of the median supraoccipital and are posterior to the sphenotic bones. In the 21 mm. larva the pterotics appear as perichondral ossifications in the region

of the posterior semicircular canal and dorsal to each perichondral ossification is seen a membranous ossification around the sensory canal, probably of the supratemporal co-ossifying with it. I have not been able to see an independent ossification of the supratemporal but it appears to develop along with the perichondral ossification. I have therefore not given a compound name to the pterotic bone. Further development of the bone is seen in the 33 mm. stage when dorsally the pterotic bone meets anteriorly the sphenotic and posteriorly the post-temporal. In the adult skull the pterotic bone is an extensive bone surrounded by the sphenotic, intertemporal, post-temporal and supraoccipital bone. Ventrally the pterotic has an extension forming the posterior and lateral portion of the auditory capsule probably taking the place of the opisthotic bone.

The epiotic and opisthotic bones are absent in *Heteropneustes*.

The intertemporals (Text-figs. 6 and 7, INT) : These have been named by a number of previous authors including Gregory (1933) and George (1954), as the dermal representative of the sphenotic bone. The intertemporal is not developed in any stages earlier than the adult skull. In the adult skull the bone is completely excluded from the otic capsule and is found between the supraorbital and the posttemporal bones. The intertemporal appears to develop outside the auditory capsule in the membrane around the sensory canal branch given off from the supraorbital sensory canal (Text-figs. 3, 6, SOS) in the pterotic bone. It is attached suturally with the postorbital anteriorly, posteriorly with post-temporal and laterally with sphenotic and pterotic bones.

4. *The occipital region :* This region of the adult skull is formed as in other teleosts by four bones ; dorsally by a large supraoccipital, ventrally by the basiccipital and laterally by a pair of exoccipital bones around the foramen magnum.

The supraoccipital (Text-figs. 1, 3, 6, and 9a, SOC) : The bone is a fairly large dorso-median bone forming the posterior end of the adult skull. In the 19 mm. and 21 mm. stages the supraoccipital ossification is seen in the region of the tecti synoticum and posterius of the chondrocranium and extends anteriorly on either side of the postero-lateral border of the dorsal fontanelle. The ossification extends anteriorly to meet the frontals, laterally to meet the supratemporal-pterotic ossifications and posteriorly extends as a supraoccipital spine. In the 33 mm. stage the ossification has further developed anteriorly and have joined the frontals on either side of a narrow posterior fontanelle, but separated from the pterotic by a strip of cartilage. The entire supraoccipital bone is formed by a single centre of ossification and a separate parietal ossification is not noticed in any of these stages. The supraoccipital has extended into the place of the parietal bone. In the adult skull the supraoccipital retains a very small posterior portion of the dorsal fontanelle in its posterior end. The bone has a long pointed spine (Text-figs, 6, 7 and 9a, SPO) almost equal in length of the entire bone. This spine extends on the dorsal surface of the united vertebrae (complex vertebrae).

The basioccipital (Text-figs. 1, 2, 3, 6, 7 and 9a, BOC) : This bone forms the posterior end of the cranium on the ventral surface. It arises in the 19 mm. and 21 mm. stages as an ossification in the posterior part of the parachordal forming the floor for the saccular recesses. In these stages and also in the 33 mm. stage the bone is almost of a triangular shape and the anterior portion overlaps the posterior pointed extension of the parasphenoid bone. Gradually in the adult skull the bone becomes extensive and possesses anteriorly a deep wedge into which fits the posterior end of the parasphenoid. Antero-laterally, the basioccipital is connected suturally with the prootics and postero-laterally with the exoccipitals. Internally the bone possesses a cavity for the accommodation of the utriculus (Text-fig. 9a, OTU) but externally the bone is smooth. The posterior end of the bone articulates with the anterior end of the centrum of the complex vertebrae (Test-figs. 1, 2, 3, 6, 7 and 9a, CV).

The post-temporals (Text-figs. 1, 2, 3, 4, 6 and 7, PTM) : These bones primarily belong to the pectoral girdle. The bone arises in the 21 mm. stage as an ossification in the region outside the postero-lateral end of the auditory capsule of the chondrocranium and at this stage it is connected with the posterior end of the supratemporal-pterotic ossification. In the 33 mm. stage the ossification extends anteriorly and completely becomes connected with the posterior end of the pterotic bone. This ossification surrounds the portion of the anterior end of the lateral line sensory canal entering the skull. In the adult skull the post-temporal bones are firmly attached to the postero-lateral ends of the skull and possess posteriorly processes. Ventrally the post-temporal bone is connected with the antero-lateral end of the bony capsule (complex vertebrae). Anteriorly the bone is suturally connected with the intertemporal and pterotic bones.

Lateral line sensory canal : The lateral line sensory canal entering the skull passes through the post-temporal bone and extends anteriorly in the supratemporal-pterotic bone as the temporal sensory canal (Text-figs. 3, 6, TSC). This canal gives off the preopercle-mandibular sensory canal branch (Text-figs. 3, 5, 6, PMS) in the supratemporal-pterotic bone which passes through the inter-temporal into the preopercle bone. The temporal sensory canal continues anteriorly as the supraorbital canal (SOS) in the sphenotic bone and gives off the infraorbital sensory canal (Text-figs. 6, SC) which extends into the suborbitals. Further the supra-orbital sensory canal passes forwards in the frontal and extends anteriorly into the nasal. The two supraorbital canals are connected behind the anterior fontanelle by means of a commissural sensory canal (COM). The suborbital branch passes through the suborbitals and in the anterior bone of the chain, the lacrimal.

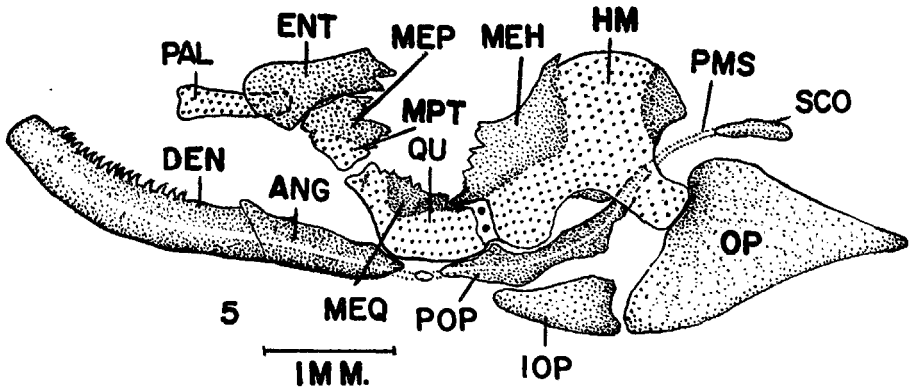
B. *The jaws and the hyobranchial skeleton.*

1. *The upper jaw :* In the osteocranium the independent part of the palato-quadratebar or the pterygoid process of the chondrocranium is ossified completely without any membranous extension, into a palatine bone (Text-figs. 3, 4, 5 and 7, PAL). The palatine is in the form of a cylindrical rod slightly swollen at the anterior end and articulates anteriorly with the maxilla. The other ossifications of the palatoquadrate can be clearly made out in the 33 mm. stage. The quadrate ossification (Text-figs. 5, 8, QU) can be seen in the quadrate portion of the hyomandibula of the chondrocranium and associated with it, is a membranous extension dorsally (Text-fig. 5, MEQ) and ventrally it articulates with the lower jaw. A piece of the original cartilage (Text-fig. 8, CAR) between the ossified hyomandibula (HM) and the ossified quadrate is left unossified and persists even in the adult skull. Anterior to the quadrate ossification, is the metapterygoid (MPT) which is also partly perichondral and partly membranous (Text-fig. 5, MEP) and closely attached to the anterior end is another small plate-like bone which is a completely membranous ossification. The latter bone probably represents the entopterygoid bone (ENT). The palatine bone is completely free from the entopterygoid articulation indicating its original independent chondrification of the chondrocranium.

An ectopterygoid bone seen in other teleosts is absent in *Heteropneustes.*

The premaxillae and maxillae which are in the anterior end of the upper jaw are membrane bones. *The premaxillaries :* (Text-figs. 1, 2, 3, 4, 6, 7 and 9a, PMX). These form the anterior end of the upper jaw on each side. Each premaxilla arises in front of the lamina precerebralis of the chondrocranium fairly early in the development and in the 21 mm. larva the bone is already developed in the form of a plate articulating ventrially with the ethmoid cornu of the lamina precerebralis. The ventral surface of the bone is covered by teeth which are pointed and of uniform size. In the 33 mm. stage the premaxillaries show thin posterior extensions which are at this stage poorly ossified. The bones in the adult skull are quite large ones with prominent posterior processes which form a sort of osseous floor for the nasal

sacs. Ventrally they are connected with the osseous ethmoid cornua of the ethmoid bone. Mesially the bones are connected by connective tissue and laterally they are connected with the maxilla.



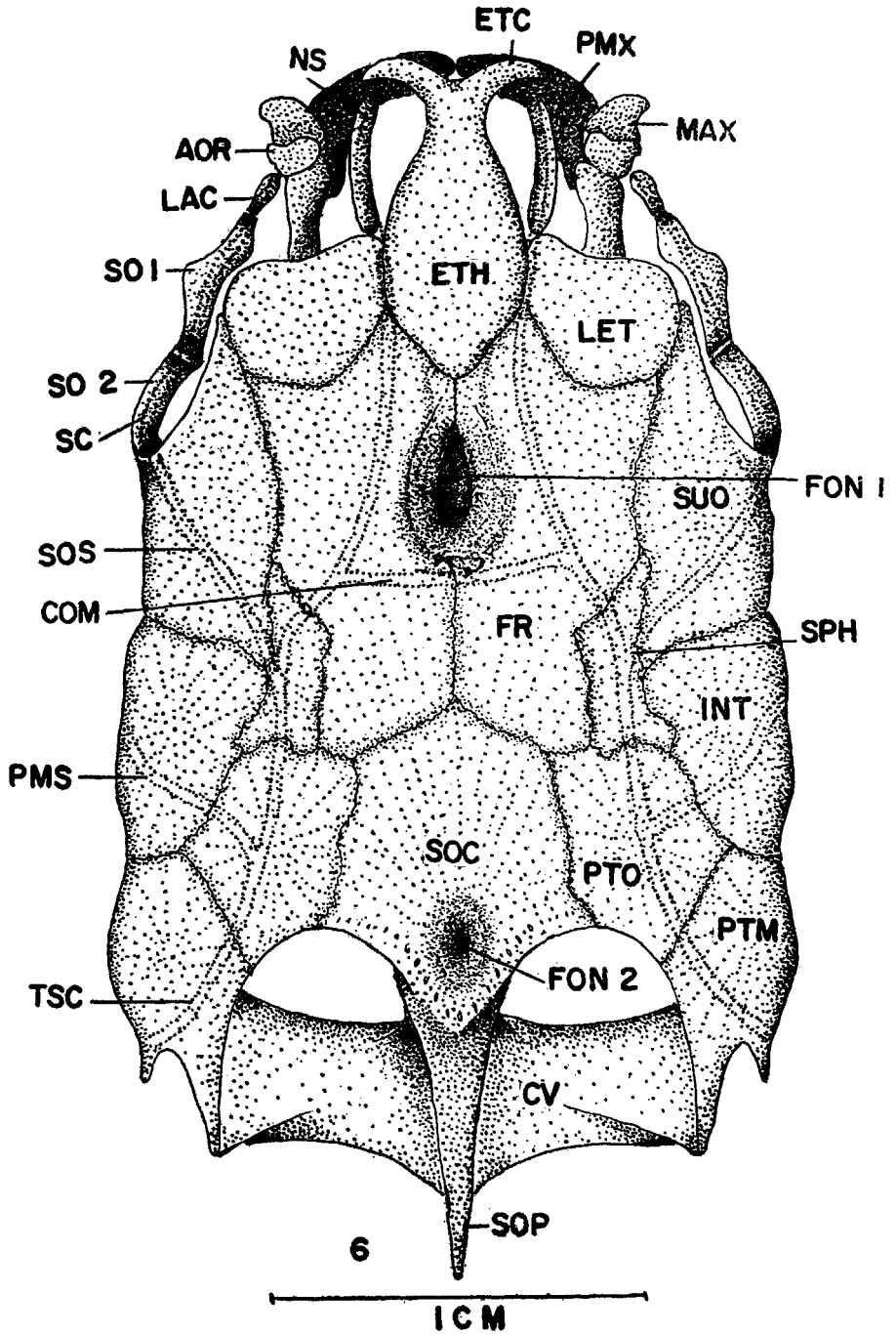
Text-fig. 5. Outer view of the left side of the upper and lower jaws with opercular bones of 33 mm. larva of *Heteropneustes fossilis* (Bloch). The perichondral ossifications are shown as thicker stipled areas.

The maxillaries (Text-figs. 1, 2, 3, 4, 6, 7 and 9a, MAX) : The maxillary bone is one of the earliest to develop in the osteocranium. In the 8 mm. larva the maxilla arises as a tiny ossification in front of the pterygoid process of the chondrocranium. In the 21 mm. larva the maxilla is already well formed postero-laterally to the premaxilla on each side. In the 33 mm. stage, when the palatine bone is formed the maxilla articulates with it by means of a hollow depression in the anterior end of the palatine. In the adult skull each maxilla is a small toothless bone which is slightly irregular in shape and supports the maxillary barbel anteriorly. These maxillaries form lateral margins of the upper jaw.

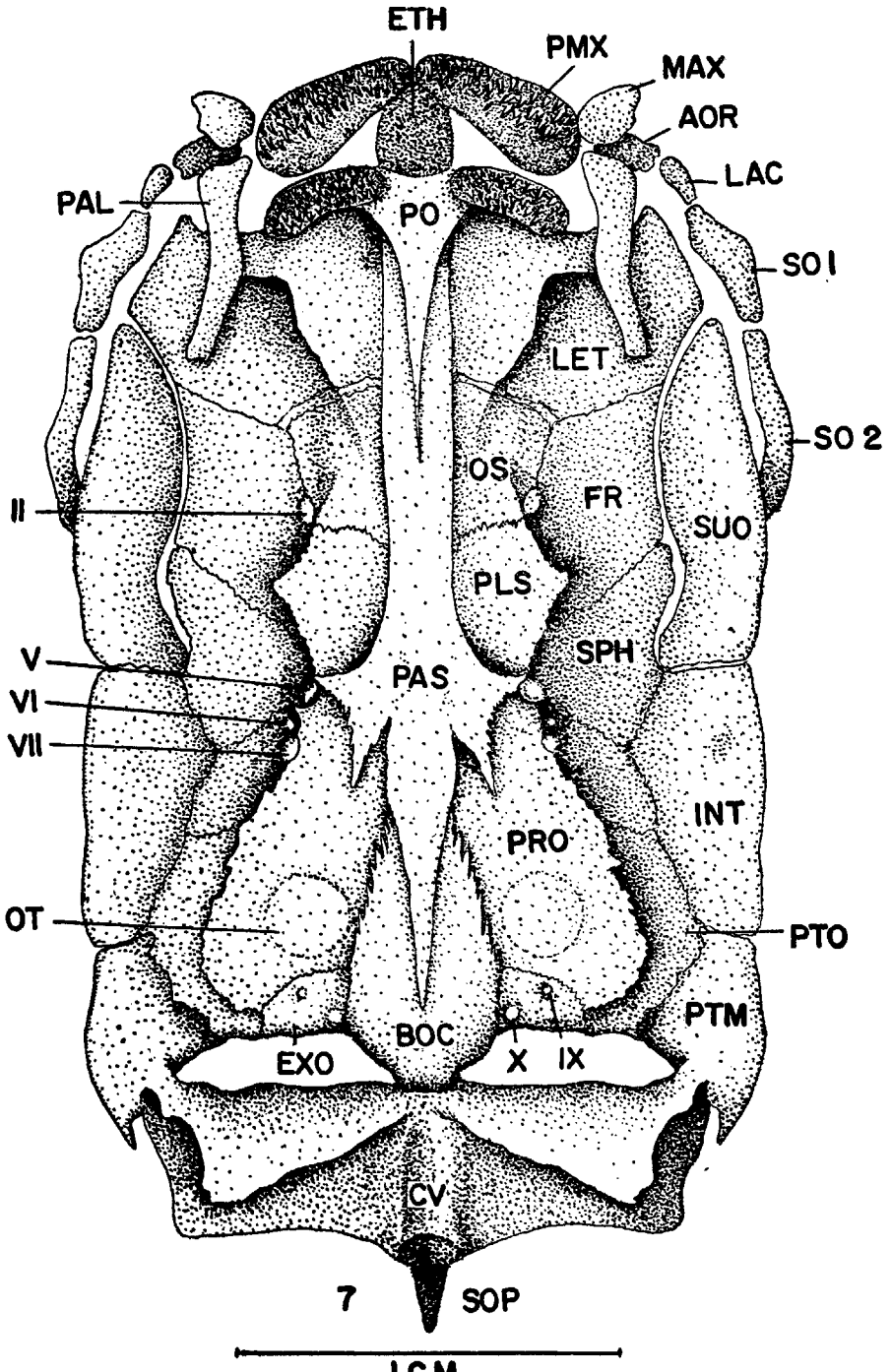
The lower jaw : The lower jaw in the adult skull consists of two halves connected mesially by a strip of connective tissue. Each half of the lower jaw consists of two bones, an anterior dentary (Text-figs. 5, 8, DEN) and a posterior angular (ANG) (articular of other authors) which later articulates with the quadrate. Both dentary and angular develop as completely membrane bones around the original Meckel's cartilage of the chondrocranium. No part of the cartilage is invaded by ossification during the development.

The dentary is fairly stout bone, anterior broad and flat and dorso-medially it possesses a number of villiform teeth. The angular bone is more or less of the same size as the dentary and has a socket posteriorly for articulation with the quadrate. Mesially the bone shows a depression in which the persisting Meckel's cartilage could be made out. A retroarticular bone seen in other teleosts is absent in *Heteropneustes*.

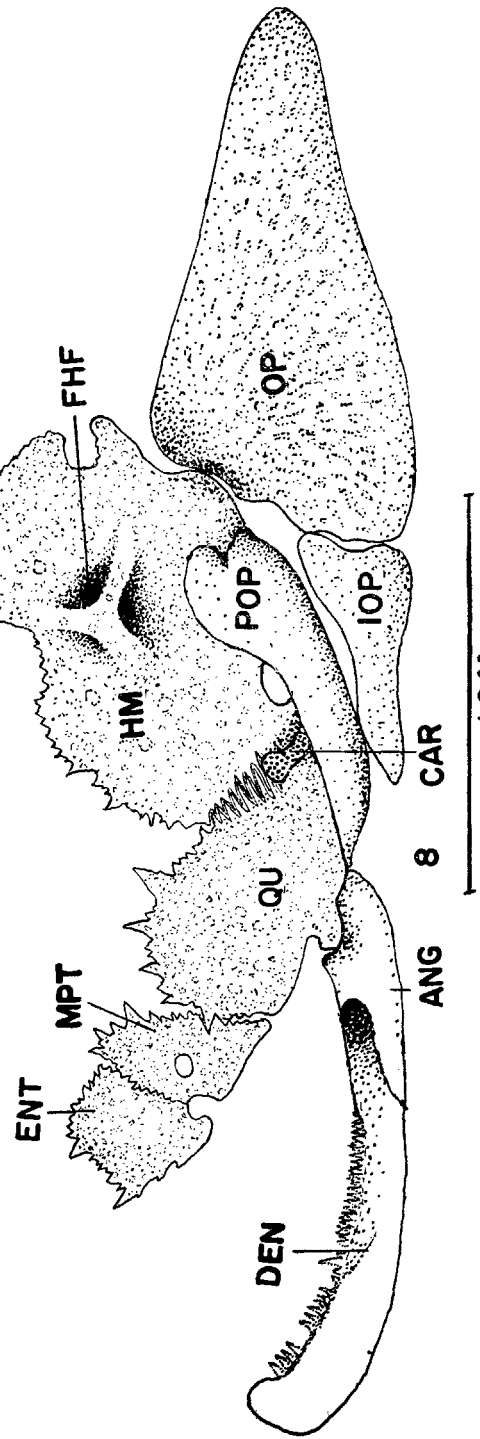
3. *The hyoid arch :* In the hyoid arch of the osteocranium, the hyomandibula which was originally fused with the quadrate in the chondrocranium, is ossified independently of the quadrate in the 33 mm. stage. The hyomandibular ossification in this stage is almost complete and possesses membranous extension (Text-fig. 5, MEH) dorsally and mesially. Ventrally the hyomandibula has a narrow process by which it articulates with the opercle bone (Test-fig., 5, 8, OP). The hyomandibula in the adult skull is a large irregular bone and articulates on the ventral surface of the sphenotic bone. It possesses laterally a number of ridges to which muscles are attached. Mesially a foramen for the exit of the hyomandibular branch of the facial nerve (Text-fig. 8, FHF) is noticed in the hyomandibula.



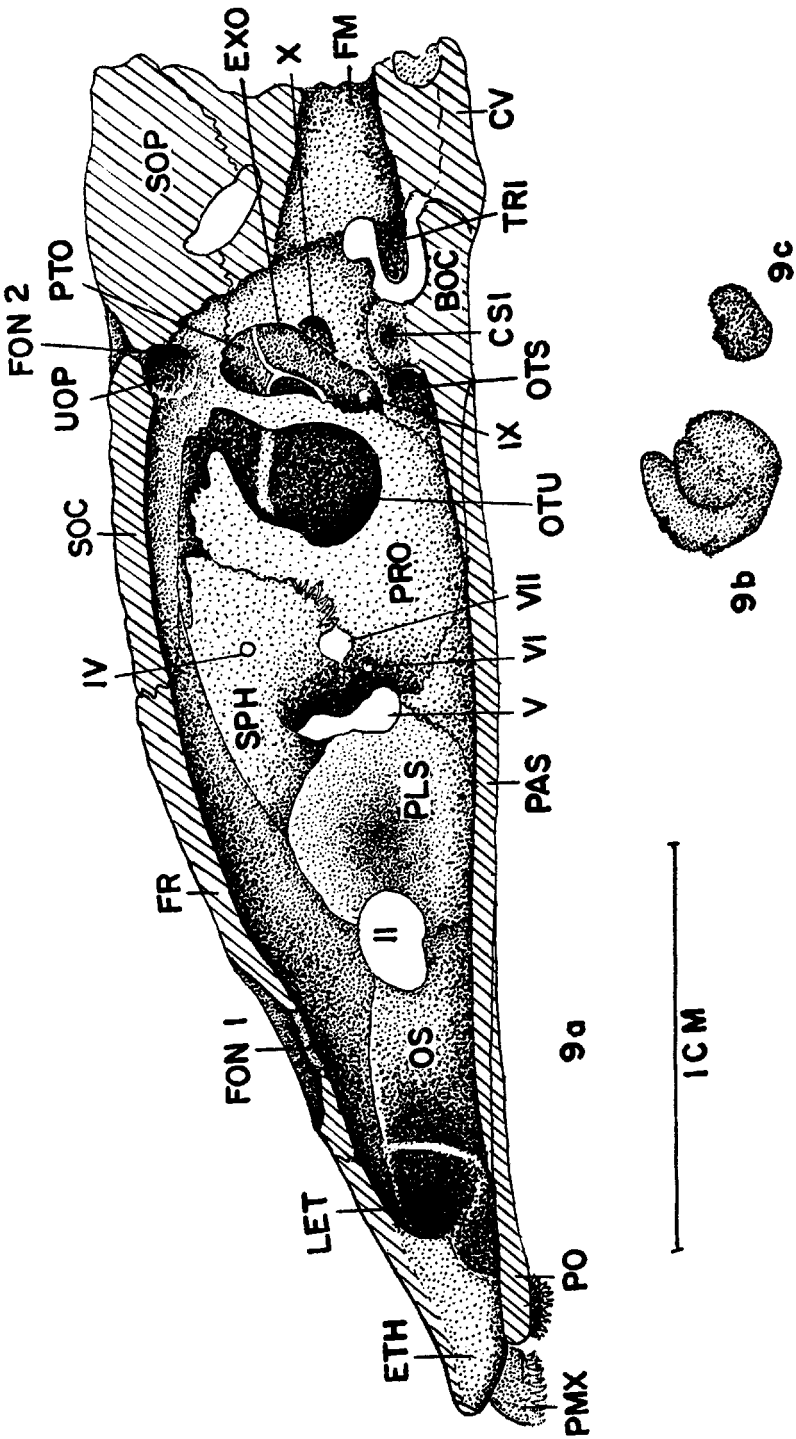
Text-fig. 6. Dorsal view of the adult skull of *Heteropneustes fossilis* (Bloch).



Text-fig. 7. Ventral view of the same.



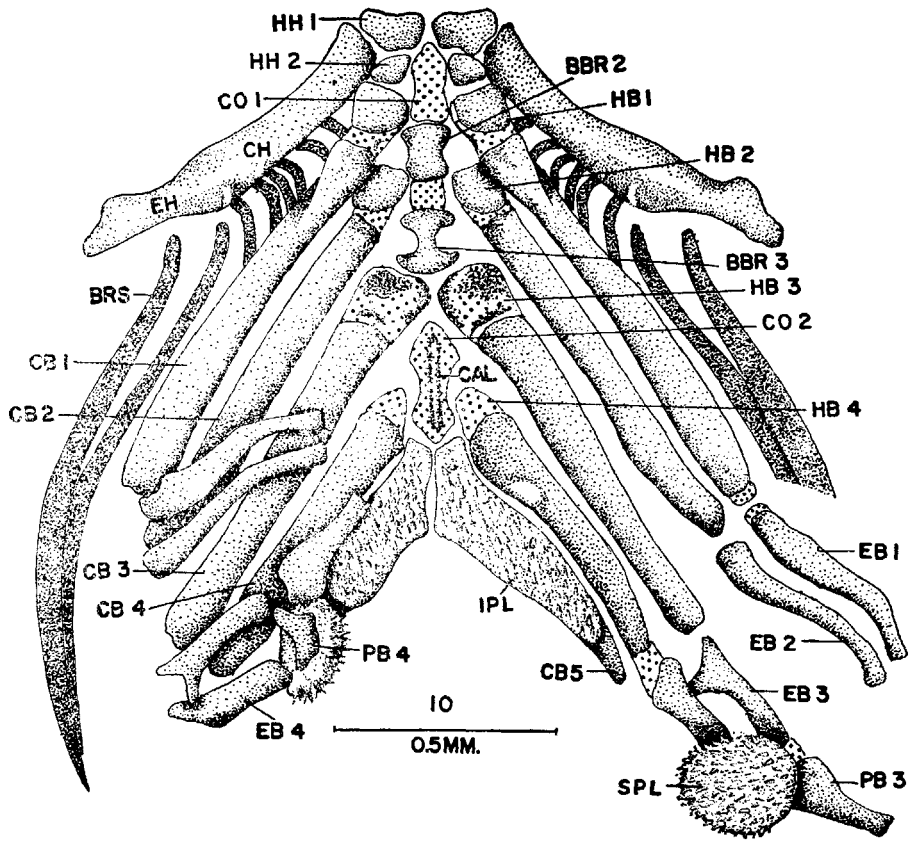
Text-fig. 8. Lateral view of the upper and lower jaws with the opercular bones of the adult skull of *Heteropneus tes fossilis* (Bloch).



Text-fig. 9a. Sagittal sectional view of the adult skull of *Heteropneustes fossilis* (Bloch).
9b. Otolith of the utriculus. 9c. Otolith of the sacculus.

It is immovably connected anteriorly with the quadrate by a piece of cartilage and also by sutures and along the ventral border, the preopercle bone is firmly attached to it. A symplectic bone is absent.

The hyoid cornu of the adult skull consists of two pieces of hypohyals (Text-figs. 10, 11, HH1, HH2), ceratohyal (CH), an epihyal (EP) and a parahyoid (Text-fig. 11, PHY) or urohyal on the mid-ventral side of the two rami of the hyoid cornua. Closely associated with hyoid cornua are the branchiostegal rays (BRS).



Text-fig. 10. Dorsal aspect of the hyobranchial apparatus of the adult *Heteropneustes fossilis* (Bloch). One side has been extended to show the structures clearly.

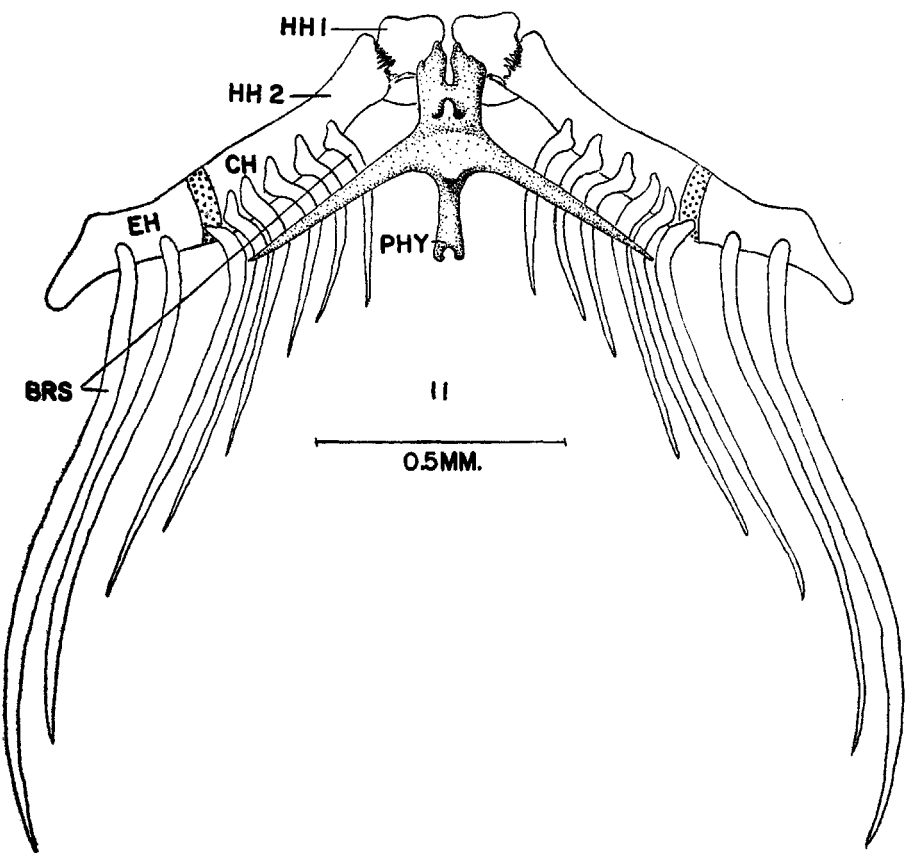
The hypohyals : The hypohyals on each side consist of the hypohyal anterior and hypohyal posterior, which are separated by a piece of unossified cartilage. The hypohyals are connected by ligaments with the corresponding bones of the other side. The anterior hypohyal is a stout piece, connected ventrally with the ceratohyal by means of sutures. The posterior hypohyal is a smaller triangular piece and lies close to the lower side of the ceratohyal. The two hypohyals are ossifications in the case of the original hypohyal cartilage which are not demarcated from the ceratohyal in the chondrocranium.

The ceratohyals : Each ceratohyal is a long bone showing a ridge on the ventral side and is flattened laterally. Anteriorly the ceratohyal is suturally connected with the hypohyal anterior and posteriorly it is connected with the epihyal by a thick piece of cartilage. On the ventral side the bone is slightly flat and gives attachment to the five branchiostegal rays.

The epihyals : Each epihyal is an ossification in the posterior end of the ceratohyal cartilage. The bone is a short piece, thick anteriorly and tapering posteriorly. The dorsal half of the epihyal is continuous with the ceratohyal and it is only in the lower half of the dorsal and ventral sides, the bone is separated from the ceratohyal by cartilage. The tapering posterior end of the epihyal is connected by a tiny piece of cartilage with the hyomandibula. The ventral side of the epihyal gives attachment to the two posterior branchiostegal rays.

A bony interhyal is absent. In the chondrocranium (Srinivasachar, 1957*b*) the interhyal which is continuous with the ventral side of the hyomandibula, connects the ceratohyal. In the ossified skull the interhyal continues to remain cartilaginous connecting the epihyal with the hyomandibula.

The parahyoid : The parahyoid (urohyal) bone is situated in the midventral line of the hyoid cornua between the hypohyals of the two sides. The parahyoid has no cartilaginous predecessor in the chondrocranium. It is a peculiarly-shaped bone connected on the ventral side to the hypohyals by means of ligaments. The bone has four rays (arms), an anterior, two lateral and a posterior arms. The anterior arm is stout having deep notch and the two portions of it are attached to the ventral side of the anterior hypohyals. The two lateral arms are fairly long pointed ones and extend ventrally obliquely on the branchiostegal rays attached to the ceratohyal. The posterior arm is a narrow portion and is bifid posteriorly-



Text-fig. 11. Ventral aspect of the hyoid cornua and the parahyoid of the adult *Heteropneustes fossilis* (Bloch).

The branchiostegal rays : There are altogether eight pairs of branchiostegals which are long pointed rays attached to the ventral surface of each hyoid cornua. These branchiosts gradually increase in length from the anterior to the posterior end. The anterior branchiostegal ray is the smallest and the posterior one is the longest of the eight rays. The anterior five branchiostegal rays are attached to the ventral surface of the ceratohyal, and the sixth ray is attached to the cartilage separating the ceratohyal from the epihyal. But the seventh and the eighth rays are attached to the ventral side of the epihyal. The eighth ray which is the longest of the lot is in the form of a large flat bone attached to the mesial side of the opercle.

The branchial arches : There are five branchial arches supporting the gills. The branchial arches are not completely ossified, but the cartilage of the chondrocranium persists in several regions. The median copula 1 (Text-fig. 10, CO1) of the chondrocranium (Srinivasachar, 1957*b*) shows two pieces of ossification representing the basibranchs, one of them between the first and second branchial arches and the other between the second and third. The rest of the portions of the original copula 1 and copula 2 (CO2) of the chondrocranium persists as unossified cartilages. The first two arches are not complete as they do not possess pharyngobranchs but the third and fourth arches are also incomplete in the absence of completely ossified hypobranchs. The fifth arch as in other teleosts is represented by ceratobranchs with patches of inferior pharyngeal teeth (IPL). In connection with the pharyngobranch of the third and fourth arches oval dentigerous patch, —the superior pharyngeal teeth (SPL) is noticed.

The basibranchs : The anterior portion of the original copula 1 of the chondrocranium persists as short piece of cartilage between the posterior ends of the hyoid cornua and the first branchial arches. The remaining portion of the copula is ossified into two pieces of bones, which may be labelled as basibranch 2 and 3 (Text-fig. 10, BBR2, BBR3) in order to differentiate between the cartilaginous and ossified portions. It may be assumed that the anterior cartilaginous piece or the copula 1 represents the fused basihyal and the first basibranch. The ossified copula represents the second basibranch. A small piece of original cartilage can be made out between the second and third basibranchs. The third basibranch is a small hour-glass shaped bone and the third branchial arch arises from the posterior end of this basibranch. Posteriorly in line with the third basibranch is a piece of cartilage biconcave laterally and is related to the fourth branchial arch. This piece of cartilage is the unossified basibranch of the fourth arch and represents the second copula (CO2) of the chondrocranium. Slight ossification (CAL) can be made out on the ventral compressed side of the cartilaginous second copula.

The hypobranchs : (Text-fig. 10, HB1–HB4) The hypobranchs of the first and second branchial arches are triangular pieces of bones connected with the respective ceratobranchs by the reminiscent cartilage. The first hypobranch is connected with the posterior end of the cartilaginous first copula, whereas the second hypobranch is at the postero-lateral end of the ossified second basibranch. The hypobranchs of the third arch are large flat pieces of cartilages showing slight ossifications in them. The cartilaginous hypobranchs extend inwards behind the third basibranch. The fourth hypobranch is probably represented as a cartilaginous piece with no ossifications and continues posteriorly as the bony fourth ceratobranch. The hypobranch arises from the postero-lateral region of the second copula. The hypobranchs are not traceable in the fifth branchial arch.

The ceratobranchs : (Text-fig. 10, CB1–CB5) All the five branchial arches show well ossified ceratobranchs. The ceratobranchs of the first three branchial arches are fairly long slightly flattened bones, and are connected posteriorly with the respective epibranchs. The ceratobranchs of fourth and fifth arches are almost of equal length and the fourth ceratobranch is connected to its epibranch by a thick piece of cartilage. The fifth ceratobranch has a thick patch of villiform

teeth of uniform size on the dorsal aspect forming the inferior pharyngeal teeth. I have not been able to see the actual origin of the teeth. The fifth ceratobranchs are situated in the posterior end of the second copula.

The epibranchs : (Text-fig. 10, EB1–EB4) The first four branchial arches possess distinct ossified epibranchs. The epibranchs of the first two branchial arches are comparatively short bent rod-like bones placed at an angle of more or less 60° to the respective ceratobranchs. These epibranchs are connected by cartilage at the ceratobranchs end while the other end is free of cartilage. The third epibranch is a small cylindrical bone having a pair of processes posteriorly, the lower process extends over the posterior end of the fourth epibranch. The upper process is attached to the ceratobranch. The fourth epibranch is a slightly curved piece connected to its ceratobranch by a strip of cartilage. Anteriorly the third and fourth epibranchs are connected to their pharyngobranchs.

The pharyngobranchs : (Text-fig. 10, PB 3–4) The first two branchial arches do not have pharyngobranchs as noticed in the early development of the chondrocranium (Srinivasachar, 1957*b*). The third and fourth branchial arches possess distinct ossified pharyngobranchs. The third pharyngobranch is a club shaped bone ; the swollen end of the bone is connected to the third epibranch by a piece of cartilage and the narrow portion extends anteriorly. The fourth pharyngobranch is a smaller bone situated below the third pharyngobranch. In the chondrocranium the third and fourth pharyngobranchs are represented by a fused piece of cartilage.

A large oval dentigerous plate, the superior pharyngeal plate is noticed on the ventral surface of the third and fourth pharyngobranchs. The dentigerous plate appears to develop independently to the pharyngobranchs. The pharyngeal plate bears uniform pointed teeth and the plate extends over the epibranchs of the third and fourth branchial arches.

The order of appearance of bones in the osteocranium of *Heteropneustes* is as follows. The bones have been arranged according to their origin (cartilage or membrane bones).

Stage	Type of ossifications	
	Perichondral ossification (Cartilage bones)	Membranous ossification (Membrane bones)
8 mm. stage		Maxilla.
12 mm. stage		Premaxilla.
19 mm. stage	Supraoccipital, Prootic, Basioccipital, Quadrate.	Parasphenoid, Frontal*, Angular*, Dentary*.
21 mm. stage	Exoccipital, Laternal ethmoid, Sphenotic*, Pterotic with supra-temporal extension*.	Posttemporal*.
29 mm. stage	Ethmoid.	
33 mm. stage	Pleurosphenoid, Orbitosphenoid, Hyomandibula, Metapterygoid, Palatine.	Prevomer, Supraorbital*, Nasal*, Preopercle*, Interopercle, Entopterygoid.
49 mm. stage and the adult skull.		Intertemporal*, Suborbitals*.

* The bones develop in association with sensory canal.

Discussion

The skull of *Heteropneustes* as in other catfishes (Gregory, 1933) shows a number of specialised features. The roof of the skull is flattened forming a cephalic shield which is actually formed by the large supraorbitals, intertemporals, pterotics and supratemporals. The skull is further broadened in *Heterobranchus* (Gregory, 1933) and *Clarias* (George, 1954).

In describing the bones of the ethmoid region of siluroid skull, the nomenclature employed is at variance. McMurrich (1884) in describing the skull of *Amiurus* called the ethmoid bone a mesethmoid ; later Kindred (1919) after studying the development of the bone in the same fish, employed the term supraethmoid as he was able to see a dermal and a perichondral ossification, following the nomenclature of Allis (1910) who described the bone in Loricati. Gregory (1933) in his figures of *Heterobranchus* and *Chrysichthys* has labelled the ethmoid bone as the dermethmoid and George (1954) has followed the same terminology in *Clarias*. In the development of *Heteropneustes*, I have observed that this bone arises completely as a perichondral ossification of the lamina precerebralis of the chondrocranium (Srinivasachar, 1957*b*) and it is only in later stages (33 mm. and 49 mm. stages) that this bone extends into the surrounding membrane. Hence I prefer to designate the bone merely an ethmoid as done by Goodrich (1909) and de Beer (1937). However, Bhimachar (1933) in describing the skull of some of the Indian catfishes has used the term supraethmoid. In the development of the osteocranium in *Heteropneustes*, it has been observed that except the palatine ossification all the other perichondral ossifications have membranous extensions into the surrounding membrane.

The other bones of the ethmoid region in *Heteropneustes* are the nasals, the lateral ethmoid and ventrally the median prevomer. The nasals develop around the anterior end of the sensory canal as narrow tubular bones. These bones resemble more the nasals of Cyprinoids (Ramaswami, 1955) than those of other siluroids studied. In *Heterobranchus* (Gregory, 1933) and *Clarias* (George, 1954) the nasals are small flat bones, but in *Silurus* (Goodrich, 1909) the nasals are large elongated plates. The lateral ethmoids are variously named in different groups of fishes. Sagemehl (1891) in Cyprinoids and Characinidae, Goodrich (1909) in *Clarias* and Gregory (1933) in *Heterobranchus* have termed the bone prefrontal and the same bone in *Amiurus* (Kindred, 1919) has been designated ectethmoid. In *Heteropneustes* the lateral ethmoid arises as a perichondral ossification in the lamina orbitonasalis of the chondrocranium and in the adult skull the bone has a large process ventrally which is connected with the antero-lateral extensions of the orbitosphenoid by a piece of cartilage. George (1954) does not report a connection of the lateral ethmoid with the orbitosphenoid in his species of *Clarias*.

The T-shaped prevomer carries two patches of teeth separated by a wide gap in *Heteropneustes*, whereas in *Clarias* (George, 1954) the bone designated as vomer is a crescent shaped one having a large patch of teeth ventrally.

The pleurosphenoids are well developed bones in *Heteropneustes* occupying the position between the optic and trigeminal foramina. These bones are seen to develop partly as perichondral ossification in the orbital cartilage and partly in membrane. Kindred (1919) has referred to this bone as alisphenoid in *Amiurus* and Bhimachar (1933) also has adopted the same nomenclature in describing the Indian catfishes. Both Goodrich (1930) and de Beer (1937) having considered the true nature of the alisphenoid have come to the conclusion that this should not be called alisphenoid in the vertebrates lower than mammals. A pleurosphenoid has not been described in *Clarias* (George, 1954).

Kindred (1919) and Bhimachar (1933) have recognised a suprasphenoid (basisphenoid) being fused with parasphenoid dorsally in *Amiurus* and other siluroids.

Such a bone is not observed in the development of skull of *Heteropneustes* and also it is absent in *Clarias* (George, 1954).

The occurrence of dorsal fontanelles between the frontals and in the supra-occipital appears to be a common feature noticed in the skull of Siluroidea. David (1935) has used the size of these fontanelles in the classification of the members of Clariidae. In *Galeichthys* and *Bagre*, Merriman (1940) described that the fontanelle might probably be meant for the passage of sensory nerves to snout and barbels. In *Heteropneustes* no nerves are seen to pass through the anterior fontanelle and it is covered by a membrane in the adult skull. These fontanelles appear to represent the remnants of the original large fontanelle of the chondrocranium, which has been reduced by the extensive growth of the frontals anteriorly and supra-occipital posteriorly. In *Clarias* (George, 1954) has also not been able to see any nerves passing through the fontanelle but has observed a foramen in the frontal bone through which passes a nerve to the skin. I have observed such foramina in the frontals on either side of the anterior fontanelle for the exit of nerves to the skin in *Clarias batrachus* which I have examined for the sake of comparison. The occurrence of frontoparietal fontanelles has been observed in large number of carp skulls like *Gobiobotia*, *Saurogobio*, *Psuedogobio* and *Abbottima* (Ramaswami, 1955), *Cyprinous carpio* (Sagemehl, 1891). Though Sagemehl (1891) did not attach much importance to the presence of the fontanelles Taranetz (1938) used the presence or absence of the fontanelles in the occipital region for dividing the gudgeons into groups. Ramaswami (1955) is of the opinion that in the bottom dwelling forms the fontanelles are necessary for some physiological functions.

There appears to be much confusion with regard to the nomenclature of bones of the otic region : the pterotic has been described by Kindred (1919) and Bhimachar (1933) as a squamoso-pterotic since the bone in *Amiurus* develops by a fusion of a perichondral and a membranous ossifications. But these ossificiations in *Amiurus* appear to be fused from the start and the membraneus part of the pterotic bone is the supratemporal which is a lateral line canal component subsequently fusing with the primary ossification. In *Heteropneustes* also I have been able to see that the membranous part (supratemporal) and the perichondral part of pterotic arises as a single ossification from the start ; I have therefore called it merely pterotic. Bhimachar (1933), however, has noticed the presence of separate supratemporal in *Rita*, *Pangasius*, *Macrones*, *Silundia* and *Plotosus*. In *Exocoetus* (Lasdin, 1913) the supratemporal and pterotic develop separately and remain separate as distinct bones, but in *Salmo* (de Beer, 1937) the two bones arise separately but fuse later.

The sphenotic has been referred to by Cuvier (1826) and Parker (1872) as postfrontal homologous to the similar bones in reptiles. Ridewood (1904) also retained the same name in his studies and similarly Goodrich (1909) has followed the same nomenclature in labelling the sphenotics of *Clarias*. It has been observed in *Heteropneustes* that the sphenotic is an ossification in the region of the anterior semicircular canal of the auditory capsule where the articulation of hyomandibula is seen. The intertemporal bone which arises as a membrane bone outside the auditory capsule in *Heteropneustes* and also probably in *Clarias*. It has been described as dermosphenotic by George (1954) and in *Heterobranchus* by Gregory (1933). But de Beer (1937) is of the opinion that "there is no reason to think that the postfrontal ever was the 'dermal representative' of the sphenotic ; the postfrontal is the uppermost bone of the postorbital series, and it is the intertemporal which comes in question as the dermal representative of the sphenotic (p. 498)". It is known that in *Dactylopterus* (Allis, 1910) and *Polypterus* (Allis, 1922) the post-frontal is fused with the sphenotic. In *Osteolepis* (Goodrich, 1930) the postfrontal, intertemporal and supra-temporal are separately present. Therefore, I have used the terms sphenotic and pterotic in describing the cartilage bones of the otic region of fishes and the terms intertemporal and supratemporal for the membrane

ossification which have been referred to by some as dermsphenotic and dermpterotic (squamosal) respectively.

It has been generally observed that the parietal bones are absent in all the siluroids studied. In this connection some authors (Goodrich, 1909 ; de Beer, 1937) have doubted whether the parietals have fused with the supraoccipital. But a study of the development of skull in *Heteropneustes* has revealed that the supraoccipital which arises as a perichondral ossification in the region of tecti synoticum and posterius of the chondrocranium, extends into the membrane both anteriorly and posteriorly, and separate parietal ossification is never observed. It is, therefore, concluded that the supraoccipital alone is developed and it extends to the region of the parietals also.

A supraoccipital spine is considerably elongated and well developed in *Heteropneustes* and in *Clarias* (George, 1954) the spine is almost absent. The supraorbital is a well developed bone in *Heteropneustes* as in *Heterobranchus* (Gregory, 1933) and *Clarias* (George, 1954).

The metapterygoid is seen to develop from the processus pterygoideus of the quadrate of the chondrocranium in *Heteropneustes* and closely attached to the metapterygoid is another membrane bone which is designated here as entopterygoid. A pterygoid (ectopterygoid) is absent. Regan (1911) opined that the metapterygoid in the Ostariophysi had moved over the top of the quadrate and taken the place of the pterygoid, and therefore, the pterygoid was absent, except in Bagridae where it formed a small plate behind the palatine. David (1935) also reports only two pterygoid bones in the members of Clariidae. Merriman (1940) in *Galleichthys* and *Bagre* and Geroge (1954) in *Clarias* have reported the presence of pterygoid lying dorsal or lateral to the metapterygoid respectively. But in *Clarias batrachus* examined by me all the three the metapterygoid, entopterygoid and the ectopterygoid bones are present ; the ectopterygoid is a small bone.

In *Heteropneustes* the palatines are completely perichondral ossifications without any membranous extension and remain independent of the metapterygoid, as observed in the development of the chondrocranium (Srinivasachar, 1957*c*). Similar palatines have been observed in other siluroids like *Heterobranchus* (Gregory, 1933) and *Clarias* (George, 1954). The independent nature of the palatines have been noticed even in the development of the chondrocranium in *Heteropneustes* and *Clarias* where the pterygoid process chondrifies independently and does not fuse with the quadrate at any time of the development. This condition has been observed by me (Srinivasachar, 1956*b*, 1957*b*, 1957*c*) in all the siluroids studied except *Arius* where the pterygoid process is fused with the quadrate.

In *Heteropnuestes* and *Clarias* the pterygoid bones are firmly attached with the prevomers by means of tendons and connective tissue. But in *Batasio* (Srinivasachar, 1956*a*) the upper jaw possesses an additional articulation of pterygoid with the orbitosphenoid bone in addition to the usual articulation with the hyomandibula. Such a condition has not been noted in any other siluroid studied.

In the lower jaw, only two bones, the angular and dentary are developed around Meckel's cartilage in *Heteropneustes* and the splenial reported in *Clarias* by George (1954) is absent. I have also not seen a splenial in *Clarias batrachus* which I have examined for the sake of comparison. However, Haines (1937) has observed the invasion of the angular ossification in Meckel's cartilage in *Mugil*, *Sardina* and *Trigla* and also the presence of an endochondral ossification in the processus retroarticularis of Meckel's cartilage. In *Heteropneustes* both angular and dentary develop outside Meckel's cartilage and a retroarticular bone is completely absent. In *Ophicephalus* (Srinivasachar, 1955) a retroarticular is seen ossifying in the retroarticular process of Meckel's cartilage.

The branchial arches of *Heteropneustes* differ considerably from the similar arches of *Clarias* (George, 1954). In *Heteropneustes* the hypobranch of the third arch is a large piece of cartilage where slight ossification has been noticed and the

hypobranch of the fourth arch is also distinct and is not ossified. But in *Clarias* (George, 1954) the hypobranchs are absent in both the third and fourth branchial arches ; and a large triangular cartilaginous plate to which the ceratobranchs of all the arches are connected, has been described by him. I have not been able to see such a structure either in the chondrocranium of *Clarias batrachus* (Srinivasachar, 1957*b*) or in the adult skull of the same that I have examined. In the chondrocranium of *Clarias* the median copula is represented by two pieces of cylindrical cartilages to which the hypobranchs are attached and not to the ceratobranchs as shown by George (1954) in the adult skull of *Clarias lazera*.

The opercular bones of *Heteropneustes* are reduced as in other siluroids (Gregory, 1933). The opercle bone is larger than in *Clarias*. The preopercle is firmly attached to the ventral edge of the hyomandibula and the quadrate in *Heteropneustes* and a subopercle is absent as in other siluroids.

The following table gives the synonymy of the terms employed by various authors in describing the skull of catfishes.

TABLE 1

Nomenclature followed in *Heteropneustes* following that of de Beer (1937)	Goodrich (1909)	Kindred (1919)	Gregory (1933)	Bhimachar (1933)	George (1954)
Ethmoid	Ethmoid	Supraethmoid	Dermethmoid	Supraethmoid	Dermethmoid
Lateral ethmoid.	Prefrontal	Ectethmoid	Prefrontal	Ectethmoid	Lateral-ethmoid.
Prevomer	—	Vomer	Vomer	Vomer	Vomer
Pleurosphenoid	—	Alisphenoid	Alisphenoid	Alisphenoid	—
Pterotic	Pterotic	Squamoso-pterotic.	Pterotic	Squamoso-pterotic.	Pterotic
Sphenotic	Postfrontal	Sphenotic	Sphenotic	Sphenotic	Sphenotic
Intertemporal	Lateral cheek bone.	—	Dermsphenotic	—	Dermsphenotic
Antorbital	Suborbital	Suborbital	Adnasal	Infraorbital	Minor maxillary.
Hypohyal	—	—	—	—	Glossohyal

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List of Abbreviations

ANG : Angular.
AOR : Antorbital.
BBR 2 : Basibranchial 2.
BBR 3 : Basibranchial 3.
BOC : Basioccipital.
BRS : Branchiostegal rays.
CAL : Ossifications.
CB 1–5 : Ceratobranchs 1 to 5.
CH : Ceratohyal.
CO 1–2 : Cartilaginous copula 1 and 2.
COM : Commissural sensory canal.

CSI : Cavum sinus impar.
CV : Complex vertebrae.
DEN : Dentary.
EB 1–4 : Epibranchs 1 to 4.
EH : Epihyal.
ENT : Entopterygoid.
ETC : Ethmoid cornu.
ETH : Ethmoid.
EXO : Exoccipital.
FHF : Foramen for the hyomandibular branch of the facial nerve.
FM : Foramen magnum.
FON 1 : Anterior fontanel in the Frontals.
FON 2 : Posterior fontanel in the Supraoccipital.
FR : Frontal.
HB 1–4 : Hypobranchs 1–4.
HH 1 : Hypohyal anterior.
HH 2 : Hypohyal posterior.
HM : Hyomandibula.
IOP : Interopercle.
IPL : Inferior pharyngel plate.
LET : Lateral ethmoid.
LAC : Lacrimal.
MAX : Maxilla.
MEE : Membranous extension of the ethmoid bone.
MEH : Membranous extension of the hyomandibula.
MEP : Membranous extension of the metapterygoid.
MEQ : Membranous extension of the quadrate.
MPT : Metapterygoid.
NS : Nasal.
OP : Opercle.
OS : Orbitosphenoid.
OT : Regon of the otolith of utriculus in prootic bone.
OTS : Cavum sacculus.
OTU : Cavum utriculus.
PAL : Palatine.
PAS : Parasphenoid.
PB 3 : Pharyngobranch 3.
PB 4 : Pharyngobranch 4.
PHY : Parahyoid.
PLS : Pleurosphenoid.
PMS : Preopercle mandibulay sensory canal.
PO : Prevomer.
POP : Preopercle.
PRO : Prootic.
PTM : Posttemporal.
PTO : Pterotic.
QU : Quadrate.
SC : Suborbital sensory canal.
SCO : Sensory canal ossicle.
SO 1–2 : Suborbitals 1 and 2.
SOC : Supraoccipital.
SOP : Supraoccipital spine.
SOS : Supraorbital sensory canal.
SPH : Sphenotic.
SPL : Superior pharyngeal plate.
SUO : Supraorbital.
TRI : Tripus.
TSC : Temporal sensory canal.
UOP : Upper opening of the posterior semicircular canal.
II : Optic foramen.
IV : Trochlear foramen.
V : Trigeminal foramen.
VI : Abducens foramen.
VII : Facial foramen.
IX : Glossopharyngeal foramen.
X : Vagus foramen.