

STUDIES ON SOME ASPECTS OF CRANIAL ANATOMY OF
INDIAN LEIOGNATHIDS (PERCIFORMES :
LEIOGNATHIDAE). PART 1. OSTEOLOGY.

By

RANI SINGH*

Zoological Survey of India, Calcutta.

AND

N. C. DATTA

*Department of Zoology Calcutta, University
Calcutta.*

(With 7 Text-figures)

INTRODUCTION

The perciform fishes are known to occupy a higher position in the ladder of teleostean evolution. Among them, leiognathids popularly known as silver-bellies, rank as one of the important groups of fishes. The leiognathids are known by 17 species from Indian waters but the knowledge of cranial osteology of these fishes is almost avoid in the literature. The present communication is an attempt to provide a reasonably detailed account of the cranial osteology of these fishes. In this connection it may be stated that Starks (1911) studied the osteology of *Leiognathus fasciatus* in brief and Delsman (1925) demonstrated the functional morphology of some bones associated with the protrusibility of mouth in *Equula dussumieri* (= *Leiognathus dussumieri*).

MATERIAL AND METHODS

The present study of the cranial osteology is based on the seven species of leiognathids belonging to three genera viz. *Leiognathus splendens* (Cuvier), *Leiognathus equulus* (Forsskal), *Leiognathus bindus* (Valenciennes), *Leiognathus brevirostris* (Valenciennes), *Secutor insidiator* (Bloch), *Secutor ruconius* (Hamilton) and *Gazza minuta* (Bloch).

The specimens were collected from various localities along the entire east coast of India. The specimens collected were first preserved in 10% formalin and the standard methods (Hollister, 1934 and Taylor, 1967)

* Part of Ph. D. thesis of the senior author under the guidance of the second author.

for the preparation of skulls were followed. Alzarine transparency of the above mentioned specimens were also prepared to show the limits of individual element in situ.

The skull of *Leiognathus splendens* is considered as a generalised type in order to provide a detailed description of each bone for further comparison with skull of other species under study. Osteological nomenclature basically followed here is after Harrington (1955) with some modifications.

ABBREVIATIONS USED IN THE TEXT AND FIGURES

A : Angular, AN : Retroarticular, BO : Basioccipital, BR : Branchiostegal ray, BS : Basisphenoid, CH : Ceratohyal, D : Dentary, DSPH : Dermosphenotic, E : Ethmoid, ECT : Ectopterygoid, EH : Epihyal, ENT : Entopterygoid, EO : Exoccipital, F : Frontal, H : Hypohyal, HM : Hyomandibular, IC : Intercalar, IH : Interhyal, IOP : Interopercular, LA : Lachrymal, LE : Lateral ethmoid, MPT : Metapterygoid, MX : Maxilla, NA : Nasal, OP : Opercular, P : Palatine, PA : Parietal, PM : Premaxilla, POP : Preopercular, PRO : Prootic, PS : Parasphenoid, PTO : Pterotic, PTS : Pterosphenoid, PTT : Post-temporal, Q : Quadrate, SO : Suborbital, SOC : Supraoccipital, SPH : Sphenotic, SPO : Supraorbital, SY : Symplectic, UH : Urohyal, V : Pre vomer.

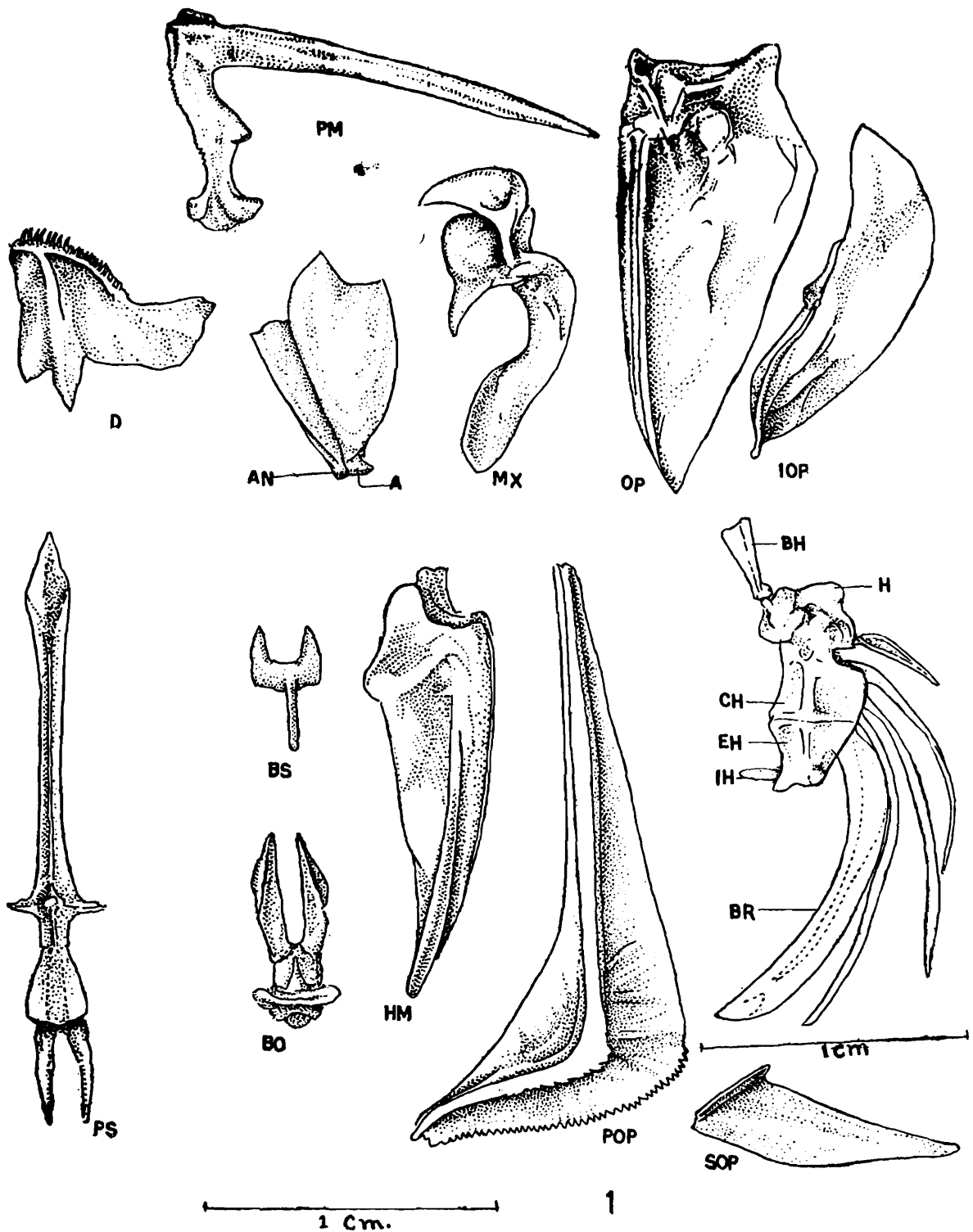
OBSERVATIONS

The skull of *Leiognathus splendens* is roughly spherical with upwardly directed supraoccipital crest and a laterally compressed orbital region which is relatively broad posteriorly. On the dorsal surface of the skull, the lateral bony ridges of the frontal along with supraoccipital form a Y-shaped structure.

The general contour of the skull in all the species of the genus *Leiognathus* is similar but the skull of the genus *Secutor* and *Gazza* differ slightly from that of *L. splendens* in having wavy rostro-occipital profile in the former and 'V' shaped structure on the dorsal aspect of the skull in the latter.

1. Olfactory Region :

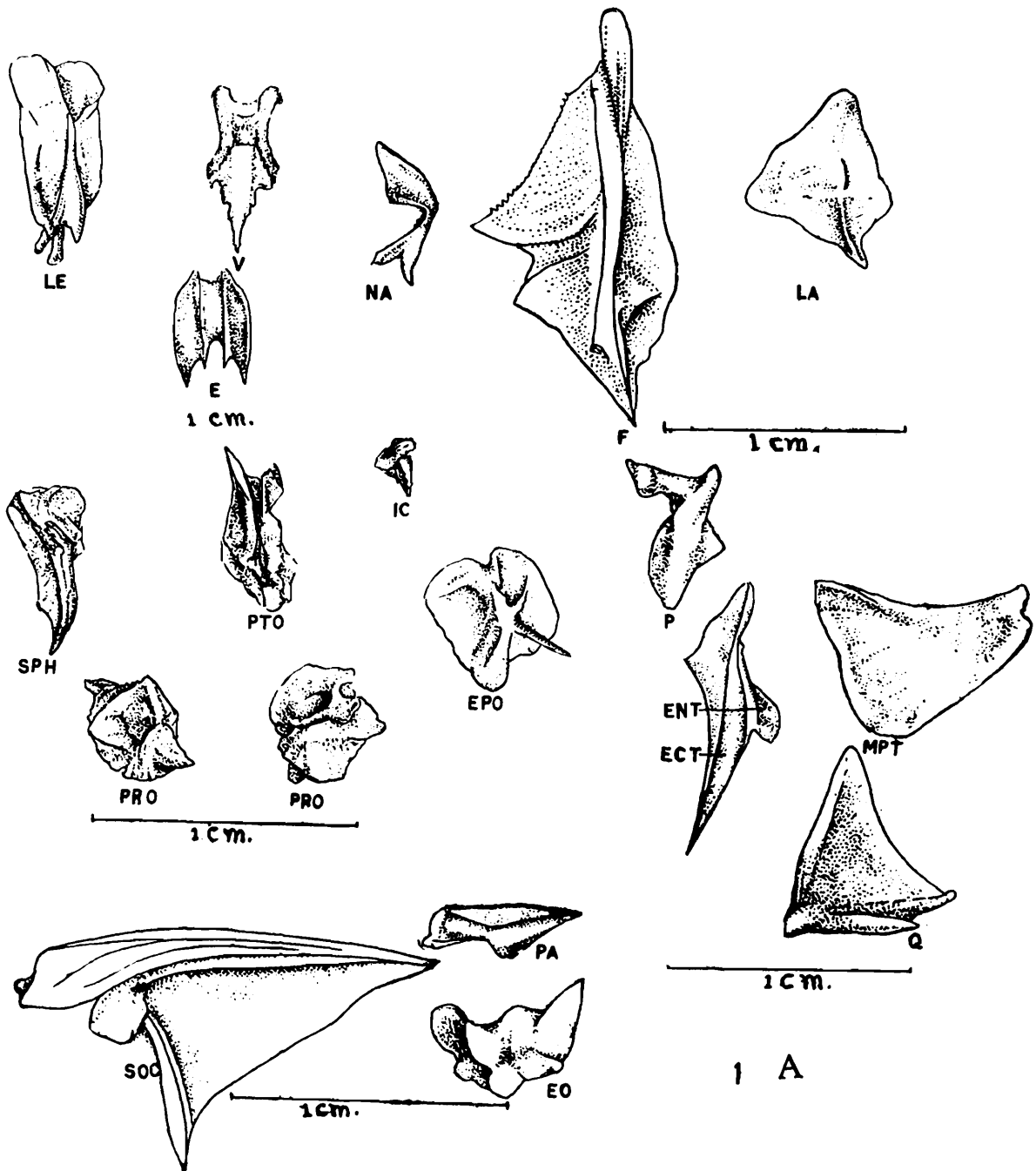
This is the anterior most region comprising paired lateral ethmoid and nasal and unpaired ethmoid and prevomer.



Text-fig. 1. Disarticulated bones of the skull of *Leiognathus splendens* (Cuvier).

1.1. Ethmoid (Text-fig. 1E and 4A) :

The ethmoid, a median endochondral bone lies between the pre-vomer and frontal. It forms the anterodorsal angle of the neurocranium and is saddle-shaped dorsally. Anteriorly it is attached to the pre-vomer by ethmovomer cartilage, laterally to the lateral ethmoid and posteriorly to the frontal. Dorsally, it is overlapped by the nasals and forms the lateral inner wall of each foramen olfactorium.



Text-fig. 1A. Disarticulated bones of the skull of *Leiognathus splendens* (Cuvier).

There is no marked difference in the disposition of this bone among the other species except that of *L. equulus* (Text-fig. 4B) and *S. ruconius* (Text-fig. 4F), where the median ridge is very much prominent. The bone is roughly lanceolate in the former species as well as in *G. minuta* (Text-fig. 4G) :

1.2. Lateral ethmoid (Text-fig. 1LE and 4A) :

The lateral ethmoid is a roughly rectangular bone, located on either side of the ethmoid and forming the outer boundary of the orbit. Posterodorsally it possesses two posteriorly directing strong antorbital spines, the outer one is more prominent than the inner. Posteroventrally, it has a narrow projection attached to the anteroventral surface

of the frontal. Laterally it forms the outer wall of the foramen olfactorium. Anterodorsally, it is attached to the lachrymal, anteriorly to the palatine and pterygoid, anterolaterally to the prevomer and posterodorsally to the nasal.

The above description equally applies to all the species although the antorbital spines are very prominent in *L. equulus*, *L. bindus* and inconspicuous in *G. minuta*. In *S. insidiator* (Text-fig. 4E), a single weak antorbital spine is present.

1.3. Prevomer (Text-fig. 1V, 4A and 5A) :

Prevomer is a toothless, square shaped bone with a thin tapering posteroventral shaft, truncated anteriorly and bears downwardly directing projections on either side. It is placed anterior to the ethmoid and forms the anteroventral part of the cranium. Overlain dorsally by premaxilla, it makes contact with maxilla anterolaterally and ethmoid posterodorsally. Laterally, the prevomer is connected with the palatine and its shaft extends into the anterodorsal groove of the parasphenoid posteroventrally.

There is no worthmentioning difference in the prevomer of other species except in *L. equuls* (Text-fig. 5B), where it is roughly dumbbell shaped and bears downwardly directed projections on either side at the anterior end with a fontanell on its ventral surface. In *S. insidiator* (Text-fig. 5E), *S. ruconins* (Text-fig. 5F), and *G. minuta* (Text-fig. 5G), it is arched along the anterior margin and bears a median fontanel on its ventral surface in the latter.

1.4. Nasals (Text-fig. 1NA and 2A) :

Each nasal is a crooked bone, located dorsal to the ethmoid and forms the roof of the nasal capsule. Anteriorly it is narrow and is attached loosely to the lachrymal and palatine and posterodorsally to the frontal and the lateral ethmoid.

The above description applies to the nasal of all the species studied, however, it is rather prominent in *L. equulus*.

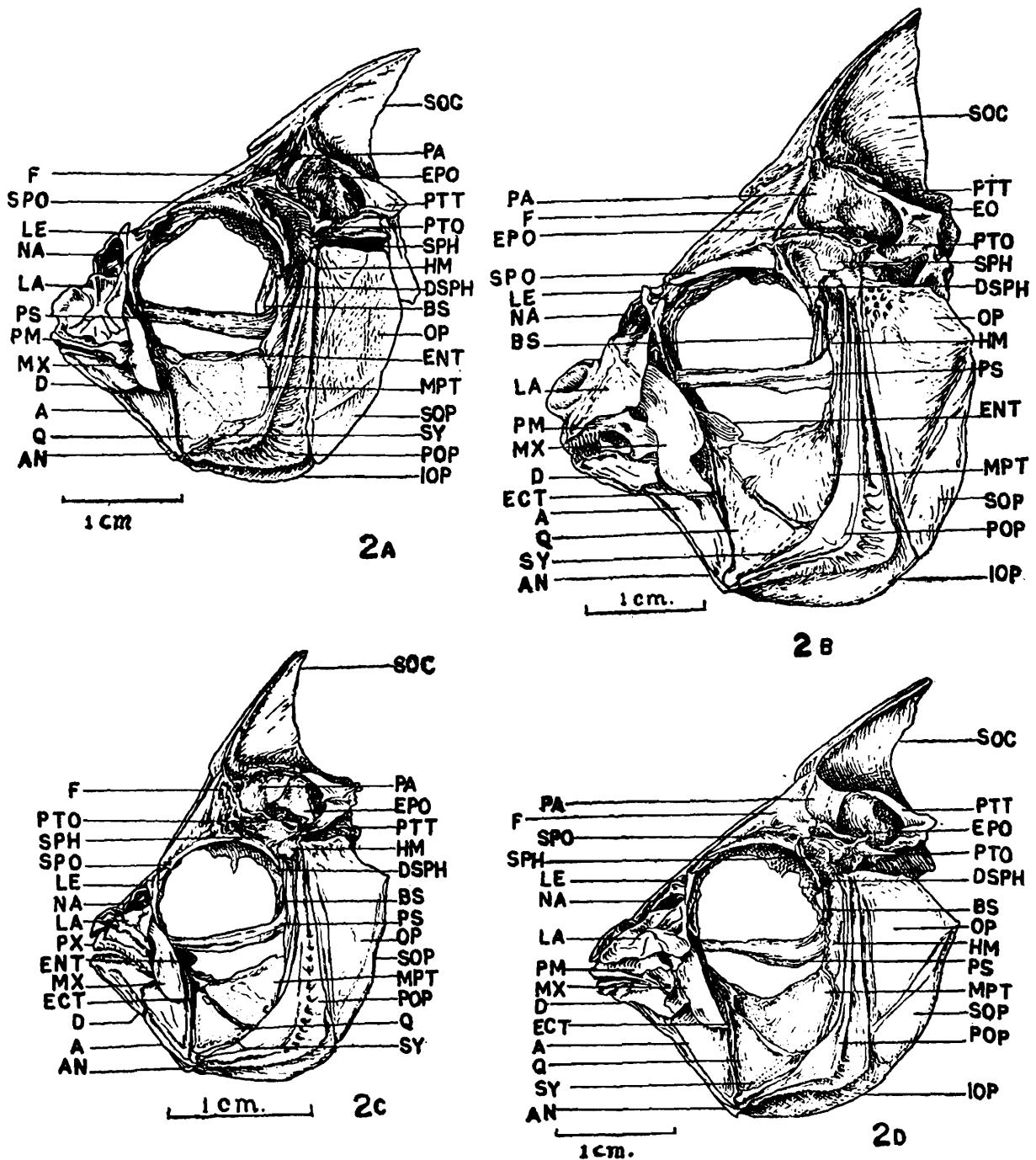
2. Orbital Region :

This region comprises all paired bones : frontal, lachrymal, supraorbital, suborbital, dermosphenotic and pterotic.

2.1. Frontal (Text-fig. 1F and 4A) :

Each frontal is a roughly hoe shaped bone and occupies nearly half of the length of the neurocranium. It lies behind the ethmoid forming the dorsal surface of the skull. Laterally it extends into a ridge forming

a Y-shaped structure which remains continuous with the lateral ridge of the supraoccipital. On the inner side of the lateral ridge, there is another poorly developed ridge at the anterior end and a comma shaped ridge, at the posterior end. Anteriorly it is broad and attached to the ethmoid, lateral ethmoid and nasal. Posteriorly it is narrow and attached to the supraoccipital along its inner surface. Anterolaterally it is fused with its respective supraorbital and posterolaterally attached to the parietal, pterotic and sphenotic.



Text-fig. 2A—D. Lateral view of the skull.

- A. *Leiognathus splendens* (Cuvier)
- B. *Leiognathus equulus* (Forsskål)
- C. *Leiognathus bindus* (Valenciennes)
- D. *Leiognathus brevisrostris* (Valenciennes)

In *L. equulus* and *L. bindus*, this bone is similar to that of *L. splendens* except slightly modified in the former species where it (Text-fig. 4B) bears an irregular outgrowth on its anterodorsal surface and lacks a comma shaped ridge at the posterior extremity. It is noticed that this irregular outgrowth is well developed in bigger specimens. In *L. brevirostris* (Text-fig. 4D), the posterodorsal surface of the frontal bears an elongated somewhat curved ridge on the inner side of the lateral ridge but the comma shaped ridge is lacking. In *S. insidiator* and *S. ruconius*, frontal is identical to that of *L. splendens* except the comma shaped ridge on its posterior surface. In *G. minuta* (Text-fig. 4G), each frontal forms a V-shaped structure in continuity with the lateral ridge of the supraoccipital and the comma shaped ridge is also wanting unlike that of *L. splendens*.

2.2. Lachrymal (Text-fig. 1LA and 2A) :

Lachrymal, the first orbital bone, forming lateral wall of the nasal capsule, is roughly triangular and lies over the dorsal surface of the proximal portion of the maxilla. Anteriorly the lachrymal of either side approaches each other. Posteriorly it is attached to the nasal, laterally to the lateral ethmoid and ventrally to the palatine, maxilla and premaxilla.

The above description applies to all the species except *L. equulus* (Text-fig. 2B) and *L. brevirostris* (Text-fig. 2D) where it is comparatively well developed and elongated anteriorly.

2.3. Supraorbital (Text-fig. 1SPO and 4A) :

Supraorbital, a well developed bone of the circumorbital series and forming the dorsal roof of the orbit, is located anterolateral to the frontal. It is roughly triangular curved bone with entirely serrated margin and is attached anteroventrally to the respective lateral ethmoid and posteriorly to the dermosphenotic and the sphenotic.

It differs specifically in respect of the serration at the outer margin. In *L. equulus*, the serration is indistinct and in *L. brevirostris*, confined to the posterior region only while in *L. bindus*, the outer margin of the bone is rugose. In *S. insidiator*, *S. ruconius* and *G. minuta*, the bone is minutely serrated along its outer margin.

2.4. Dermosphenotic (Text-fig. 3A and 4A) :

Dermosphenotic, the last bone of the circumorbital series, is thin and elongated. Attached to the supraorbital proximally, it lies above the sphenotic and connects the suborbital distally.

It is identical in all the species.

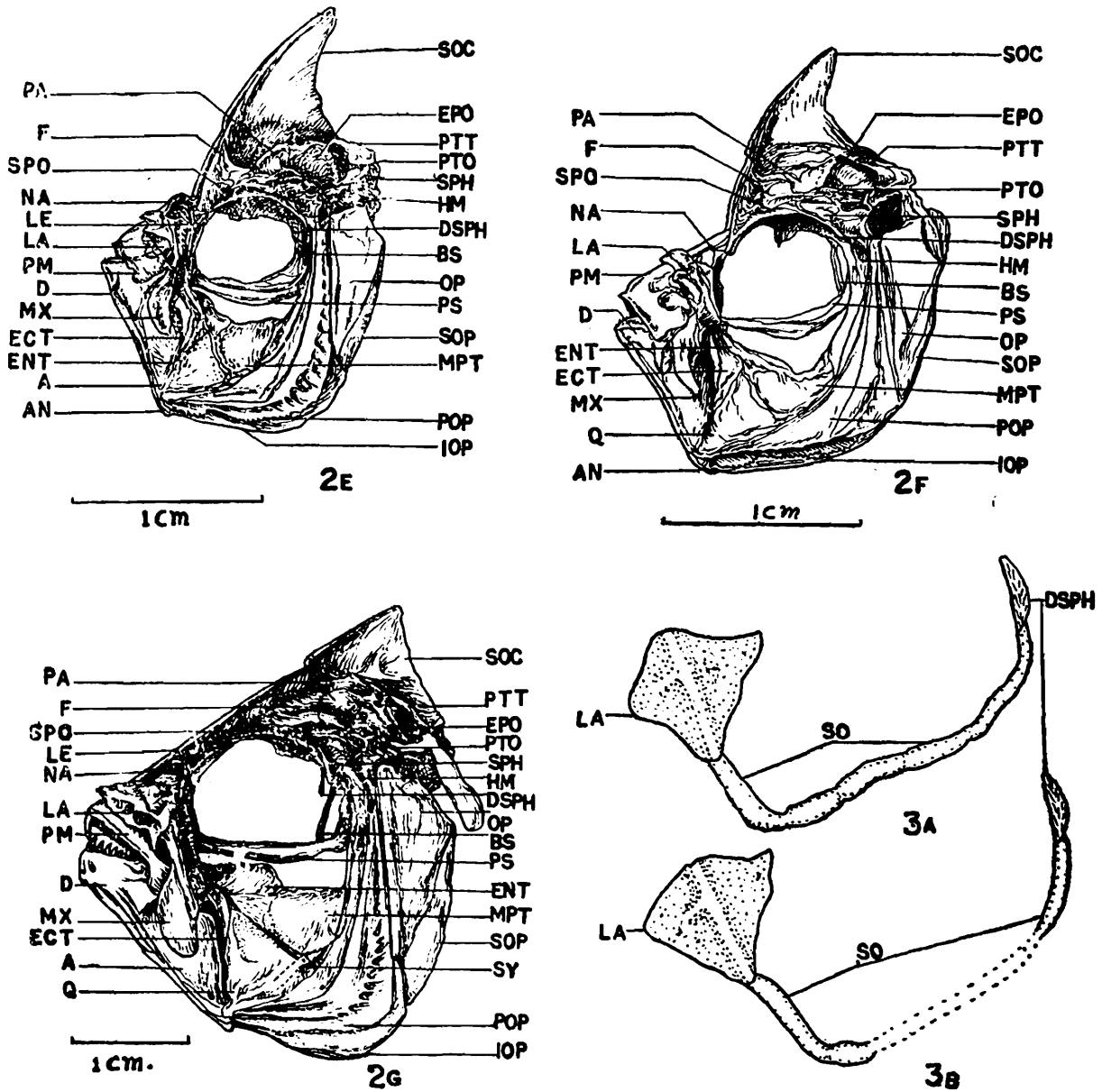
2.5. Suborbitals (Text-fig. 3A) :

The suborbital series, forming the ventral wall of the orbit is reduced to a thin bony tube and can not be demarcated into a number of discrete bones like some of other fishes.

There is no worthmentioning difference in the suborbitals of *L. equulus*, *L. brevirostris*, *S. insidiator* and *S. ruconius*. However, the suborbital series is incomplete in *L. bindus* and *G. minuta* (Text-fig. 3B).

2.6. Pterosphenoid (Text-fig. 5A) :

Pterosphenoid, a well developed irregular shaped bone, is situated anterior to the basisphenoid and prootic. Dorsoanteriorly it is attached to the sphenotic, posteriorly to the prootic and basisphenoid and mesially to its fellow of the other side.



Text-fig. 2E—G. E. *Secutor insidiator* (Bloch)
 F. *Secutor ruconius* (Hamilton)
 G. *Gazza minuta* (Bloch)
 Text-fig. 3A & B. Circumorbital series.
 A. *Leiognathus splendens* (Cuvier)
 B. *Leiognathus bindus* (Valenciennes)

The above description is applicable to all the species.

3. Otic Region :

The otic region, comprises nine well ossified bones (sphenotic, pterotic, epiotic, prootic, intercalar, exoccipital, supraoccipital, parietal and posttemporal). Collectively the bones of this region form the endocranial vault and the otic capsule and provide protection to the brain and parts of the cranial nerves and also afford the attachment area to the branchiocanium as well as the vertebral column. This region also serves as a foothold for the pectoral girdle through the posttemporal.

3.1 Sphenotic (Text-fig. 1SPH and 2A) :

The sphenotic is an irregular shaped bone having an anterior thin and a posterior broad thick triangular portion. It is located anterior to the pterotic. Ventrolaterally it bears a cup like articulating facet for dorsoanterior condyle of respective hyomandibula. Proximally it is attached to the frontal and supraorbital, distally to the pterotic, ventrally to the prootic and is overlapped dorsally by the dermosphenotic.

The above description applies to the sphenotic of all the species.

3.2 Pterotic (Text-fig. 1PTO and 2A) :

The pterotic is an irregular shaped bone forming the postero-lateral surface of the cranium and lies posterior to the sphenotic. The thin proximal portion of this bone bears a sensory tunnel which proximally communicates with the frontal system of the sensory tunnel. Its heavy distal portion is triangular posteriorly and forms a cup like structure with the prootic on its ventral surface for articulation of the posterodorsal condyle of the hyomandibula. It is attached to the epiotic as well as to the exoccipital. Posteroventrally it is overlapped by the intercalar.

There is no marked difference in the disposition of this bone among the other species except *L. equulus* (Text-fig. 2B) and *L. brevirostris* (Text-fig. 2d) where a posteriorly directed postero-ventral spine like prominent process is present.

3.3. Epiotic (Text-fig. 1EPO and 2A) :

Each bone resembles a hollow cup, capping the posterodorsal surface of the cranium and encloses the posterior semicircular canals. The epiotic bears a median ridge and an outward directed epiotic process which provides the attachment area to the lateral muscles. Anterodorsally, it is partially overlapped by the parietal and is attached to the pterotic anteroventrally, to the exoccipital posteroventrally and to the

supraoccipital posteriorly. Mesially it bears a depression for receiving the dorsal arm of the posttemporal.

The above description is more or less applicable to all the species studied here.

3.4. Prootic (Text-fig. 1PRO and 5A) :

The prootic, a large irregular shaped bone, forming the anteromesial and anterodorsal wall of the auditory capsule, bears a carotid foramen and the foramen for the Vth and VIIth cranial nerves. The anterior part of the bone joins mesially with its fellow of the other side and is distally attached to the basisphenoid and laterally to the sphenotic. Dorsally, its posterior part is attached to the ventral margin of sphenotic, pterotic and intercalar, posteriorly to the exoccipital, ventrally to the parasphenoid and posteroventrally to the basioccipital.

The above description applies to prootic of all the present species.

3.5. Intercalar (Text-fig. 1IC and 5A) :

Intercalar, the smallest bone of otic region, lies posterior to the pterotic and extends to the prootic anteroventrally. It is an irregular shaped bone with somewhat concave dorsal surface. It is thicker along its outer margin, bears a horizontal ridge for providing the attachment to the ventral arm of the posttemporal and overlaps the exoccipital partially at the distal end.

There is no worthmentioning difference in the intercalar of all the species studied here.

3.6. Exoccipital (Text-fig. 1EO and 5A) :

The exoccipital is roughly fan-shaped with a dorsomedian ridge, forms the posterior wall of the cranium and lies posteroventral to the supraoccipital and epiotic. It bears three foramina for ixth and xth cranial nerves. The anterior one is smaller than the others. The bone forms the wall of the foramen magnum posteriorly and bears a condylar surface posteroventrally for the articulation with the centrum of the first vertebra. The condyle of one side joins its fellow of the other side midventrally through a median piece of cartilage. The bone is overlapped by the intercalar and is attached to the pterotic and epiotic dorsally, to the supraoccipital along its ventral margin and to the prootic anteriorly.

The exoccipital is similar in all the species except the genus *Secutor* (Text-fig. 5E and F) where two foramina are present.

3.7. Supraoccipital (Text-fig. 1SO, 2A and 4A) :

It is a well developed median bone, lying between the frontals posteriorly and forming the posterodorsal wall of the cranium. The bone is divided into a thick anterodorsal portion with a median and two lateral ridges converging posteriorly to form the supraoccipital crest. A thin, broad, blade like ventral portion of the bone extends ventrally upto the dorsal groove of the foramen magnum and forms an angle of less than 60° with the median longitudinal axis of the skull. The supraoccipital crest is convex dorsally and gradually merges to the thin portion ventrally. Anteriorly the lateral ridges of this bone are continuous with the lateral ridges of the frontals. Parietal is placed along its anterior margin but exoccipital lies ventral to it.

This bone varies specifically among all the species under study in respect of its shape, relative size and disposition. Anteriorly the median ridge of the supraoccipital forms a knob in *L. equulus* (Text-fig. 4B). In *L. bindus*, the thin ventral portion does not extend upto the furrow of the foramen magnum. In case of the species belonging to the genus *Secutor*, the supraoccipital crest is short and convex and the ventral thin blade like portion is oblique (Text-fig. 2E and F) like that of *L. splendens*. In *G. minuta* (Text-fig. 2G), the occipital crest is straight and the posterior margin of the ventral thin portion is vertical.

3.8. Parietal (Text-fig. 1PA and 2A) :

Located posterolateral to the frontal each parietal is a triradiate bone and contributes little to the formation of the roof of the cranium. It possesses a prominent concave ridge on the dorsal surface and another small ridge on the posterior surface in conjunction with the median ridge of the epiotic. Anteriorly the parietal is attached suturally to the pterotic, dorsally to the frontal and posteriorly to the supraoccipital. It overlaps the dorsal margin of the epiotic ventrally.

There is a marked difference in the shape of this bone among all the species studied here. In *L. equulus* (Text-fig. 2B) and *L. brevirostris* (Text-fig. 2D), the parietal is roughly petal shaped. In the former it does not bear a ridge like that of *L. splendens* but in latter there is a prominent ridge on its posterior surface. In *L. bindus* (Text-fig. 2C), it is roughly tetra-radiate with a prominent ridge on its posterior surface. In *S. insidiator* (Text-fig. 2E), *S. ruconius* (Text-fig. 2F) and *G. minuta* (Text-fig. 2G), this bone is irregular in shape and is elongated dorsoventrally. It is provided with a median ridge instead of anteroposterior elongation having concave ridge.

3.9 Posttemporal (Text-fig. 2A) :

Posttemporal serves as a bridge between the neurocranium and the pectoral girdle. It is a hook shaped bone having an elongated dorsal and small ventral arms. The dorsal arm is attached to the dorsomedian surface of the epiotic and the ventral arm to the intercalar. Posteriorly it is attached to the supracleithrum.

4. Basicranial Region :

This region contributes to the formation of the floor or base of the cranium and comprises the basioccipital, basisphenoid and parasphenoid of which the former two take part in the formation of auditory capsule.

4.1 Basioccipital (Text-fig. 1BO and 5A) :

This median bone takes part in the formation of the posterior wall of the myodome and is located posterior to the parasphenoid. Its lateral walls extend anteriorly so as to form a trough like structure (posterior myodome) and are attached to the prootic anterodorsally. The bone is partly overlapped by the parasphenoid. Posterodorsally it is attached to the exoccipital. The thick posterior end of the bone, has a deep concavity similar to that of centrum of a typical vertebra which bears a small median ridge at its posteroventral surface. Mesiolaterally it provides attachment to the Baudelot's ligament.

The general contour of this bone is more or less similar in all the species studied but for the shape of myodome is oval in *L. bindus* (Text-fig. 5C) and *S. insidiator* (Text-fig. 5E), conical in *L. equulus* (Text-fig. 5B), slender in *L. brevirostris* (Text-fig. 5D), *S. ruconius* (Text-fig. 5F) and *G. minuta* (Text-fig. 5G). In *L. brevirostris*, a thin elongated interoccipital septum exists at the posteroventral extremity of this bone.

4.2 Basisphenoid (Text-fig. 2A) :

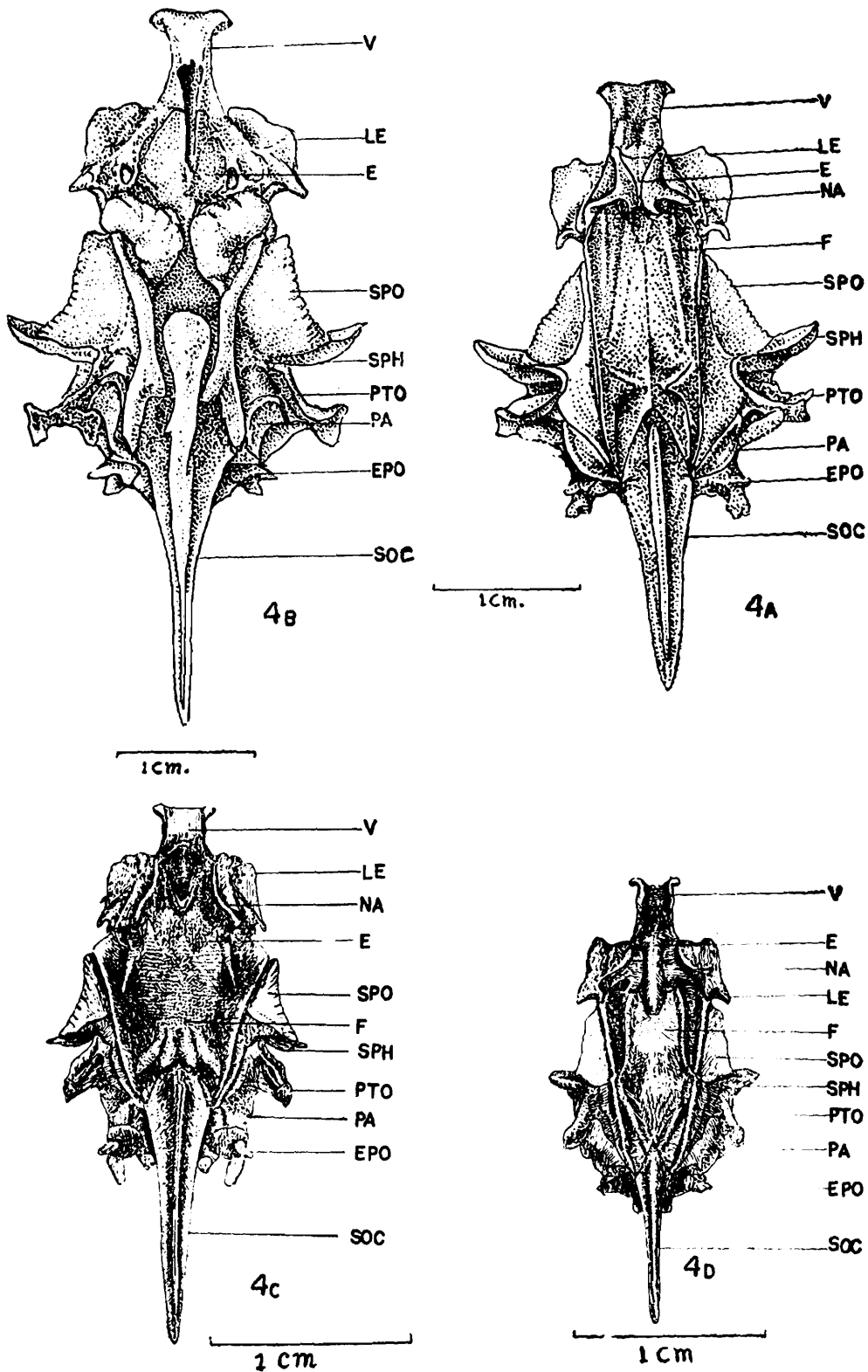
Basisphenoid is a small median Y-shaped bone and forms the ventral wall of the anterior myodome. It lies nearly vertical in the posterior region of the anterior half of the skull. The shank of Y is thin, elongated, directed downwards and forwards and is attached to the dorsomedian surface of the parasphenoid. The two arms of the Y are somewhat wide, dorsally concave and bounded by the prootic along its lateral as well as caudal region.

The bone is identical in all the species studied here.

4.3 Parasphenoid (Text-fig. 1PS and 2A) :

Parasphenoid, an elongated curved bone, bridging the otic and olfactory regions, is anteriorly dagger shaped and bears a groove for

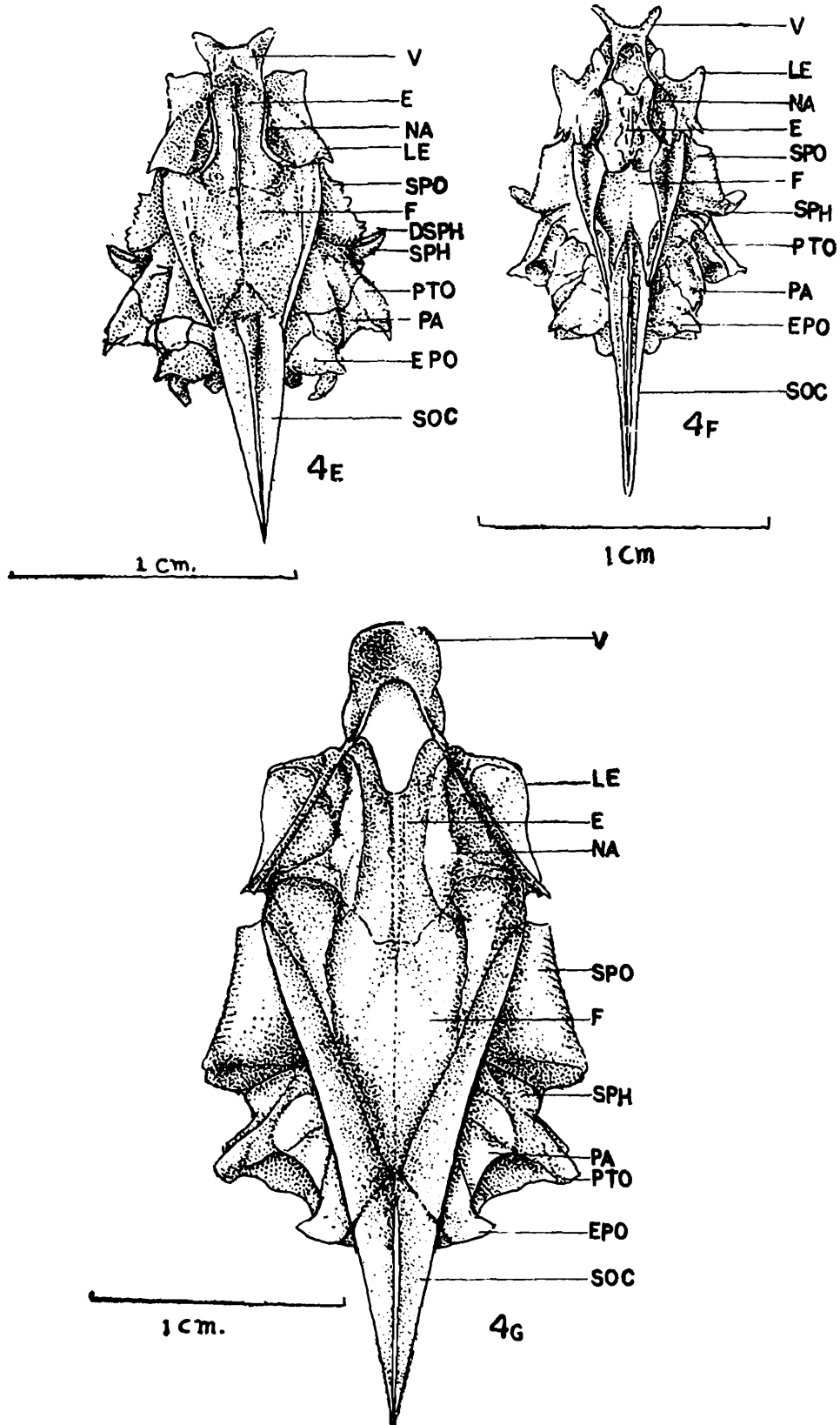
receiving posteriorly the pointed end of prevomer. Mesially it is keeled having two lateral wings, one on either side which impinges on the prootic. Posteriorly the bone bifurcates into slivers which overlap the



Text-fig. 4A—D. Dorsal view of the neurocranium.

- A. *Leiognathus splendens* (Cuvier)
- B. *Leiognathus equulus* (Forsskal)
- C. *Leiognathus bindus* (Valenciennes)
- D. *Leiognathus brevirostris* (Valenciennes)

basioccipital but do not extend up to the posterior extremity of the latter. Behind its lateral wing, it bears a small notch which is followed by a knob. It forms an angle less than 60° with the dorsomedian longitudinal axis of the skull.



Text-fig. 4E—G. E. *Secutor insidiator* (Bloch)
 F. *Secutor ruconius* (Hamilton)
 G. *Gazza minuta* (Bloch)

This bone is similar in all the species. However, in *S. insidiator* (Text-fig. 2E) and *S. ruconius* (Text-fig. 2F.), the parasphenoid forms an angle of more than 75° with dorsomedian longitudinal axis of the skull whereas in other species it forms an angle less than 60°.

5. Oromandibular Region :

The bones of this region contribute to the formation of the lower wall of the orbit, roof and floor of the mouth and connect the neurocranium with the branchiocranium through the palatine and the hyomandibula. This region comprises paired palatine, quadrate, metapterygoid, angular, pterygoid, premaxilla, maxilla, dentary and retroarticular.

5.1 Palatine (Text-fig. 1P and 6A) :

Palatine, a small and edentulous bone, connects the branchiocranium with the neurocranium. It has an anterodorsal arm and a broad ventroposterior shank which joins suturally with its respective ectopterygoid and entopterygoid distally. The proximal end of the palatine arm is overlapped by the lachrymal and is loosely connected with the nasal anterodorsally. It is attached to the lateral ethmoid dorsally, to the head of the prevomer anteroventrally and to the maxilla along its mesial and anterior end.

The above description is also applicable to *L. equulus* but in other species some differences exist. In *L. bindus* (Text-fig. 6C) and *L. brevirostris* (Text-fig. 6D), the palatine arm is thin elongated and directed upwards anteriorly. In *S. insidiator* (Text-fig. 6E), *S. ruconius* (Text-fig. 6F) and *G. minuta* (Text-fig. 6G), the arm is narrow and comma shaped.

5.2. Quadrate (Text-fig. 1A and 6A) :

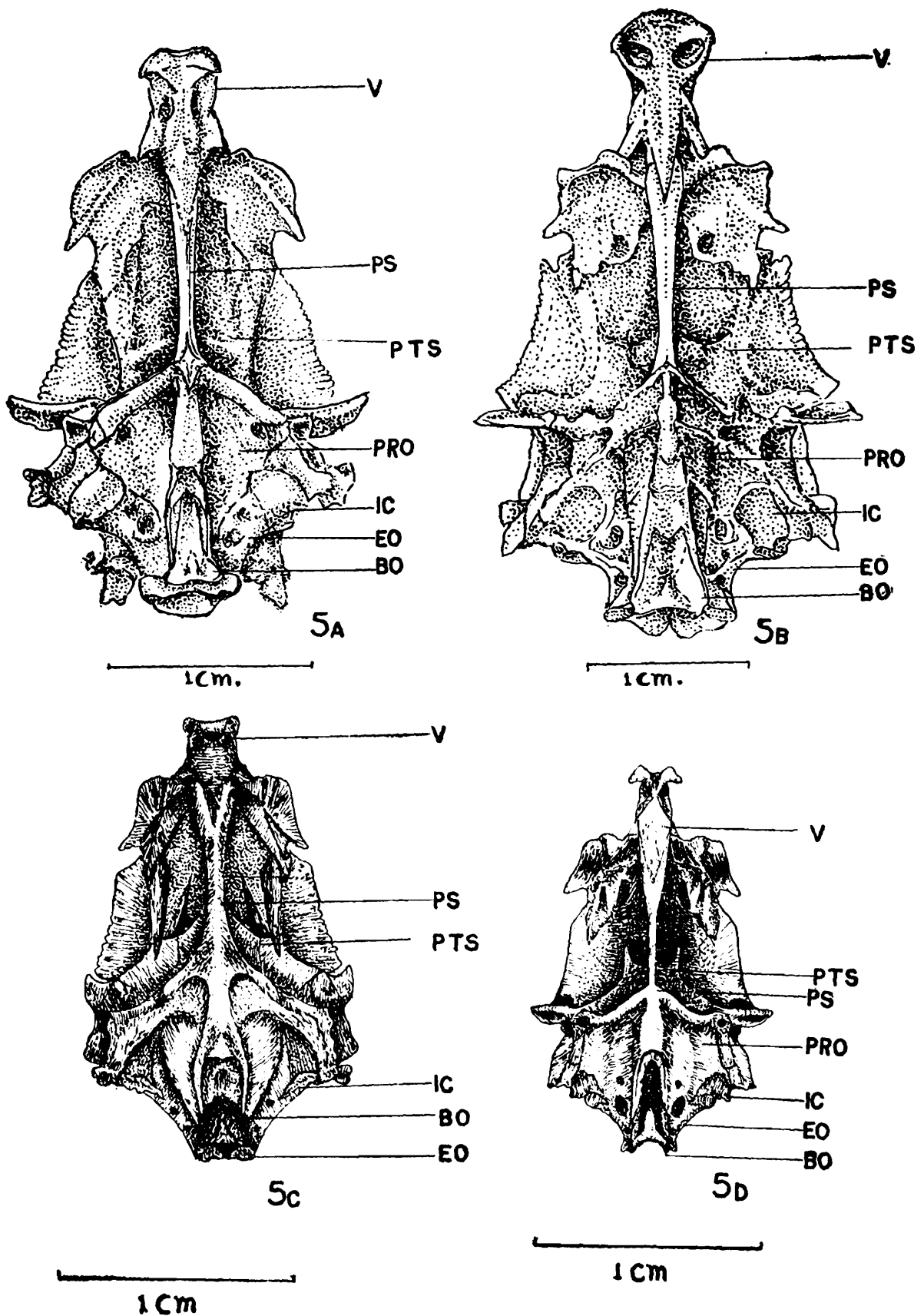
Quadrate, a triangular bone, is located anterior to the horizontal arm of the preopercular and possesses a double headed condyle along its apex that articulates with the angular. Its anterior arm forms a groove for providing attachment area to the ectopterygoid and the posterior arm is connected with the metapterygoid. Along its inner surface, it bears a groove that lodges the symplectic. Dorsoanteriorly it is attached to the entopterygoid.

There is no notable difference in respect of morphology of the quadrate in all the species studied.

5.3. Metapterygoid (Text-fig. 1MPT and 6A) :

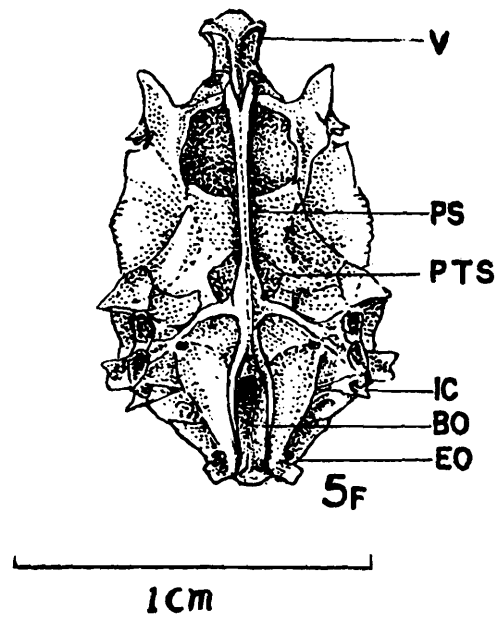
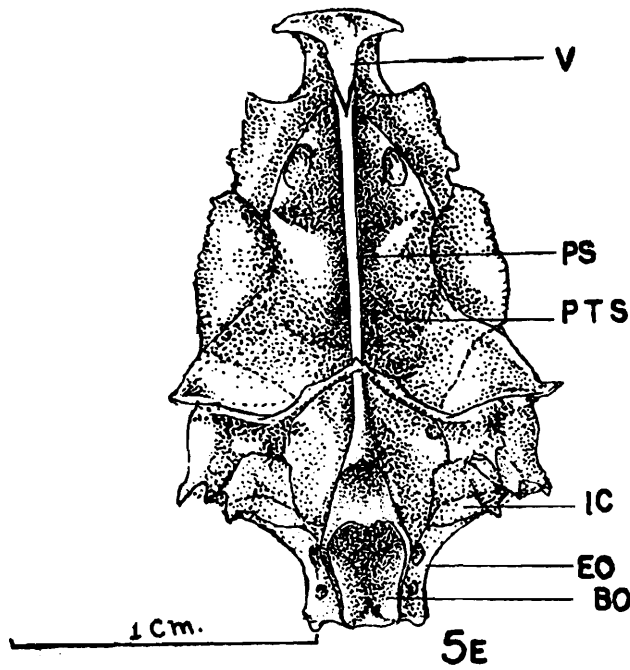
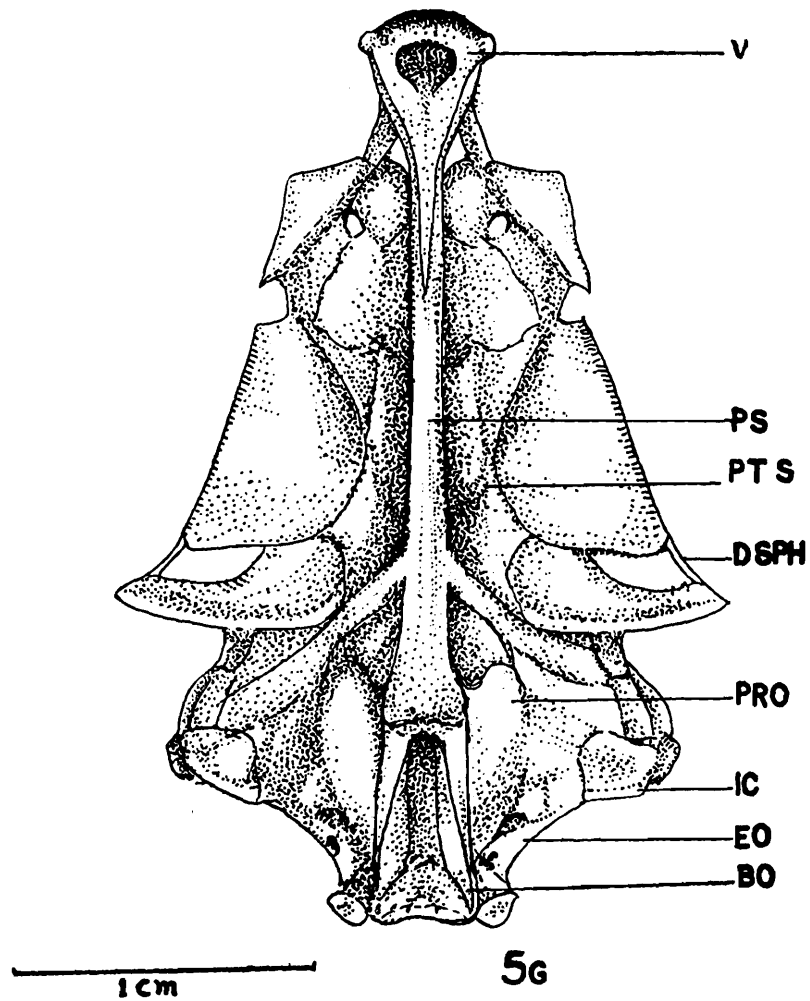
Metapterygoid, roughly crescentic, forming a part of the ventral wall of the orbit, lies dorsal to the quadrate. Anteriorly it is attached to the entopterygoid and joins the quadrate anteroventrally by a thin strip of cartilage. It is attached to the preopercular along its posterior margin and to the interhyal by ligament along its inner surface.

There is no worthmentioning difference in the metapterygoid of other species.



Text-fig. 5A—D. Ventral view of the neurocranium.

- A. *Leiognathus splendens* (Ouvier)
- B. *Leiognathus equulus* (Forsskal)
- C. *Leiognathus bindus* (Valenciennes)
- D. *Leiognathus brevirostris* (Valenciennes)



Text-fig. 5E—G. E. *Secutor insidiator* (Bloch)
 F. *Secutor ruconius* (Hamilton)
 G. *Gazza minuta* (Bloch)

5.4. Angular (Text-fig. 1A and 2A) :

Angular, roughly wedge shaped, slightly concave, lying behind the dentary, is proximally broad and inserted into the ventral pocket of the dentary. Distally the narrow portion forms the articulating facet for the head of quadrate. Anteriorly it is closely applied to the angular. The maxillo-mandibular ligament is inserted at its inner aspect.

The above description applies to the other species but in *I. equulus*, it is semiellipsoidal in shape with almost straight anterior margin.

5.5. Ectopterygoid (Text-fig. 1ECT and 6A) :

The ectopterygoid is an elongated curved bone and is located behind the palatine. Its proximally broad portion is attached with the distal surface of the palatine and the distally narrow portion running over the quadrate is attached to the entopterygoid posteriorly.

This bone is similar in all the species under study.

5.6. Entopterygoid (Text-fig. 1ENT and 6A) :

Entopterygoid, a thin irregular shaped bone, taking part in the formation of the lower wall of the orbit, lies posterior to the ectopterygoid. Proximally it is attached to the distal surface of the lateral ethmoid and distally to the quadrate and metapterygoid. The bone is not well ossified in comparison to ectopterygoid.

There is no worthmentioning difference in the entopterygoid of other species.

5.7. Premaxilla (Text-fig. 1 PM and 2A) :

Each premaxilla consists of a curved elongated ventral portion and a slender ascending process which extends posteriorly up to the posterior half of the frontal. The ventral portion bears a knob posteromedially and is rounded distally. The bone is slender and is attached to its fellow of either side proximally. It is overlapped by the maxilla distally, specially when the mouth is closed. Dorsally it is loosely attached to the lachrymal and possesses a single row of small villiform teeth along its entire portion forming the gape of mouth.

The above description applies to *L. bindus* and *L. brevirostris* except a distinct anterodorsal projection in the latter species. In *L. equulus* (Text-fig. 2B), the teeth are present only in half of its total length towards the symphysis and the bone bears a deep broad notch below the teeth bearing portion. In *S. insidiator* (Text-fig. 2E) and *S. ruconius* (Text-fig. 2F) its distal portion is flattened. In *G. minuta* (Text-fig. 2G), the distal end of this bone is triknobed and presence of a caninoid tooth along with the villiform teeth readily distinguishes this species from the other species.

5.8. Maxilla (Text-fig. 1MX) :

Maxilla, is a toothless, long, S-shaped bone and lies posterior to the premaxilla. Its proximal end bears two projections forming a cup like depression in conjunction with the fellow of the other side and provides a sliding movement to the premaxillary process. Posteriorly it extends into a shaft which is free and lies over the dentary. The bone is overlapped by the lachrymal proximally and gives the attachment to the maxillo-mandibular ligament along its inner aspect.

The bone is similar in all the species under study.

5.9. Dentary (Text-fig. 1D) :

Dentary, the anterior most element of the lower jaw, is roughly plough shaped and bears minute villiform teeth along its entire portion and forms the gape of the mouth. The anterior portion of this bone proximally meets its fellow of the other side at the symphysis and its posterior somewhat narrow portion is outwardly oblique and overlapped by the premaxilla. Posteroventrally the bone bears a pocket for the insertion of the anterior process of the angular and its narrow distal portion is attached to the retroarticular.

In *L. equulus*, *L. brevirostris* and *L. bindus*, the shape of this bone is identical with that of *L. splendens* but the arrangement of teeth differs specifically. In the first species the teeth are present in many rows along the half of its total length towards the symphysis while in *L. brevirostris*, teeth are uniformly present in many rows along its entire length (Text-fig. 2B). In *G. minuta*, the bone bears caninoid teeth (Text-fig. 2G). In *S. insidiator* and *S. ruconius*, the dentary is hook-shaped.

5.10. Retroarticular (Text-fig. 1AN) :

Retroarticular, the smallest bone of the lower jaw lies anteroventral to the angular. It is triangular in shape and bears a shallow concavity along its base for providing the attachment area to the mandibulo-interopercular ligament. It is attached posteriorly to the angular.

There is no marked difference in respect of disposition of this bone in all the species.

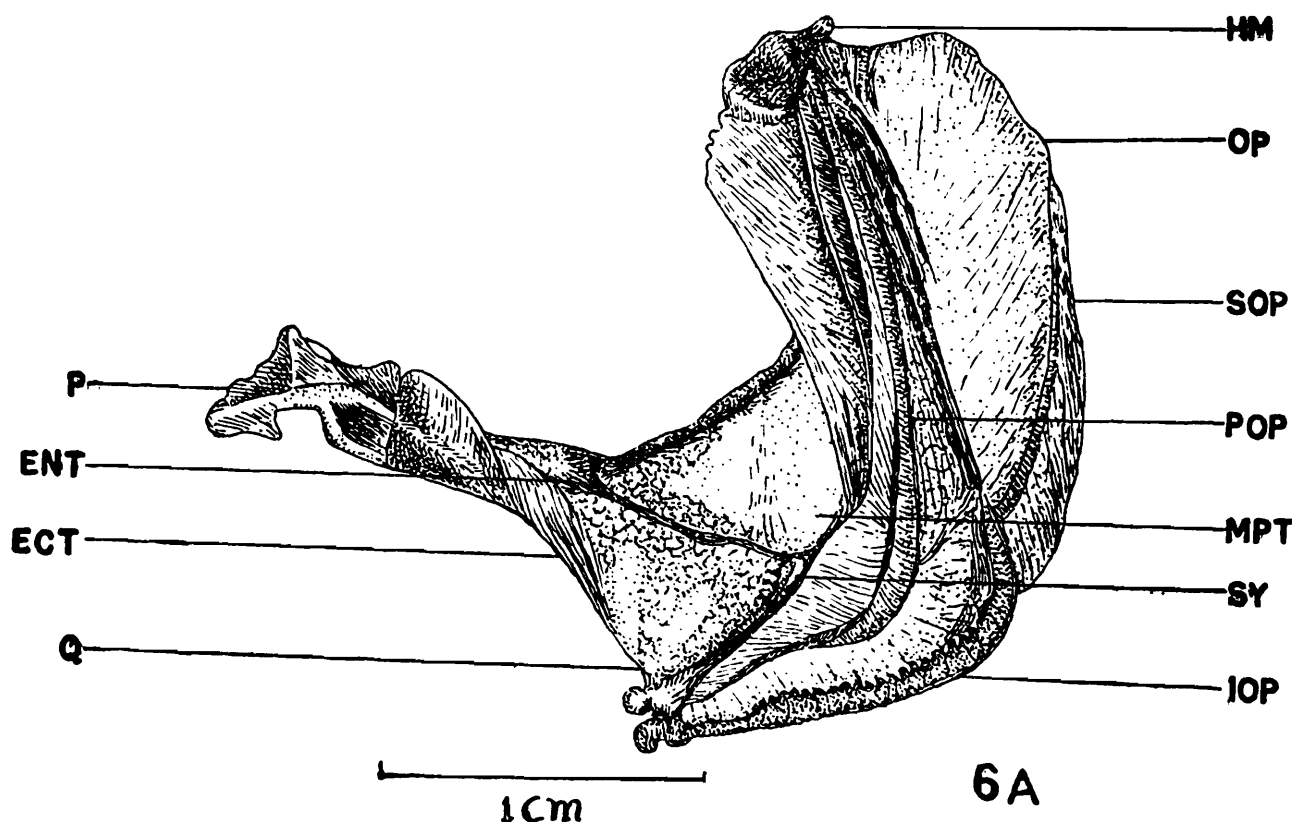
6. Hyoid Region :

The hyoid region which connects the oromandibular and the otic region is composed of paired hyomandibula, symplectic, interhyal, epihyal, opercular, preopercular, subopercular, interopercular, branchiostegal as well as unpaired urohyal and basihyal. The bones of this region take part in the respiratory and feeding movements of the jaws.

6.1. Hyomandibula (Text-fig. 1HM and 6A) :

Hyomandibula is a fan shaped bone with a distinguished head and an elongated distally narrow blade which bears a shallow groove along its posterior surface for receiving the anterodorsal arm of preopercular. Anteriorly it is bounded by the metapterygoid. The head of this bone consists of three condyles, the anterior condyles articulate with the ventrolateral facets of sphenotic and pterotic respectively and the posterior condyle articulates with the anterior articulating surface of the opercular. The hyomandibula bears a poorly developed channel like fossa on its proximal half of the ventromesial region for the passage of nerves. It connects the suspensorial bone with the neurocranium.

The above description applies also to other species as well.



Text-fig. 6A—G. Suspensorial bones of the left side.

A. *Leiognathus splendens* (Cuvier)

6.2. Symplectic (Text-fig. 2A) :

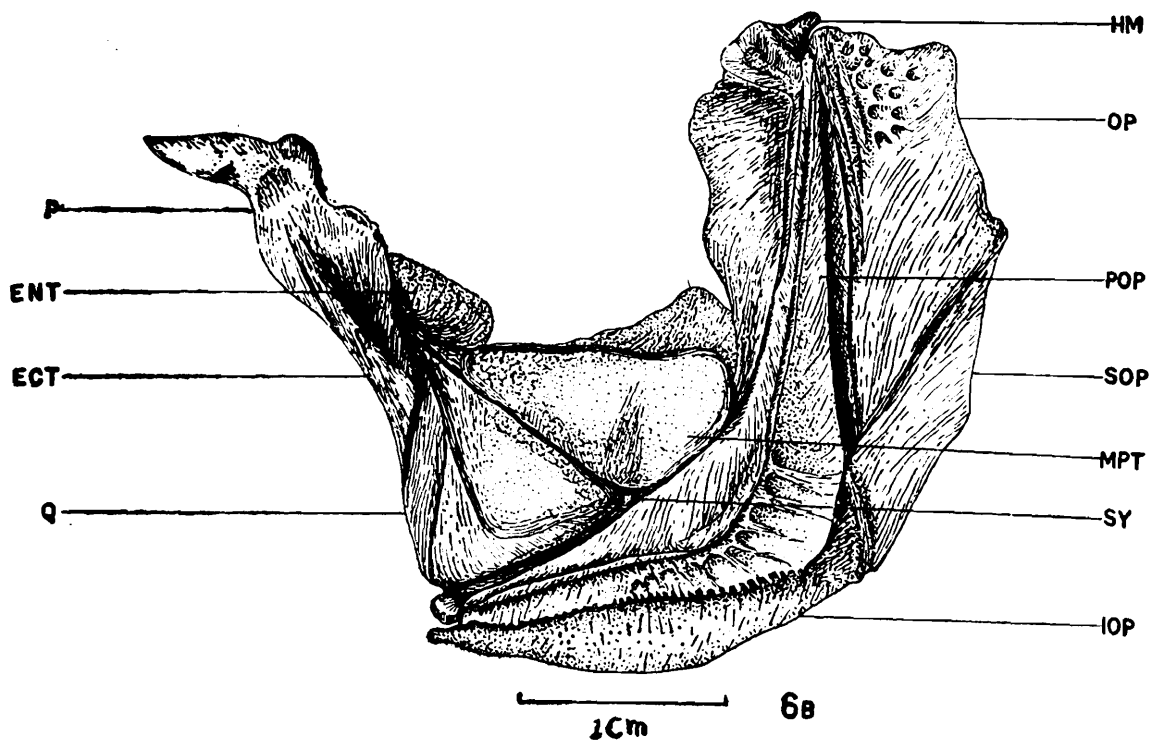
Symplectic is a poorly developed elongated bone lying in the posterior groove of the quadrate. Proximally it is attached to the metapterygoid and preopercular and joins the hyomandibula by a thin ligament.

There is no difference in respect of this bone among the species of the genera *Leiognathus* and *Gazza*. However, it is absent in *S. insidiator* and *S. ruconius*.

6.3. Interhyal (Text-fig. 1IH) :

Interhyal, a tiny rod shaped bone serving as the posterior suspensory element, is located anterior to the epihyal. At one end it is attached to the metapterygoid by ligament and at the other end to the epihyal. Laterally the bone is jointed with the preopercular and ventrally with the quadrate. Hyomandibula does not have any attachment with this bone like those of other percoid fishes.

This bone is similar in all the species under study.



Text-fig. 6B. *Leiognathus equulus* (Forsskal)

6.4. Epihyal (Text-fig. 1EH) :

Epihyal is a roughly triangular bone lying behind the interhyal with which it articulates along the narrow apex. The broad base of the bone is sutured with the ceratohyal.

The bone is similar in all the species.

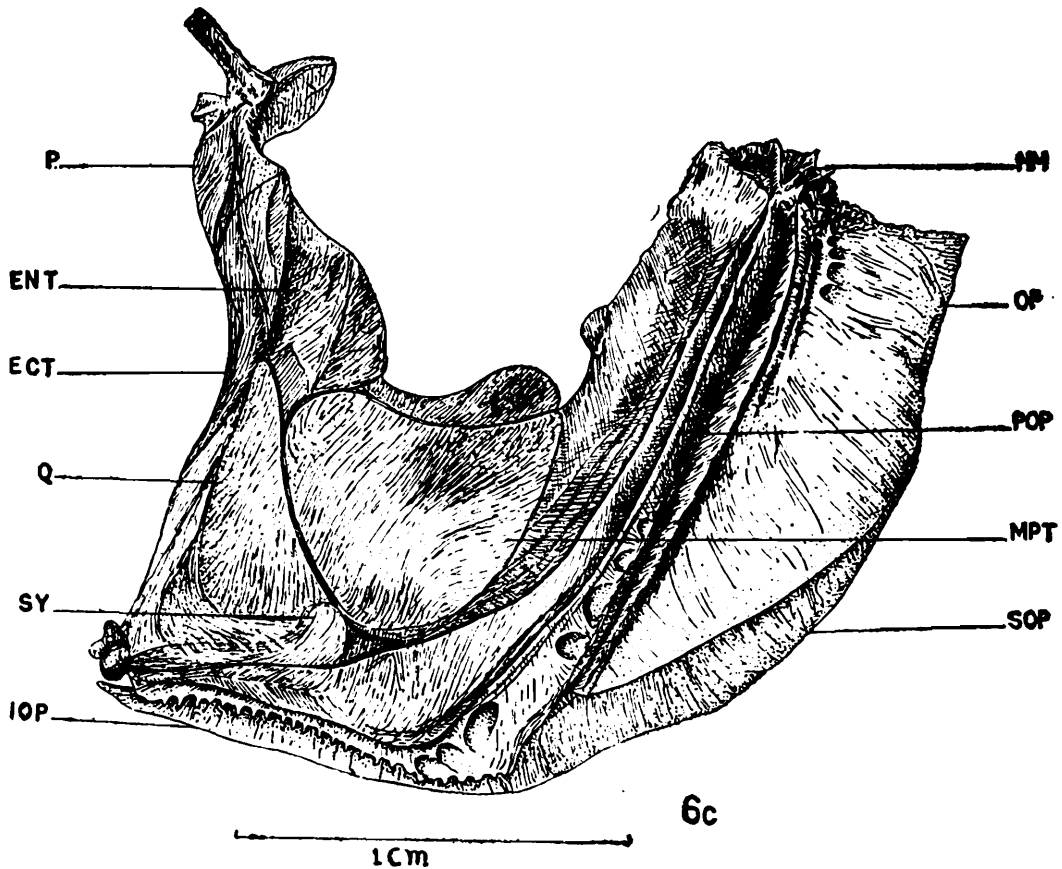
6.5. Ceratohyal (Text-fig. 1CH) :

Ceratohyal, the biggest element of the hyoid cornu, lies inner to the metapterygoid. It is narrow anteriorly and bears a knob like projection anteroventrally which articulates with the hypohyal. Posteriorly its broad portion is attached to the epihyal. Ventrally the ceratohyal gives attachment to the branchiostegal rays.

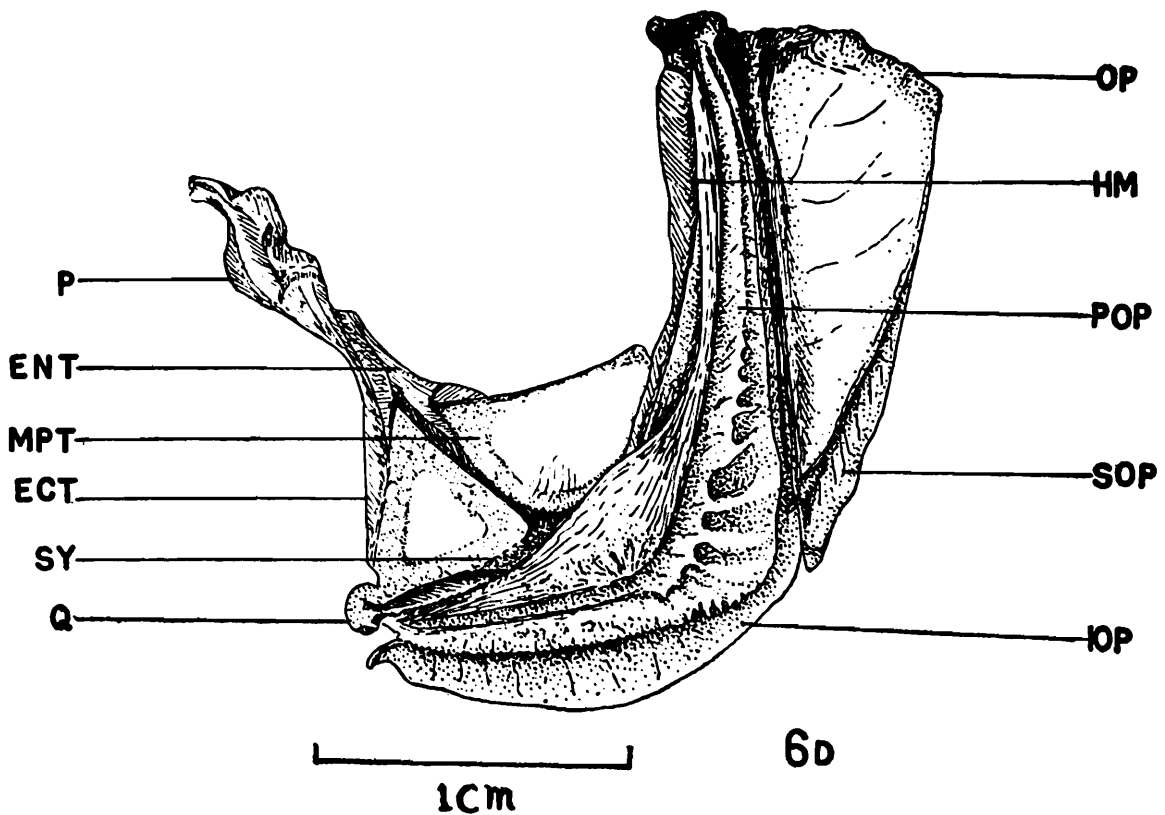
In all the species this bone is similar to that of *L. splendens*,

6.6. Hypohyal (Text-fig. 1H) :

The hypohyal presents the upper and lower elements in it. The upper element i. e. upper hypohyal is thick, broad and joins its fellow



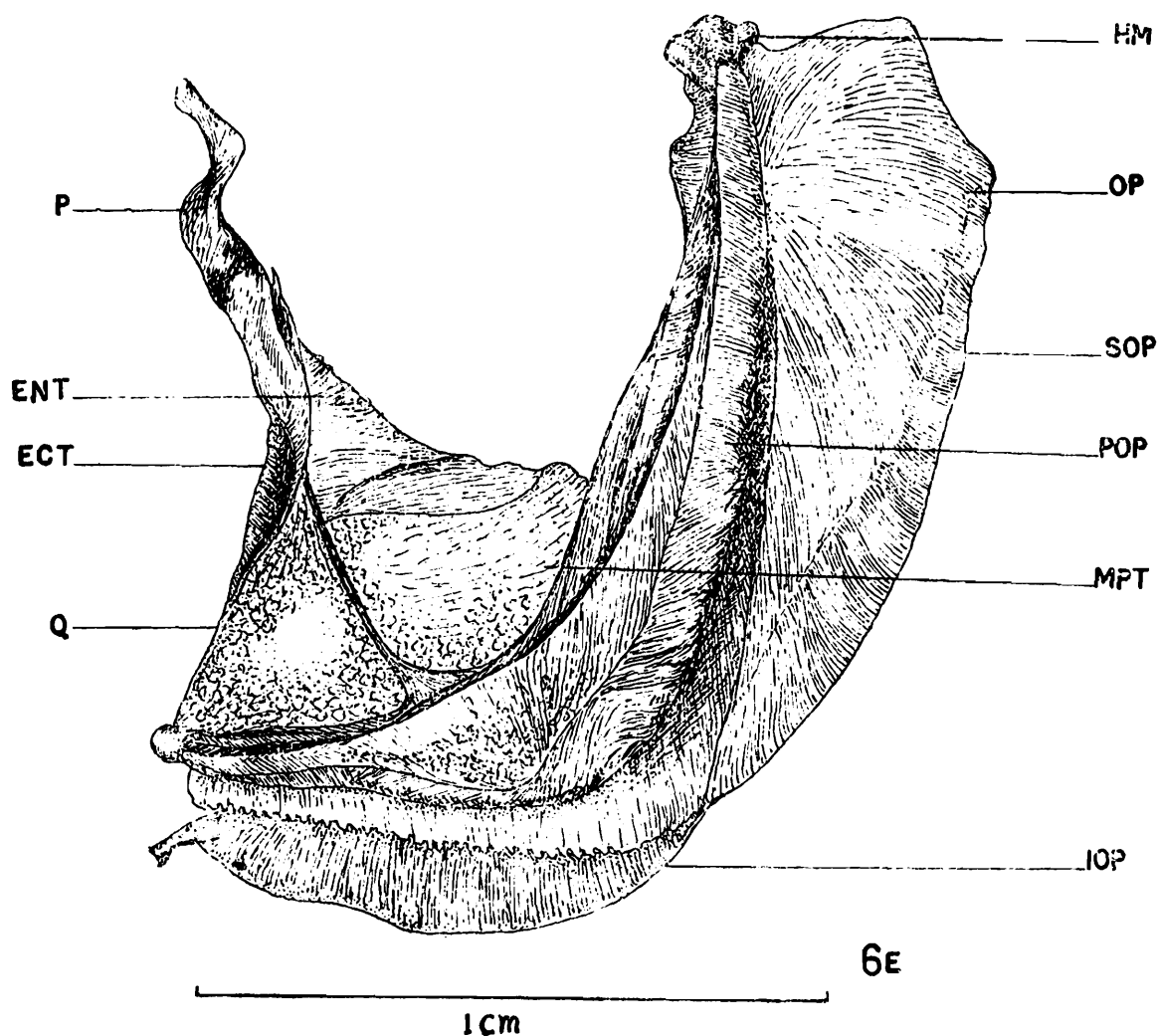
Text-fig. 6C. *Leiognathus bindus* (Valenciennes)



Text-fig. 6D. *Leiognathus brevisrostris* (Valenciennes)

of the opposite side at the middle and gives attachment to the basihyal dorsoanteriorly. It is attached to the ceratohyal posteriorly and to the lower hypohyal ventrally. The lower element i. e. lower hypohyal is a comparatively small curved bone and bears a concavity for the articulation of the ceratohyal.

The above description also applies to other species.



Text-fig. 6E. *Secutor insidiator* (Bloch)

6.7. Basihyal (Text-fig. 1BH) :

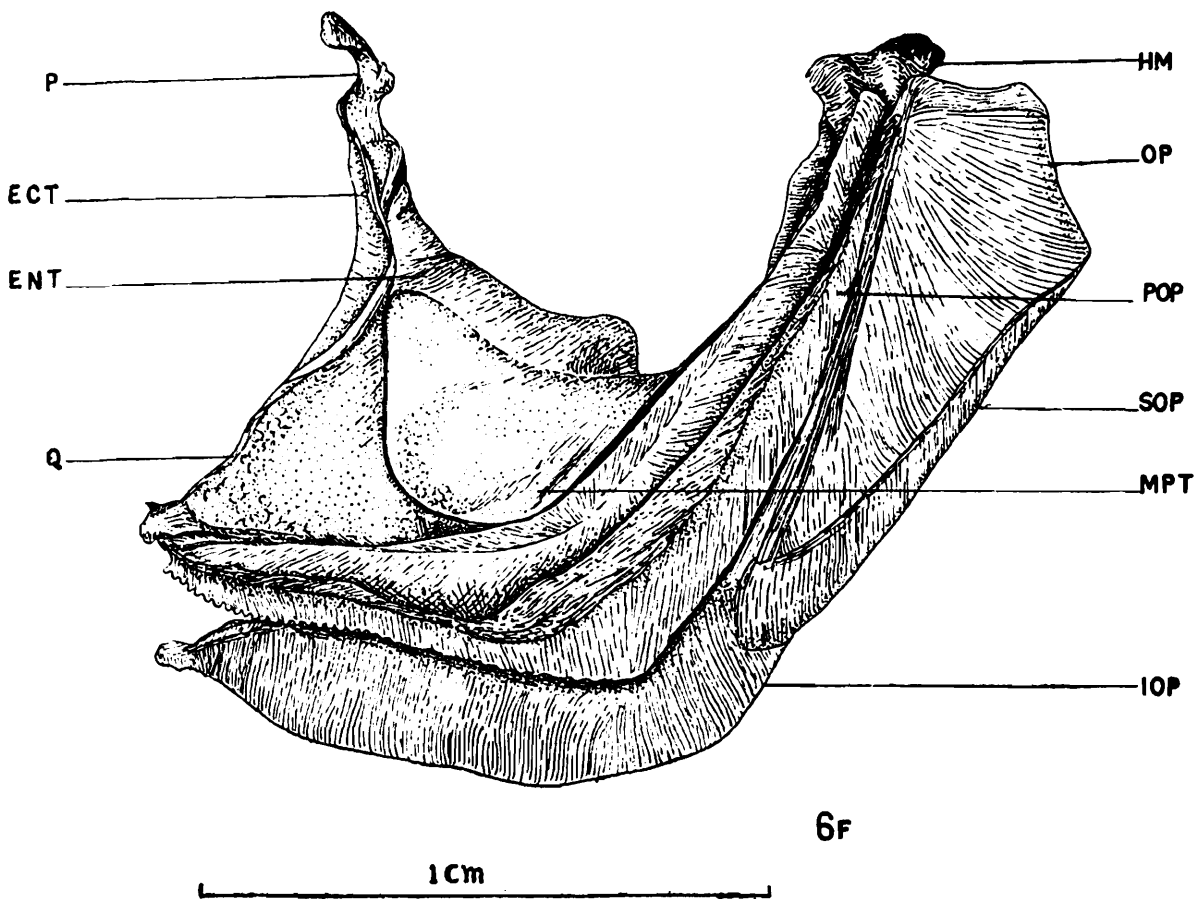
Basihyal is roughly a tumbler-shaped bone with a broad, free anterior end and narrow disc-like posterior end which is attached to the anterodorsal surface of the hypohyals. There is a ligamentous attachment between it and hypohyals ventrally.

The above description applies to all the species studied except *L. equulus*, where it is triangular in shape.

6.8. Preopercular (Text-fig. 1POP, 2A and 6A) :

Preopercular is a crescentic bone, lying proximally over the postero-dorsal surface of the head of hyomandibula and is located anterior to

the preopercular. It consists of a narrow elongated vertical and a broad horizontal arm. It is comparatively broad at the junction between its vertical and horizontal arm. The horizontal arm is slightly oblique along its lower margin and possesses dentated edge as well as ridge. The vertical arm forms a socket anteriorly for receiving the hyomandibular blade and is attached to the opercular posteriorly. Anteromesially it is attached to the metapterygoid and to the interopercular anteroventrally.



Text-fig. 6F. *Secutor ruconius* (Hamilton)

There is no marked difference in the position of this bone among other species except that the ridge of the horizontal arm is smooth. The horizontal arm is somewhat rounded along its posterior margin in *S. insidiator* (Text-fig. 2E), *S. ruconius* (Text-fig. 2F) and *G. minuta* (Text-fig. 2G).

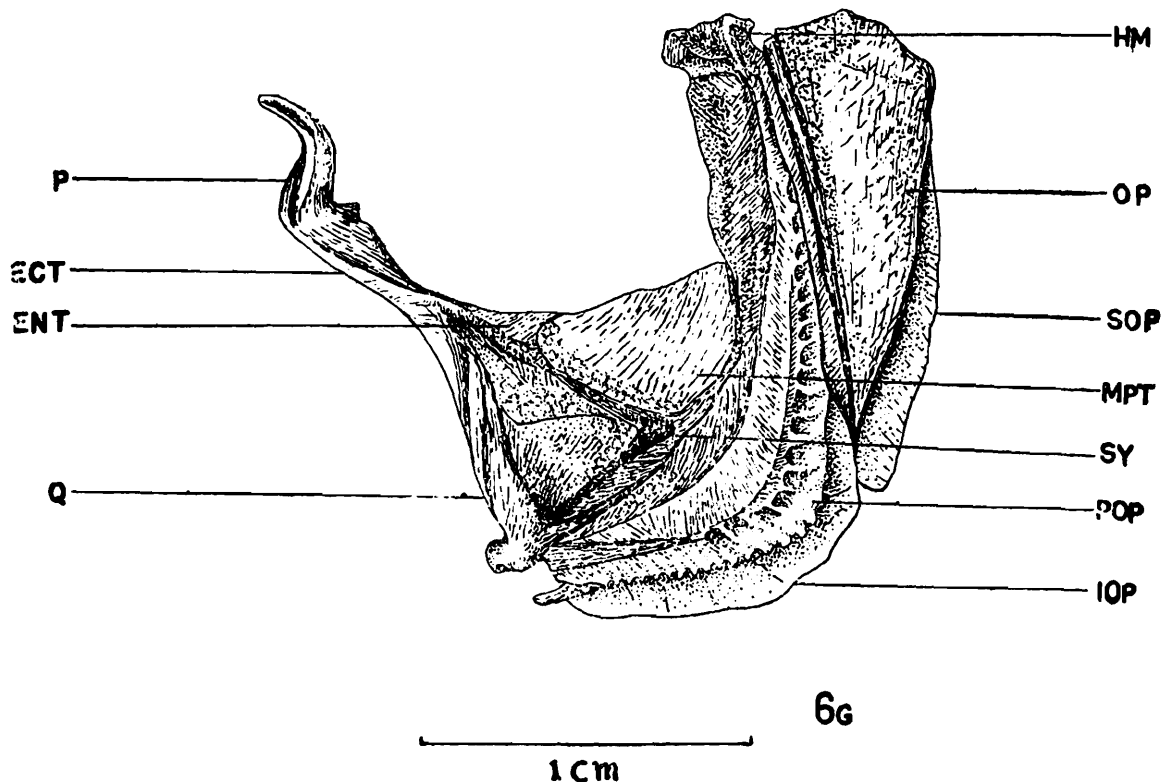
6.9. Interopercular (Text-fig. 1IOP) :

A thin chopper-shaped interopercular is situated anterior to the subopercular. It is thickened along its anterolateral margin and bears a notch ventromesially for lodging the apex of the epihyal. Proximally it is narrow and is attached to the retroarticular by mandibulo-interopercular ligament and distally to the subopercular by means of connective tissue.

The above description also applies to other species.

6.10. Subopercular (Text-fig. 1SOP and 2A) :

The subopercular is a thin flat bone with a broad blunt proximal end and a pointed distal end. Dorsally it is attached to the distal portion of the preopercular and proximally to the interopercular.

Text-fig, 6G. *Gazza minuta* (Bloch)

It is similar in all the species studied.

6.11. Branchiostegal (Text-fig. 1BS) :

There are five branchiostegal rays on the either side of the skull. Distally they are free but connected with each other by a membrane. Proximally the first four rays are attached to the ventral edge of ceratohyal and the fifth one is attached at the junction of the epihyal and ceratohyal. The fifth, posterior most ray is longest and leaf like while the others decrease in size gradually in the posteroanterior direction.

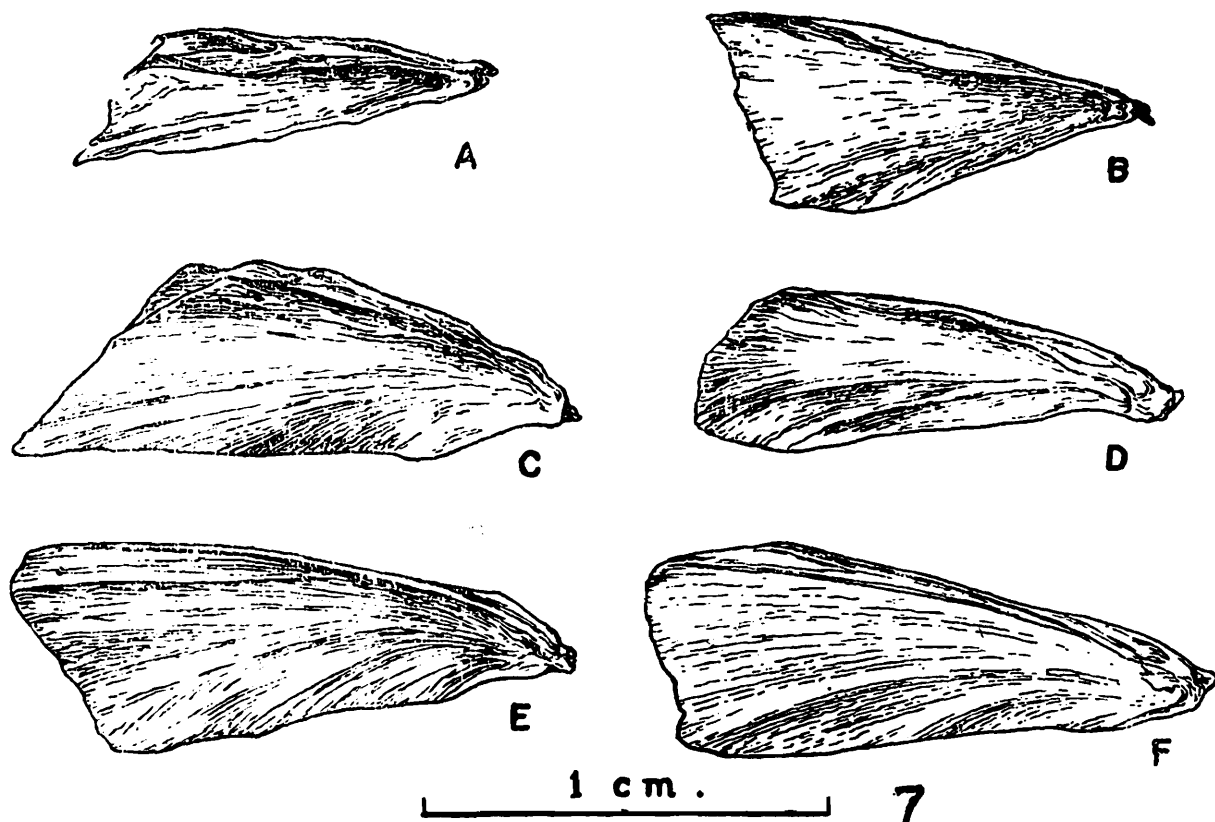
The above description applies to all the species, although in *S. insidiator*, *S. ruconius* and *G. minuta*, the last ray (5th) is attached to the epihyal only.

6.12. Urohyal (Text-fig. 7A) :

Urohyal, a well developed triradiate bone is located in the midventral line between the two halves of the hyoid cornu. It consists of one vertical and two horizontal wings. The proximal narrow and distally broad horizontal wings form a rhomboid. The urohyal is

attached to the hypohyals by ligament proximally and lies between the posteroventral surface of the cleithra distally.

The ventral aspect of this bone differs specifically. In *L. equulus* (Text-fig. 7C), it is wedge shaped, in *L. bindus* (Text-fig. 7B), spear shaped and slender in *S. insidiator*, *S. ruconius* (Text-fig. 7E), and *G. minuta* (Text-fig. 7F).



Text-fig. 7A—F. Lateral view of the urohyal.

- A. *Leiognathus splendens* (Cuvier)
- B. *Leiognathus bindus* (Valenciennes)
- C. *Leiognathus equulus* (Forsskal)
- D. *Leiognathus brevirostris* (Valenciennes)
- E. *Secutor insidiator* (Bloch)
- F. *Gazza minuta* (Bloch)

DISCUSSION

The comparative study of the cranial osteology in the three genera (*Leiognathus*, *Secutor* and *Gazza*) comprising seven species of leiognathids reveals that the general pattern of their osteocranium agrees with the typical percoid characters. Berg (1940), Regan (1913), Starks (1911), Delsman (1925) and Greenwood *et al.* (1966) have described such characters of the percoids. The common percoid characters as listed in the seven species include protractile mouth, development of a large frequently mobile premaxilla, exclusion of maxilla from the gape of mouth, the loss of maxillary, parasphenoid and pterygoid teeth, forked

posttemporal, reduction in size of the infraorbital (=Suborbital) bones, ethmoid (=mesethmoid of Berg, 1940) in contact with the prevomer, presence of Baudelot's ligament which extends up to the basicranium, presence of basisphenoid and loss of the orbitosphenoid.

The present comparative study records a great number of intergeneric and intrageneric variations in respect of the various regions of the osteocranium. The bones of the olfactory regions exhibit some intrageneric variations in respect of the configuration of the lateral ethmoid and prevomer. For example, there is only one antorbital spine in *S. insidiator* while two such antorbital spines are present on each lateral ethmoid in all the other species. Moreover, there is a single fontanel on the ventral aspect of the prevomer in *G. minuta*, two in *L. equulus* and no fontanel in other species.

The bone of the orbital region seems to be of much taxonomic significance since they reveal intergeneric difference such as the frontals forming a Y-shaped structure in the genera *Leiognathus* and *Secutor* vs. V-shaped in *Gazza*. The intrageneric variations include the presence of comma-shaped ridge on the posterior half of the frontals in *L. splendens* and *L. bindus* while other species do not possess any such structure. In addition the circumorbital sereis are incomplete in case of *L. bindus* and *G. minuta* but complete in the rest of the species.

In the otic region three bones i. e. supraoccipital, exoccipital and parietal show differences in respect of their configuration and relative disposition at generic as well as specific level. Starks (1911) interpreted the disposition of supraoccipital crest in terms of phylogenetic relationships among the scombroid fishes. The relative size and shape of supraoccipital crest seems to be diagnostic features in the identification of leiognathids genera. For example, the supraoccipital crest is elongated and curved in the genus *Leiognathus*, short and curved in *Secutor* and short and straight in the genus *Gazza*. In *L. fasciatus*, Starks (*op. cit.*) pointed out that the supraoccipital did not reach the foramen magnum and considered it as a family character. However, such a character varies specifically inasmuch as it extends upto the furrow of the foramen magnum in all species studied except in *L. bindus*. Further, the disposition of the posteroventral margin of the supraoccipital process plays an important role in the generic diagnosis of the family Leiognathidae since it is oblique (Text-fig. 2a, b, c, d, e and f) in the genera *Leiognathus* and *Secutor* and vertical to the median longitudinal axis of the skull in the genus *Gazza*. The general contour of the exoccipital does not vary significantly but the number of foramina present on this bone reveals intergeneric differences. Starks

(1911) observed three foramina in the exoccipital of *L. fasciatus* and opined that this was a characteristic feature of the family Leiognathidae. Presence of two foramina in the species of the genus *Secutor* and three in the other species of the genera *Leiognathus* and *Gazza* clearly indicate that the number of foramina in exoccipital as well as the relative length and shape of the supraoccipital crest can not be taken as a diagnostic character of the family as pointed out by Starks (*op. cit.*).

In the basicranial region the shape of the posterior myodome and the disposition of parasphenoid vary specifically. The extension of bifurcated portion of the parasphenoid upto the posterior end of the basioccipital is a constant feature of the species belonging to the genera *Secutor* and *Gazza* while species specific variation occurs among the species of the genus *Leiognathus*. The disposition of this bone also differs at a generic level since it forms an angle of more than 75° with the dorsomedian longitudinal axis of the skull in the genus *Secutor* and less than 60° (Text-fig. 2g) in the genera *Leiognathus* and *Gazza*. It seems that the disposition of basioccipital is associated with the direction of the protrusibility of the mouth since the oral tube protrudes upwards in *Secutor* but horizontally forwards or slightly downwards in *Leiognathus* and *Gazza*.

The bones of the oromandibular region are of much taxonomic and phylogenetic significance. The movable premaxillaries with a long posterior process exhibit a typical percoid character. Moreover the configuration of this bone shows intergeneric differentiation. In the genus *Leiognathus* it bears villiform teeth and its distal end is rounded. In the genus *Secutor*, the teeth are also villiform but the distal end of the bone is truncated. In *Gazza* it bears caninoid teeth and its distal end is triknobed. Further relative size of the premaxillary process is species specific which helps in the extent of protrusion of the mouth. The ontogenic gradation of the symplectic bone, which is poorly developed in the species of the genera *Leiognathus* and *Gazza* and is totally absent in the species of the genus *Secutor*, shows a departure from other percoids where the bone remains well developed. The attachment of the interhyal with the metapterygoid instead of hyomandibula is another specialized feature of these fishes since it is attached to the hyomandibula, in other percoids. Starks (1911) reported it as a family character. Day (1887), Regan (1913), Weber and de Beaufort (1931), Munro (1955) and James (1978) reported the preopercular's edge of these fishes is serrated (a characteristic feature of the family Leiognathidae). However, we have also observed the preopercular's

ridge as serrated in two species of the genus *Leiognathus* (*L. splendens* and *L. indicus*) in addition to the serrated preopercular's edge. This character seems to be of an additional aid in elucidating the systematic identity of the species of the genus *Leiognathus*. The general contour and configuration of the urohyal bone depicts intrageneric variations (Text-fig. 7A, B, C, D, E and F).

In view of foregoing discussion it is concluded that the osteological attributes as exhibited by the osteocranium of these fishes play an important role in the derivation of phylogenetic relationships and also in delineating the taxonomic identity of various taxa at generic as well as specific level. The osteological key for differentiating the genera as well as species under each genus is provided below.

Key to the genera

- | | | |
|--|-----|--------------------|
| 1. Supraoccipital crest convex, posteroventral margin of supraoccipital process oblique forming an angle of less than 60°. Caninoid teeth absent. Distal end of premaxilla rounded or truncated. ... | ... | 2 |
| Supraoccipital crest straight, posteroventral margin of supraoccipital process vertical. Caninoid teeth present. Distal end of premaxilla triknobed. ... | ... | <i>Gazza</i> |
| 2. Symplectic present, distal end of premaxilla round, parasphenoid forms an angle of less than 60° with dorsomedian longitudinal axis of the skull, exoccipital with three foramina. ... | ... | <i>Leiognathus</i> |
| Symplectic absent, premaxilla with truncated distal end, parasphenoid forms an angle more than 75° with the dorsomedian longitudinal axis of the skull, exoccipital with two foramina. ... | ... | <i>Secutor</i> |

Key to the species of genus *Secutor*

- | | | |
|---|-----|--|
| 1. One antorbital spine, posterior myodome oval...
Two antorbital spines, posterior myodome slender. ... | ... | <i>insidiator</i>

<i>ruconius</i> |
|---|-----|--|

Key to the species of genus *Leiognathus*

- | | | |
|--|-----|---|
| 1. Gape of mouth (premaxilla + dentary) entirely toothed. Prevomer square shaped without any fontanel on its ventral surface. Basihyal tumbler shaped. ... | ... | 2 |
|--|-----|---|

- Gape of mouth (premaxilla+dentary) not toothed entirely. Vomer dumbbell shaped with two fontanelle on its ventral surface. Basihyal triangular. ... *equulus*
2. Circumorbital chain complete. Parietal petal shaped or triradiate. Ventral thin portion of supraoccipital extends upto furrow of foramen magnum. Urohyal rhomboidal in its ventral aspect. ... 3
- Circumorbital chain incomplete, Parietal tetraradiate. Ventral thin portion of supraoccipital not extends upto the furrow of foramen magnum. Urohyal spear shaped in its ventral aspect. ... *bindus*
3. Parietal triradiate. Frontal with a comma shaped ridge on its posterior aspect. Premaxillary process extends upto the posterior half of the frontal. Posterior myodome oval. ... *splendens*
- Parietal petal shaped. Frontal without comma shaped ridge on its posterior aspect. Premaxillary process extends upto the supraoccipital. Posterior myodome slender. ... *brevirostris*

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