

COMPARATIVE OSTEOLOGY OF THE FISHES OF THE FAMILY
LEIOGNATHIDAE

PART I : OSTEOLOGY

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ABSTRACT

The paper deals with the comparative osteology of 17 species of the three genera, *Leiognathus*, *Secutor* and *Gazza*, in the family Leiognathidae. While giving a detailed description of the osteology of *L. jonesi*, representing the genus *Leiognathus*, the osteological features of the other two genera are compared. The distinctive features of the various species are listed. The relationships among the genera and the species are discussed, and osteological keys to the genera and the species are provided.

The results of the study indicate that within the genus *Leiognathus* the species constitute four groups: the first represented by *L. smithursti*, *L. splendens*, *L. jonesi* and *L. dussumieri*; second by *L. fasciatus* and *L. equulus*; third by *L. leuciscus*, *L. berbis* and *L. lineolatus*; and fourth by *L. daura*, *L. blochi* and *L. brevisrostris*.

The species *L. bindus* stands apart from all the other species of *Leiognathus* and shows affinity to genus *Secutor* on one hand and genus *Gazza* on the other, and incidentally exhibits certain specialised characters like the upwardly directed protrusible mouth of the former and the development of prominent teeth of the latter. The species of *Secutor* and *Gazza* remain distinct within the respective genera and from species of the genus *Leiognathus*.

INTRODUCTION

According to recent authors, the family Leiognathidae includes three genera, *Leiognathus* Lacepede, *Secutor* Gistel and *Gazza* Ruppell. From the entire range of their distribution in the Indo-Pacific, 19 species of *Leiognathus*, 3 species of *Secutor* and 2 species of *Gazza* have so far been reported, of which 15 species of *Leiognathus*, 2 species of *Secutor* and 2 species of *Gazza* are now known to occur in the seas around India. A systematic review of 18 species of this family (excepting *L. indicus* reported recently) has been made by the author (James 1975**).

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** For the details of the references cited in this part of the paper, Part I, see end of Part II, in Number 4 of this Volume.

Although some aspects of the biology and fishery of different species of this family have been investigated in different areas of their distribution, so far no detailed study has been made on the osteology of this family. Earlier observations on the osteology of these fishes include those of Agassiz (1837) on the skeleton of *L. fasciatus* under *E. setigera*, of Bertin and Arambourg (1958b) on the mechanism of the mouth slip, of Boulenger (1904) on the osteology of *Equula* and *Gazza*, of Delsman (1925) on the mechanisms of mouth protrusion in Leiognathidae, of Gregory (1933) on the skeleton of *Equula*, of Husaka (1974) on the urohyal bone of some species of leiognathids, of Starks (1911, 1926) on the osteology of *L. fasciatus* and of Whitehead (1975) on the mechanism of the mouth slip. A systematic study of the group indicated that a few of the species described need comment and clarification as to their position in the system. Some of the characters described by earlier authors for the species are difficult to ascertain or are even contradictory. Therefore, an attempt is made for a comprehensive and comparative study of the osteology of these fishes to draw a clear distinction between the different species based on osteological characters since many similarities and differences have been noticed among the species under investigation. The systematic significance of these characters is discussed and an osteological key provided.

In comparing the osteology of the species, it was noticed that, while they have many features in common, the three genera *Leiognathus*, *Secutor* and *Gazza* basically differ from one another osteologically. Therefore, a detailed description of the osteology of *L. jonesi*, representing the genus *Leiognathus*, is given, with which the other two genera are compared. The species within the three genera have also been compared for similarities and differences in important osteological characters. Thus, the intergeneric and interspecific osteological differences and similarities have been studied and the affinities between species and genera outlined.

MATERIAL AND METHODS

The material for this study has been collected from various fish landing centres along the east and west coasts of India, especially from the Palk bay and the Gulf of Mannar in the vicinity of Mandapam, where the group forms an important fishery. Skeletons were prepared for study by cooking the fresh fish in water. The bones of the skulls of all the species were disarticulated and studied.

OSTEOLOGY

The main features of the skeleton may be summarised as follows: The skull is small and compressed (Figs. 1 and 2) and its bones are thin and light, neurocranium laterally compressed, short and high with bony ridges and a nuchal spine on the dorsal side, supraoccipital crest low or high, lying wholly behind

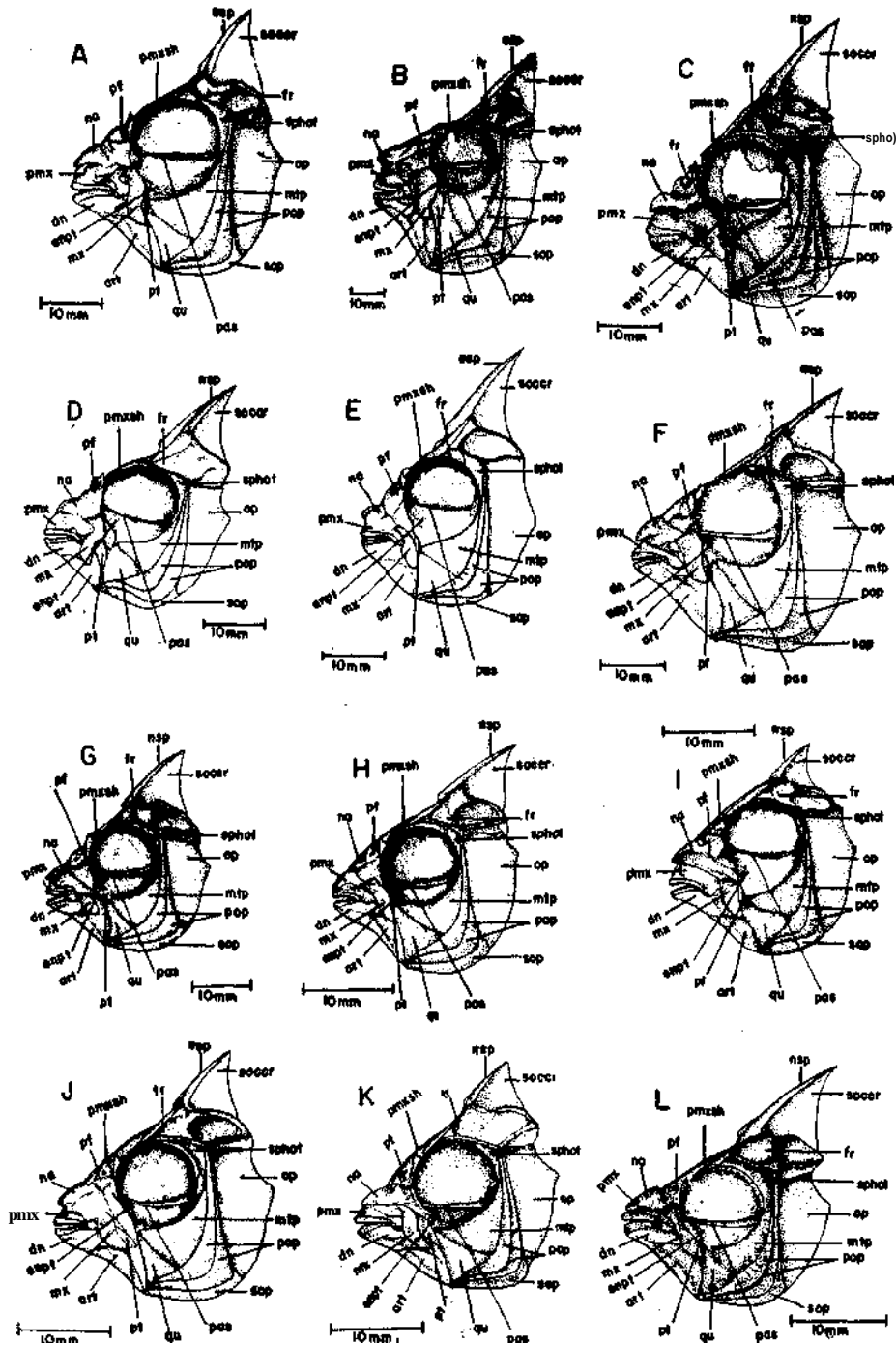


FIG. 1. Skull lateral view: A. *L. fasciatus*, B. *L. equulus*, C. *L. smithursti*, D. *L. splendens*, E. *L. jonesi* and F. *L. dussumieri*. G. *L. daura*, H. *L. blochi*, I. *L. brevirostris*, J. *L. leuciscus*, K. *L. berbis*, L. *L. lineolatus*. (For abbreviations, see Fig. 2.)

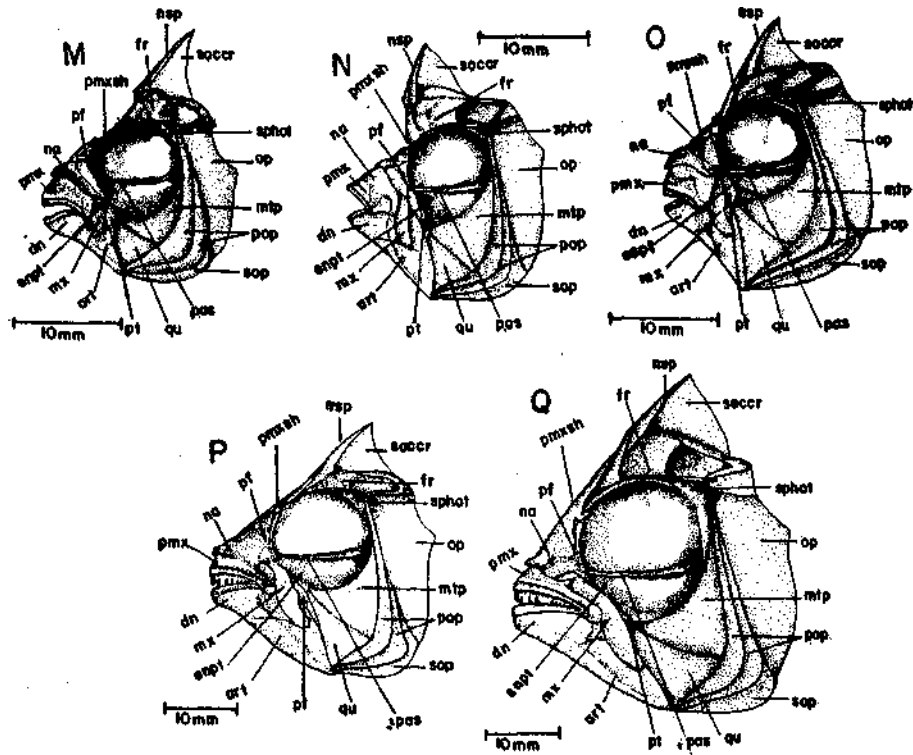


FIG. 2. Skull, lateral view: M. *L. bindus*, N. *S. ruconius*, O. *S. insidiator*, P. *G. minuta*? Q. *G. achlamys*.

art: articular; dn: dentary; enpt: entopterygoid; fr: frontal; mtp: metapterygoid; mx: maxilla; na: nasal; nsp: nuchal spine; op: opercle; pas: parasphenoid; pf: prefrontal; pmx: premaxilla; pmxsh: premaxillary sheath; pop: preopercle; pt: pterygoid; qu: quadrate; soccr: supraoccipital crest; sop: subopercle; sphot: sphenotic.

the frontals; supraorbital bony ridge of each side continued posteriorly as outer border of nuchal spine; vomer devoid of teeth, broad at the anterior end and tapering to a sharp point posteriorly; palate toothless. Teeth in jaws minute, in a single setiform series, or, in upper jaws, a series of sharp teeth and a curved canine tooth on each side of symphysis; in lower jaw, a series of curved, pointed teeth, with a pair of symphyisial canine-form teeth with a notch between them to receive the upper canine-form teeth. Mouth very protractile, the long intermaxillary pedicels lying in a groove formed by the bifurcation of the occipital crest; when fully protracted it forms a tube directed horizontally, dorsally or downwards. Proximal extremity of maxillary curved, slipping under preorbital, distal extremity exposed, without a supplemental bone. Lower margin of preopercle serrate; four to five branchiostegals; gill rakers 11 to 22 of various

lengths. Vertebrae 22 to 24; ribs fragile, interneurals and interhaemals do not correspond to neural and haemal spines. Pectoral and pelvic girdles prominent and deep; single dorsal fin with 8 spines and 15-16 rays; anal with 3 spines and 14 rays; the second dorsal and anal spines the longest.

NEUROCRANIUM

The neurocranium (Figs. 3 to 14) is somewhat narrow in the front and broad behind. The vomer forms the anterior end and the nuchal spine the posterior end of the neurocranium. The sides of the neurocranium are not entire but are formed by the spinous projections or processes of the frontals, sphenotics and pterotic bones. On the dorsal side, the two prominent supraorbital bony ridges which arise at the inner one of a pair of more or less pronounced post-nasal spines run posteriorly in a converging manner and form the outer borders of the nuchal spine. The interorbital concavity is deep. The neurocranium of

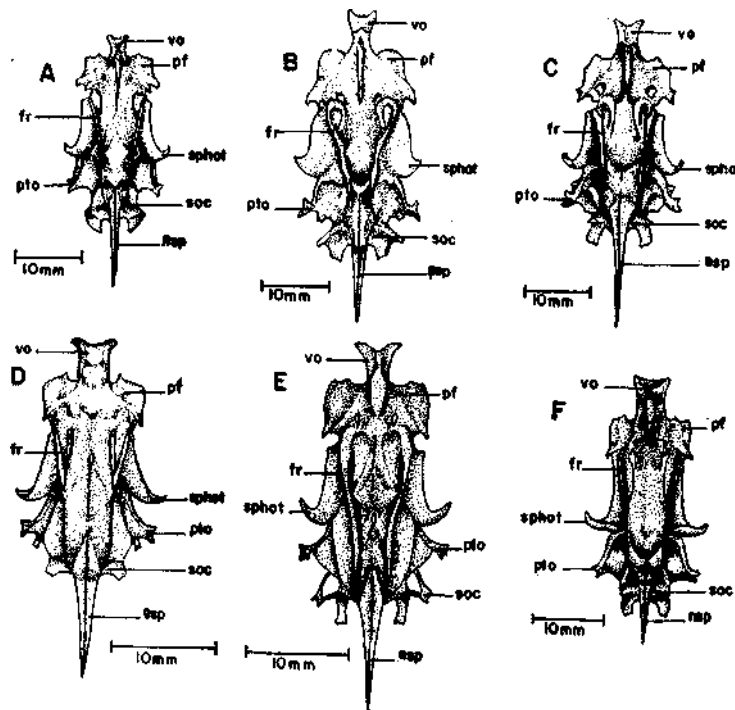


FIG. 3. Neurocranium, dorsal view: A. *L. fasciatus*, B. *L. equulus*, C. *L. smithursti*, D. *L. splendens*, E. *L. jonesi*, F. *L. dussumieri*.

it: frontal; nsp: nuchal spine; pf: prefrontal; pto: pterotic; soc: supraoccipital; sphot: sphenotic; vo: vomer.

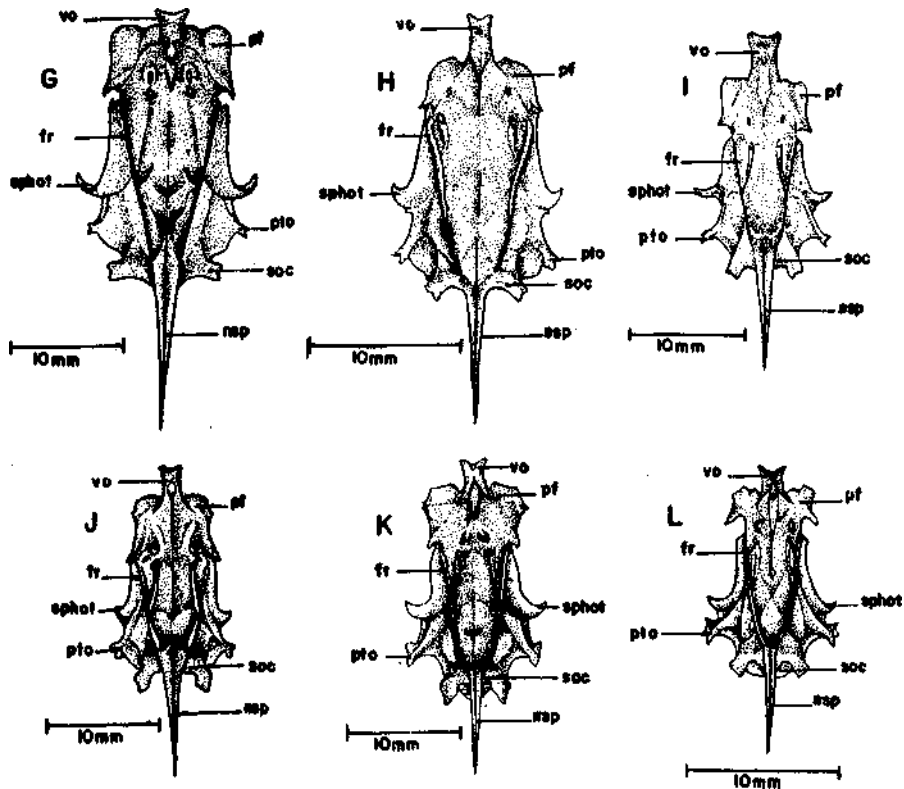


FIG. 4. Neurocranium, dorsal view: G. *L. daura*, H. *L. blochi*, I. *L. braviostris*, J. *L. leuciscus*, K. *L. berbis*, L. *L. lineolatus*.

fr: frontal; nsp: nuchal spine; pf: prefrontal; pto: pterotic; soc: supraoccipital; sphot: sphenotic; vo: vomer.

Leionathus and *Gazza* resemble closely in that the front end is only slightly narrower than posterior end, whereas in *Secutor* the front end is strikingly narrower than the posterior end. Further, the nuchal spine is less prominent in the former two genera compared to that of the latter.

On the ventral side of the neurocranium, seven major parts stand out conspicuously, beginning from the anterior end, the vomer, the frontals, the sphenotics, the pterotics, the nuchal spine, the occipital bones and the parasphenoid. Among the genera, *Leionathus* and *Secutor* resemble more closely between themselves in that the sphenotic and pterotic regions are close to each other (or somewhat continuous), whereas in *Gazza* the pterotic region remains apart from the sphenotic region. Within the genus *Leionathus*, *L. equulus* and *L. jonesi* differ from others in having lateral cavities in the pterotic region.

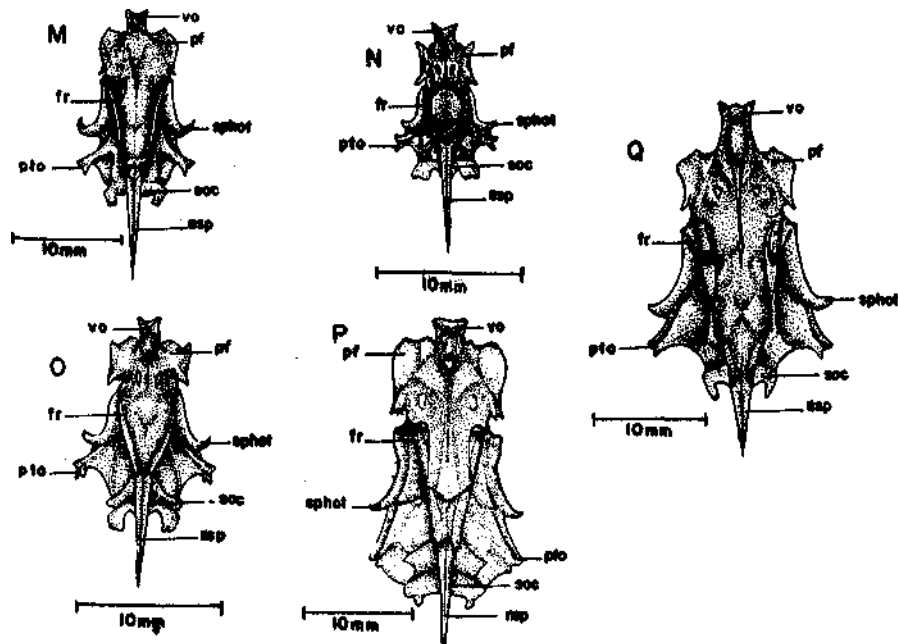


FIG. 5. Neurocranium, dorsal view: M. *L. bindus*; N. *Secutor ruconius*; O. *S. insidiator*; P. *G. minuta*; Q. *G. achlamys*.

fr: frontal; nsp: nuchal spine; pf: prefrontal; pto: pterotic; soc: supraoccipital; sphot: sphenotic; vo: vomer.

In the lateral view of the neurocranium, the orbital cavity is prominent, underlined by the vomer and the parasphenoid. The posterior portion forms a solid mass composed of the occipital complex and the otic bones. Whereas the front half is more or less horizontal in *Leiognathus* and *Gazza*, it is upturned in *Secutor*. Unlike in the genera *Leiognathus* and *Secutor*, in the genus *Gazza* the nuchal spine is carried forwards as far as the postnasal spines. In the genus *Leiognathus*, in *L. dussumieri* and *L. bindus* the posterior part of neurocranium behind the orbital cavity, instead of being inclined upwards as in most of the other species, is almost horizontal in position.

In the posterior view of the neurocranium, in addition to the occipital and otic regions of the skull, the ventral view of front part of neurocranium (consisting of the vomer, frontals, part of sphenotics and parasphenoid) is also visible because of the differential elevation of the front and hind parts of the neurocranium. The posterior views of the neurocrania of *Leiognathus* and *Secutor* resemble closely each other in shape and differ from *Gazza*. Within the genus *Leiognathus*, the nuchal spine of *L. equulus* and *L. daura* appear more conspicuous (longer) than in other species. *L. jonesi* is distinct in that two

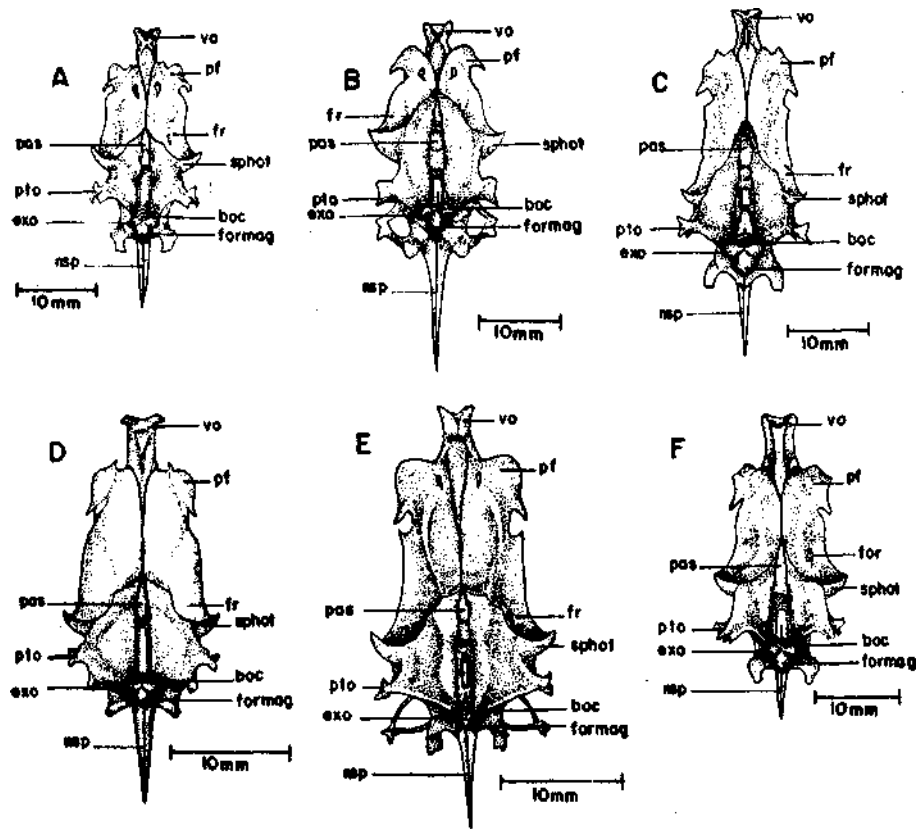


FIG. 6. Neurocranium, ventral view: A. *L. fasciatus*; B. *L. equulus*; C. *L. smithursti*; D. *L. splendens*; E. *L. jonesi*; F. *L. dussumieri*.

boc: basioccipital; expo: exoccipital; formag: foramen magnum; fr: frontal; nsp: nuchal spine; pas: parasphenoid; pf: prefrontal; pto: pterotic; sphot: sphenotic; vo: vomer.

lateral cavities are formed in the occipital | pterotic region. Orbits are large, more than $1/3$ length of neurocranium. Among the three genera, they are largest in *Gazza*. While there is a slight variation among species of *Leiognathus*, within the other two genera, the orbital cavity is larger in *S. insidiator* than in *S. rucconius* and larger in *G. achlamys* than in *G. minuta*.

INDIVIDUAL BONES OF THE SKULL

Olfactory region: The *dermethmoid* (*deth*) is median, fits in tightly at the forked posterior portion of the vomer. Its posterior end is closely grasped by the prefrontals. At the anterolateral positions, the dermethmoid supports the nasals.

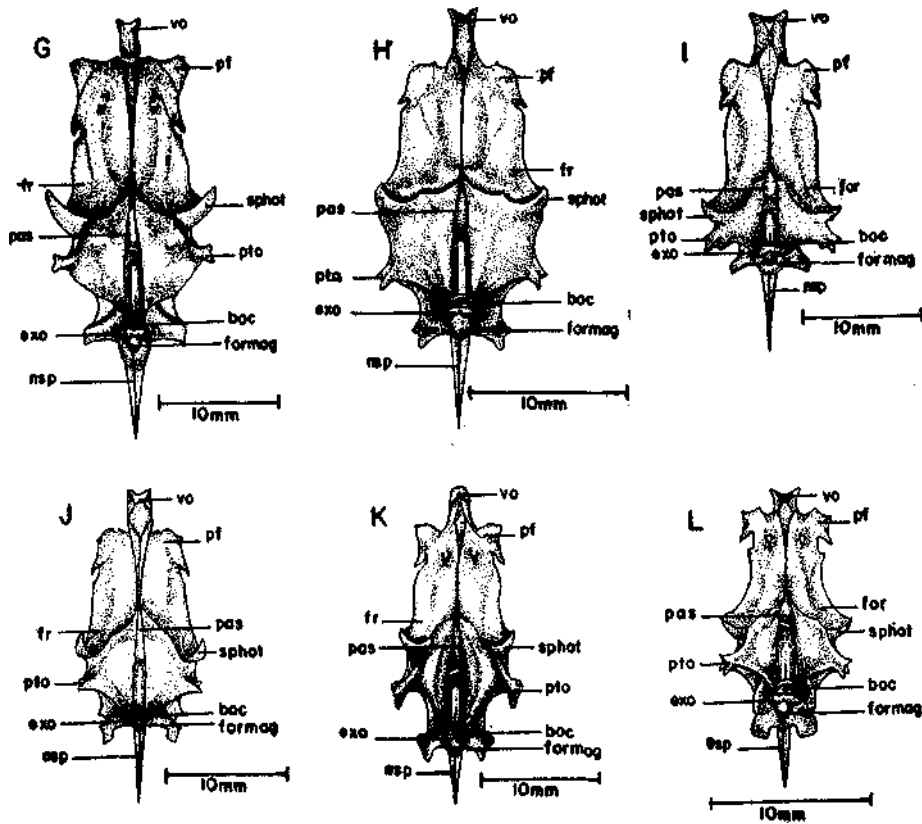


FIG. 7. Neurocranium, ventral view: G. *L. daura*; H. *L. blochi*; I. *L. brevisrostris*; J. *L. leuciscus*; K. *L. berbis*; L. *L. lineolatus*.

boc: basioccipital; expo: exoccipital; formag: foramen magnum; fr: frontal; nsp: nuchal spine; pas: parasphenoid; pf: prefrontal; pto: pterotic; sphot: sphenotic; vo: vomer.

About one-third length from the anterior end, on the ventral side, a backwardly directed process from the dermethmoid lies dorsal to the anterior end of the parasphenoid. The shape of the dermethmoid is similar in *Leiognathus* and *Gazza*. In *Secutor*, the dermethmoid is inverted T shaped, the vertical limb directed anteriorly and the horizontal limb posteriorly, the former closely fitting between the two prefrontals and the latter articulating with the frontals. It does not directly meet the vomer. The dermethmoid bears median ridges ventrally and dorsally, the dorsal ridge of a lesser height than the ventral.

The *prefrontals* (pjf) are two irregular bones, forming the anterior wall of the orbit and posterior mesial walls of the nasal cavity. They articulate with

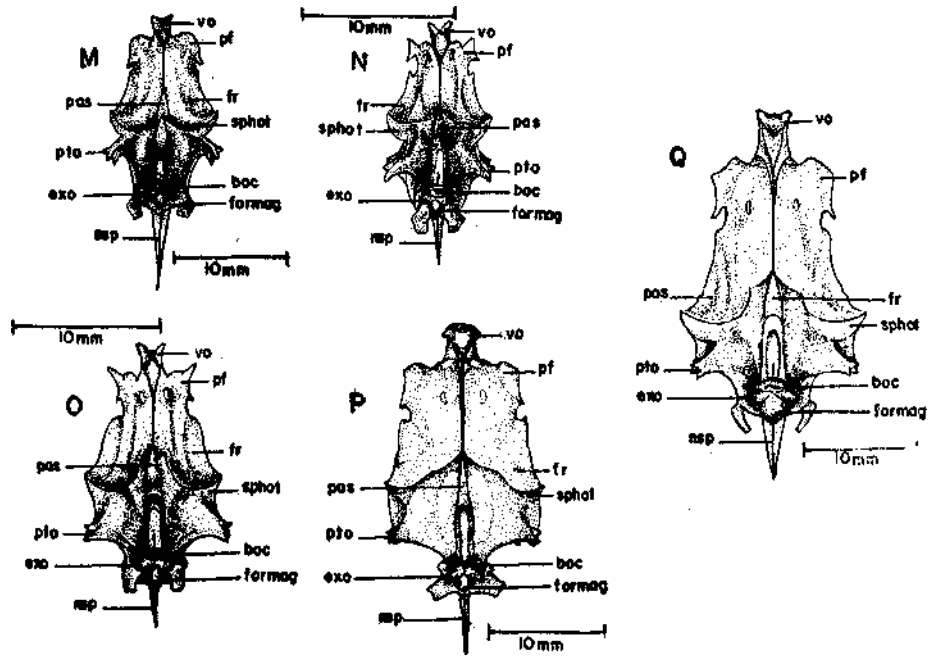


FIG. 8. Neurocranium, ventral view: M. *L. binous*; N. *S. ruconius*; O. *S. insidiator*; P. *G. minuta*; Q. *G. achlamys*.

boc: basioccipital; expo: exoccipital; formag: foramen magnum; fr: frontal; nsp: nuchal spine; pas: parasphenoid; pf: prefrontal; pto: pterotic; sphot: sphenotic; vo: vomer.

vomer, dermethmoid, frontals and parasphenoid. The prefrontals in *Leiognathus* and *Gazza* resemble closely in shape and bear dorsally an oblique ridge, which is absent in *Secutor*. Their shape is also different in *Secutor*.

The *hasals* (*na*) are small, thin bones attached loosely at the anterolateral portions of the dermethmoid. The anterior portion of nasal in *Secutor* is narrower and sharper than the anterior portions of nasals in *Leiognathus* and *Gazza*.

The *vomer* (*vo*) (Fig. 15) is broad anteriorly and narrow posteriorly, where it ends in a sharp point. The anterior end presents a quadriradiate head, two of the processes directed dorsally and two ventrally. Anteriorly it articulates with the prefrontals and the maxillae and posteriorly it lies in the groove on the outer side of the anterior end of parasphenoid. The dermethmoid rests on the anterior broad portion. The vomer is devoid of teeth. The shape of vomer in *Secutor* and *Gazza* is somewhat similar in that the posterior portion is longer

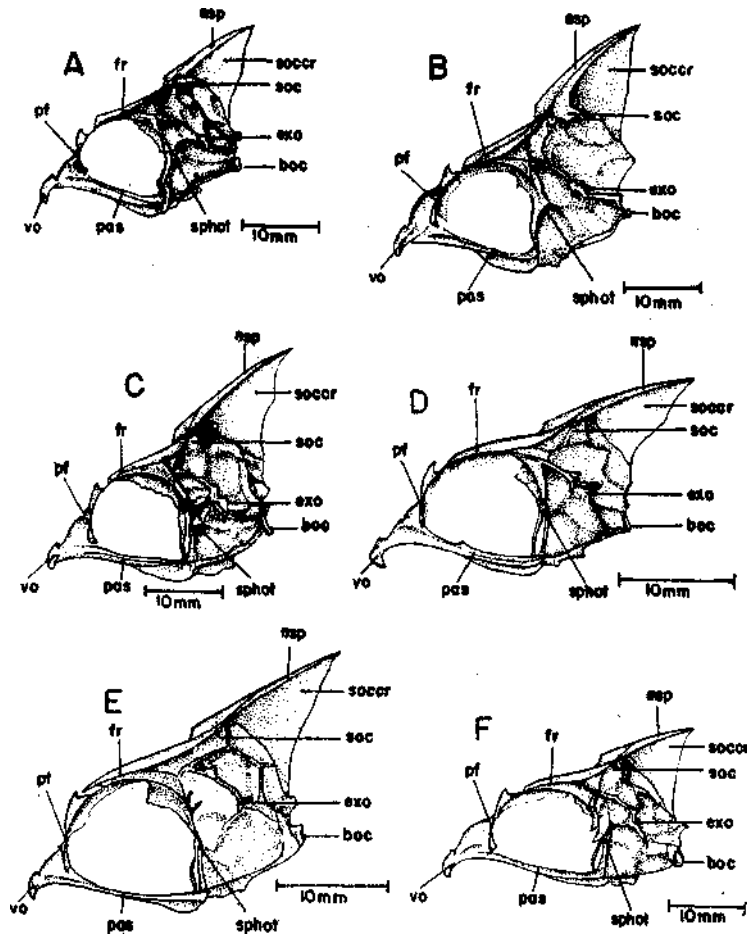


FIG. 9. Neurocranium, lateral view: A. *L. fasciatus*; B. *L. equulus*; C. *L. smithursti*; D. *L. splendens*; E. *L. jonesi*; F. *L. dussumieri*.

boc: basioccipital; exo: exoccipital; formag: foramen magnum; fr: frontal; nsp: nuchal spine; pas: parasphenoid; pf: prefrontal; pto: pterotic; sphenot: sphenotic; vo: vomer.

and sharper, whereas that of *Leiognathus* is short and stout, especially its posterior portion. The anterior portion also differs strikingly in shape. Anteriorly, the head of the vomer constitutes the tip of neurocranium.

Orbital region: The *frontils* (*fr*) (Fig. 16) form the largest portion of the roof of the skull. They articulate with the dermethmoid, profrontals, supraoccipital, sphenotics, parietals and alisphenoid. The frontals are broad with sharp ridges

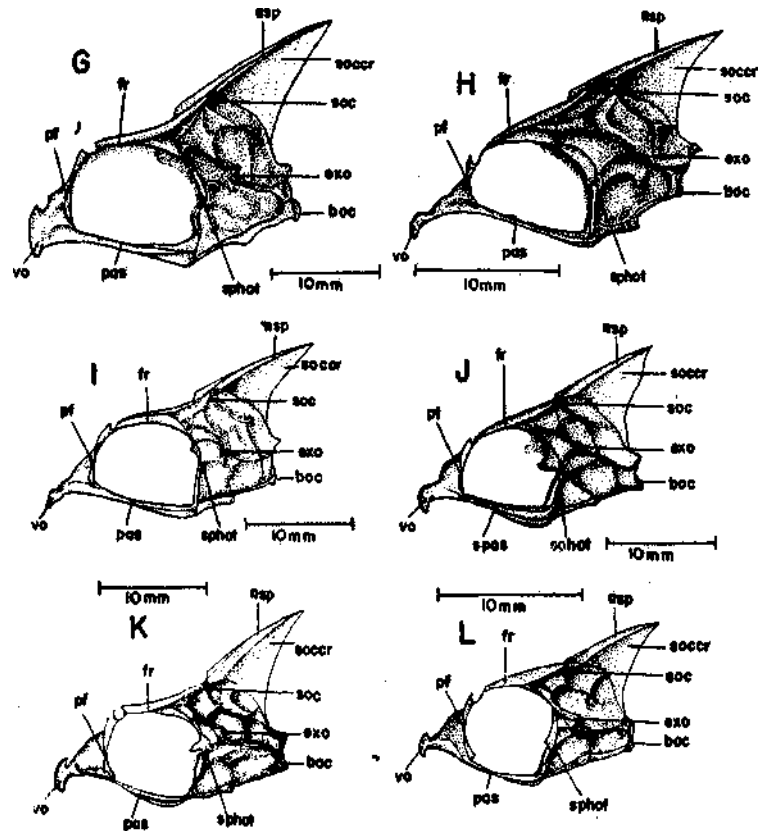


FIG. 10. Neurocranium, lateral view: G. *L. daura*; H. *L. blochi*; I. *L. brevisrostris*; J. *L. leuciscus*; K. *L. berbis*; L. *L. lineolatus*.

boc: basioccipital; expo: exoccipital; formag: foramen magnum; fr: frontal; nsp: nuchal spine; pas: parasphenoid; pf: prefrontal; pto: pterotic; sphot: sphenotic; vo: vomer.

on top in *Secutor* and *Gazza*. In *Leiognathus*, they are narrow and the ridges are blunt and are excessively ossified in older fish. The median elevated ridge is continuous behind with the supraoccipital crest.

The *alisphenoids* (*alsp*) are more or less rectangular in shape, forming the posteriodorsal angle of the orbit wall and articulate with the frontals, sphenotics, pterotics and parasphenoid. They are rectangular in shape in *Leiognathus* and *Gazza* but oval in *Secutor*. On the inner side, a prominent ridge is present in *Gazza* which is less prominent in *Secutor* and absent in *Leiognathus*. The brain chamber opens between the alisphenoids.

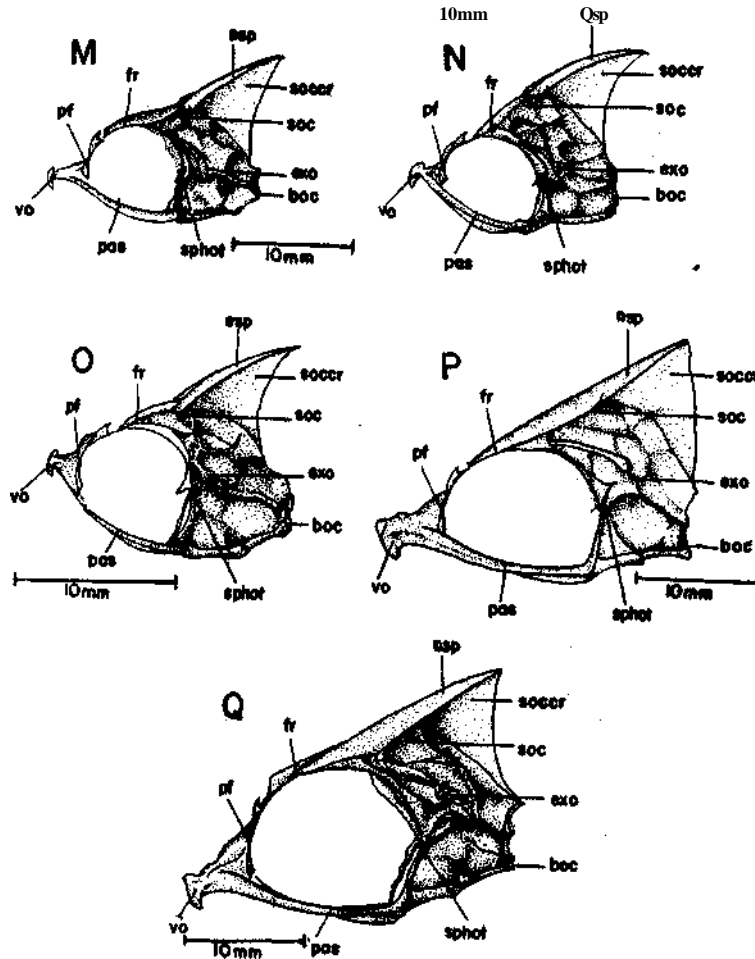


FIG. 11. Neurocranium, lateral view: M. *L. bindus*; N. *S. ruconius*; O. *S. insidiator*; P. *G. minuta*; Q. *G. achlamys*.

boc: basioccipital; exo: exoccipital; formag: foramen magnum; fr: frontal; nsp: nuchal spine; pas: parasphenoid; pf: prefrontal; pto: pterotic; sphot: sphenotic; vo: vomer.

The *parasphenoid* (*pas*) (Fig. 17) differs significantly in shape in the three genera which will be described in detail under the basicranial region.

The *lacrymal* (*la*) is the largest bone of the suborbital ring and is characterised by the sculpture that decorates it. The shape of the bone varies in the three genera, especially the anteroventral portion which is long and sharp in *Gazza*, less so in *Secutor* and blunt in *Leiognathus*.

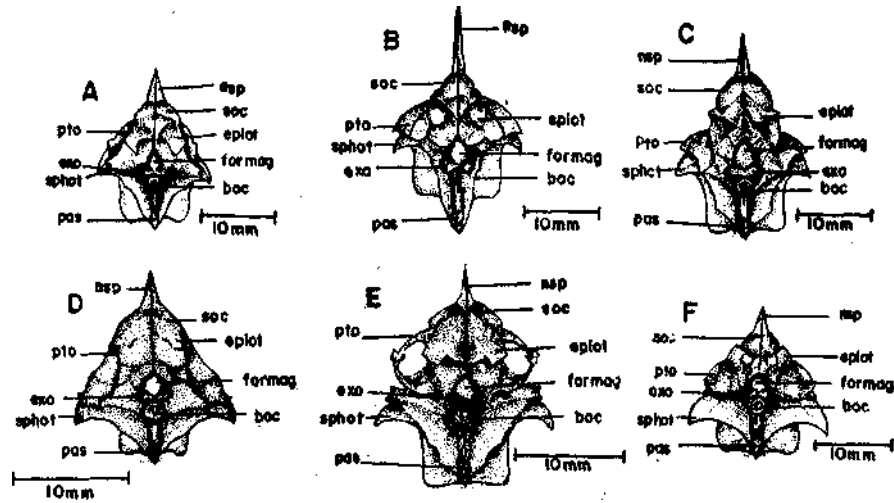


FIG. 12. Neurocranium, posterior view: A. *L. fasciatus*; B. *L. equulus*; C. *L. smithurstii*; D. *L. splendens*; E. *L. jonesi*; F. *L. dussumieri*.

boc: basioccipital; expo: exoccipital; formag: foramen magnum; fr: frontal; nsp: nuchal spine; pas: parasphenoid; pf: prefrontal; pto: pterotic; sphot: sphenotic; vo: vomer.

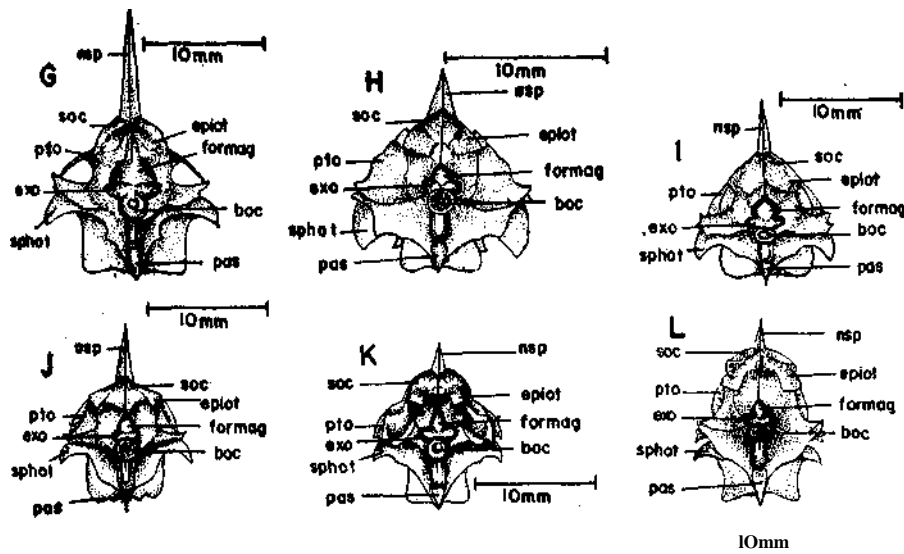


FIG. 13. Neurocranium, posterior view: G. *L. dattra*; H. *L. blochi*; I. *L. brevirostiti*; J. *L. leuciscus*; K. *L. berbis*; L. *L. lineolatus*.

boc: basioccipital; expo: exoccipital; formag: foramen magnum; fr: frontal; nsp: nuchal spine; pas: parasphenoid; pf: prefrontal; pto: pterotic; sphot: sphenotic; vo: vomer.

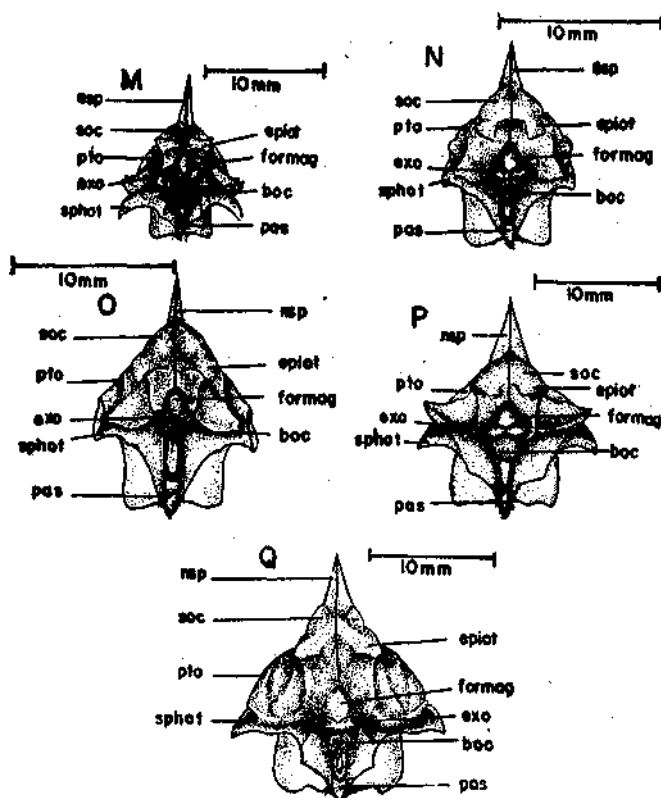


FIG. 14. Neurocranium, posterior view. M. *L. bindus*; N. *S. ruconius*; O. *S. insidiator*; P. *G. minuta*; Q. *G. achlamys*.

boc: basioccipital; expo: exoccipital; formag: foramen magnum; fr: frontal; nsp: nuchal spine; pas: parasphenoid; pf: prefrontal; pto: pterotic; sphot: sphenotic; vo: vomer.

Two other bones are present in the circumorbital series. One of them, situated at the posterior dorsal corner of the eye, is smaller than the second, the *dermosphenotic* (*dsph*) which is a narrow bone, freely lying in a groove at the upper corner of the hind margin of orbit. In *Leiognathus* and *Secutor* only the dermosphenotic is present but in *Gazza* both the bones are present.

Otic region: The *parietals* (*pa*) (Fig. 18) are paired small bones on the anterior sides of the supraoccipital and bear dorsally a small elevated ridge, which forms part of the temporal ridge. Anteriorly, the parietals unite with frontals and posteriorly with the epiotics. In *Leiognathus*, the parietals are somewhat rectangular with strong bony ridges, which excessively ossify in the older fish. In *Secutor* they are oblong, with a narrow dorsal ridge. In *Gazza* they are ovoid with a posteriolateral process and a delicate small dorsal ridge.

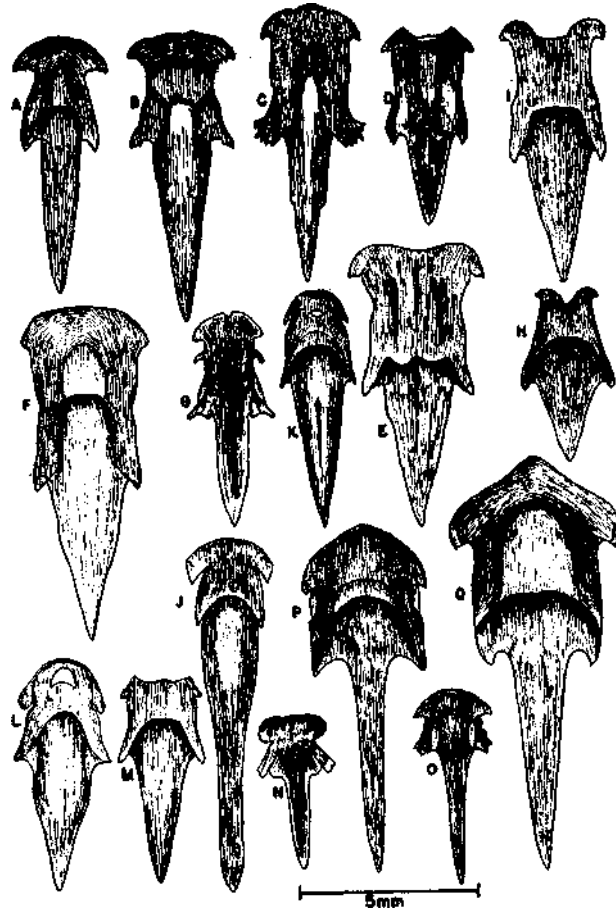


FIG. 15. Vomer of A. *L. fasciatitis*; B. *L. equulus*; C. *L. smkhursti*; D. *L. splendens*; E. *L. jonesi*; F. *L. dussumieri*; G. *L. daitra*; H. *L. blochi*; I. *L. brevirostris*; J. *L. leuciscus*; K. *L. berbis*; L. i. *Lineolatus*; M. i. *bittdus*; N. *S. ruconius*; O. *S. insidiator*; P. *C. minuta*; Q. *G. achlamys*.

The *supraoccipital (soc)* (Fig. 19) forms the dorsomedian portion of the posterior end of the neurocranium. It is convex, broad in the middle region and narrow at either end. The posterior end extends between the epiotics. The supraoccipital bears a ridge middorsally, its ridge separating the supratemporal grooves of the two sides. The supraoccipital joins the frontals anteriorly, the parietals anterolaterally and the epiotics laterally. The supraoccipital bears a prominent dorsomedian crest, the anterior portion of which is in the form of a strong spine. The supraoccipital is more convex in *Leiognathus* than in *Secutor* and *Gazza*. In the bend, about $1/3$ length of the supraoccipital spine, some

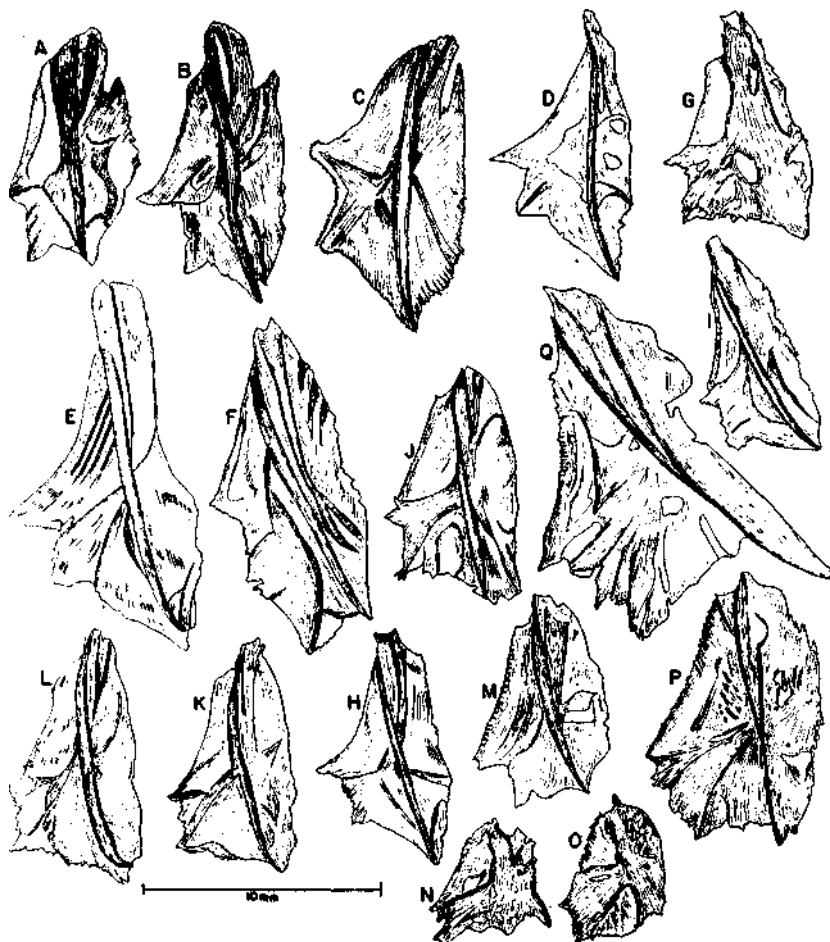


FIG. 16. Frontal of A. *L. fasciatus*; B. *L. equulus*; C. *L. smithursti*; D. *L. splendens*; E. *L. jonesi*; F. *L. dussumieri*; G. *L. daura*; H. *L. blochi*; I. *L. brevirostris*; J. *L. leuciscus*; K. *L. berbis*; L. *L. lineolatus*; M. *L. bindus*; N. *S. ruconius*; O. *S. insidiator*; P. *G. minuta*; Q. *G. achlamys*.

resemblance is seen between *Secutor* and *Gazza*, whereas no such bend is found in *Leiognathus*, resulting in a low supraoccipital crest in the former two genera and an elevated crest in the latter genus. While the supraoccipital crest is confined to the length of the bone in *Leiognathus* and *Secutor*, in *Gazza* it extends posteriorly beyond the bone. The upper half of the posterior margin of the crest is crenulated in *Leiognathus* and smooth in *Secutor* in both of which the lower half is concave. In *Gazza*, the entire posterior margin of supraoccipital crest is wavy.

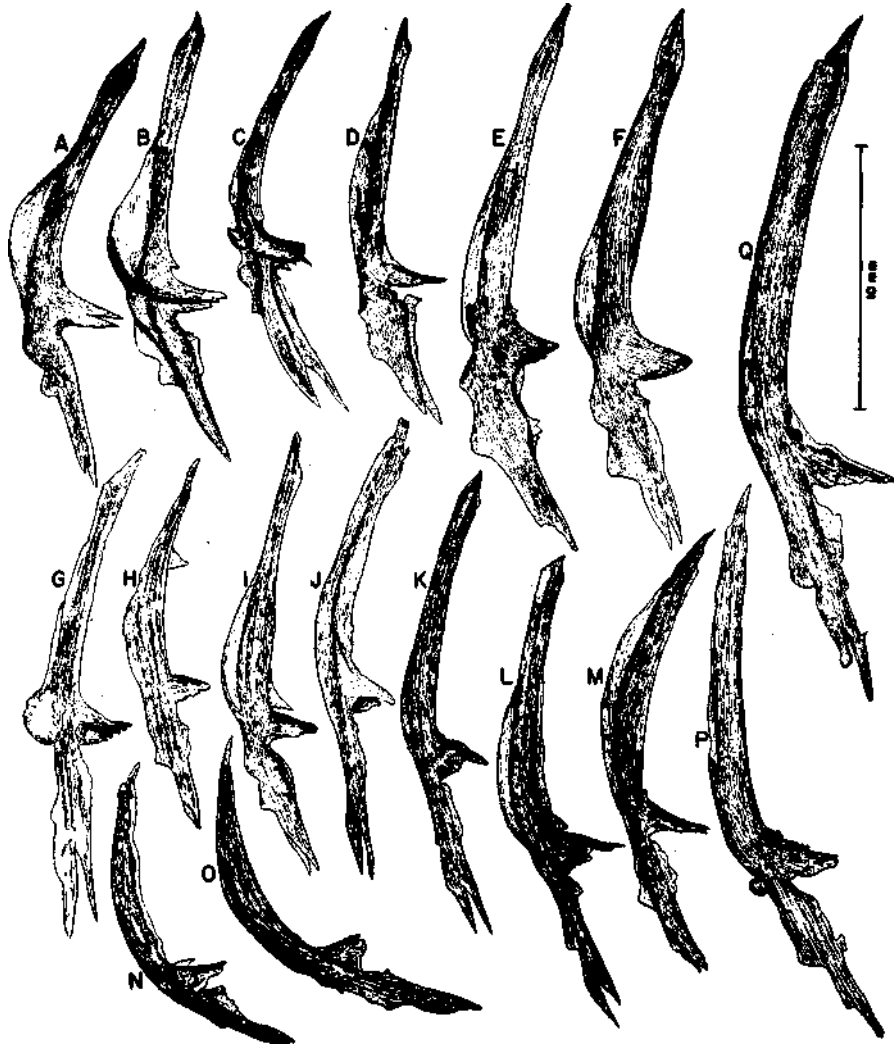


FIG. 17. Parasphenoid of A. *L. fasciatus*; B. *L. equulus*; C. *L. smithursti*; D. *L. splendens*; E. *L. jonesi*; F. *L. dussumieri*; G. *L. daura*; H. *L. blochi*; I. *L. brevirostris*; J. *L. leuciscus*; K. *L. berbis*; L. *L. Lineolatus*; M. *L. bindus*; N. *S. ruconius*; O. *S. insidiator*; P. *G. minuta*; Q. *G. achlamys*.

The *pterotics* (*pto*) (Fig. 20) form the posterolateral corners of the skull, each with a lateral spine-like process. They also contribute to the formation of the temporal and dilator groves and to the main portion of the pterotic ridge. The pterotic of *Leiognathus* bears a cavity larger than that of *Secutor* and *Gazza*. The pterotic process in *Gazza* is broader and wing-like compared to the same in the other genera.

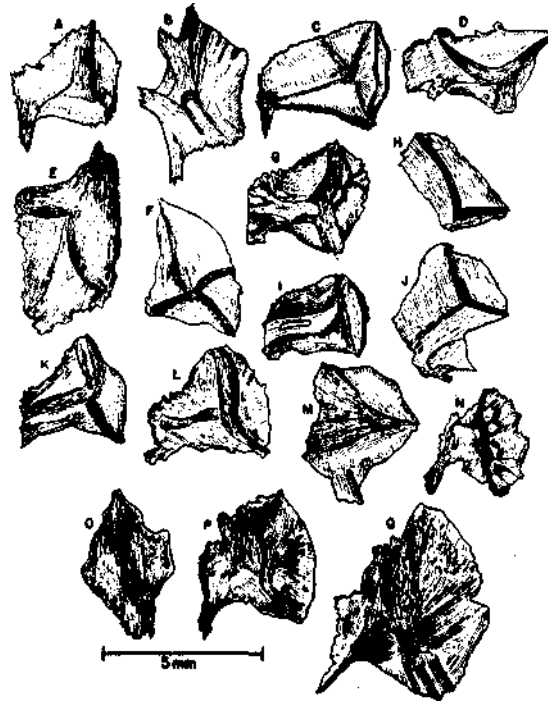


FIG. 18. Parietal of A. *L. fasciatus*; B. *L. equulus*; C. *L. smithursti*; D. *L. splendens*; E. *L. jonesi*; F. *L. dussumieri*; G. *L. daura*; H. *L. blochi*; I. *L. brevirostris*; J. *L. leuciscus*; K. *L. berbis*; L. *L. Lineolatus*; M. *L. bindus*; N. *S. ruconius*; O. *S. insidiator*; P. *G. minuta*; Q. *G. achlamys*.

The *Prootics* (*proot*) are irregular in shape, articulate with the parasphenoid, sphenotics, pterotics and basioccipital. The prootics of *Secutor* and *Gazza* resemble closely in shape.

The *epiotics* (*epiot*) (Fig. 21) are small, almost square-shaped bones. Dorsally, a process at the posterior end of temporal ridge receives the upper end of the post-temporal, thus forming a connection between the pectoral girdle and neurocranium. Anteriorly, the epiotics join the supraoccipital. Posteriorly, they unite with the exoccipitals and laterally with the pterotics. The epiotics of *Secutor* and *Gazza* resemble closely, in that the convexity of the bones is greater and the process longer than in *Leiognathus*.

The *sphenotics* (*sphot*) form the posterior part of the orbital roof and laterally a segment of the articular fossa for the head of the hyomandibular. The shallow, open dilator grooves traverse the surface of the sphenotics. In the shape of the bone and the presence of a partition in its cavity, *Secutor* and *Gazza* generally resemble each other although the sphenotic of the latter is



FIG. 19. Supraoccipital of A. *L. fasciatus*; B. *L. equulus*; C. *L. smithursti*; D. *L. splendens*; E. *L. jonesi*; F. *L. dussumieri*; G. *L. daura*; H. *X. blochi*; I. *L. brevisrostris*; J. *L. leuciscus*; K. *L. berbis*; L. *L. lineolatus*; M. *£. bindus*; N. *S. ruconius*; O. *S. insidiator*; P. *O. minuta*; Q. *G. achlamys*.

broader and shorter than that of the former and also of *Leiognathus* where the cavity is not partitioned. In *Leiognathus*, the sphenotic is larger and bears a prominent process at the posterior end. The sphenotics unite with frontals parietals, epiotics, pterotics and pterotics.

The *opisthotics* (*opo*) are very small, rectangular bones interposed between the pterotics and exoccipitals. They unite in front with the epiotics, anterolaterally with the pterotics and posterolaterally with the exoccipitals.

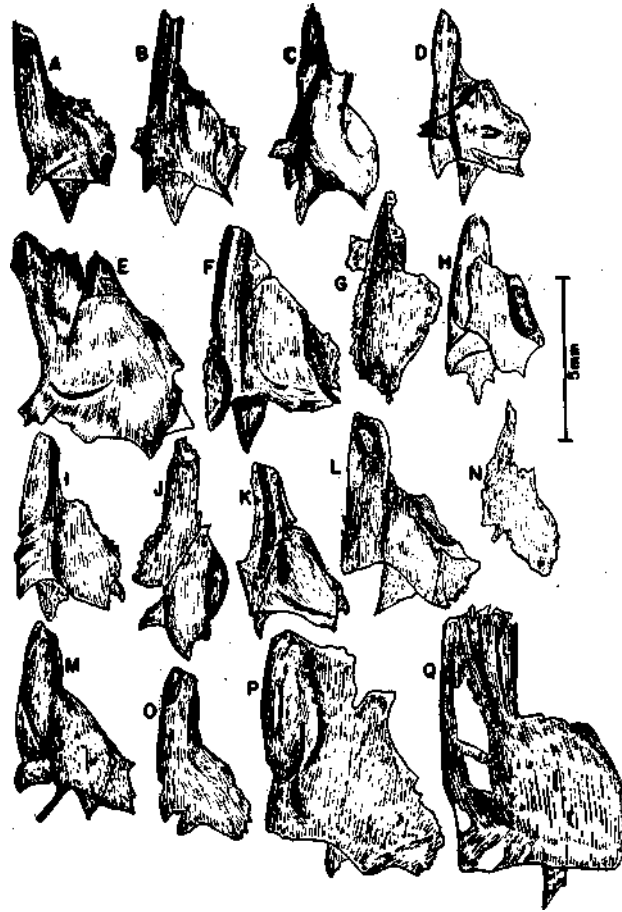


FIG. 20. Pterotic of A. *L. fasciatus*; B. *L. eqmilus*; C. *L. smithursti*; D. *L. splendens*; E. *L. jonesi*; F. *L. dussumieri*; G. *L. daura*; H. *L. blochi*; I. *L. brevisrostris*; J. *L. leuciscus*; K. *L. berbis*; L. *L. linealatus*; M. *£. bindus*; N. *S. ruconius*; O. *S. insidiaior*; P. *G. minuta*; Q. *G. achlamys*.

The *exoccipitals (exo)* (Fig. 22) are fan-shaped bones which enclose the foramen magnum and articulate with the basioccipital along the median line. Anterodorsally, they unite with the epiotics, anteriorly the prootics, laterally the pterotics, ventrally the basioccipital and along the inner margin with opisthotics. Their vertebral or paraoccipital condyles to the atlas are flat in *Leiognathus* and *Gazza* but concave in *Secutor*. The foramen for the passage of the vagus nerve is prominent. The exoccipitals of *Secutor* and *Gazza* resemble closely especially in their prominent paraoccipital condyles which are small in *Leiognathus*.

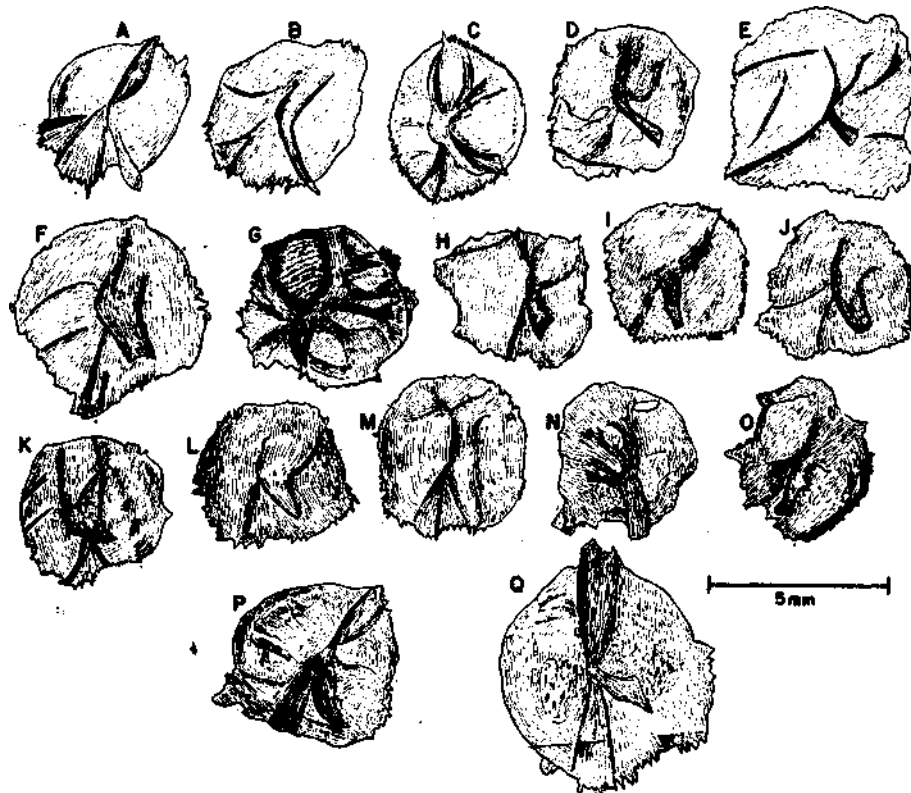


FIG. 21. Epiotics of A. *L. fasciatus*; B. *L. equulus*; C. *L. smithursti*; D. *L. splendens*; E. *L. jonesi*; F. *L. dussumieri*; G. *L. daura*; H. *L. blochi*; I. *L. brevirostris*; J. *L. leuciscus*; K. *L. berbis*; L. *L. Lineolatus*; M. *Z. bindus*; N. *5. ruconius*; O. *5. insidiator*; P. *G. minuta*; Q. *G. achlamys*.

Basicranial region: The *parasphenoid (pas)* (Fig. 17) is a long bone, forming the greater portion of the basicranial region of the neurocranium. It extends the entire length of the ventral median line between the olfactory region in front and otic region behind. Posteriorly, it bears two small lateral ascending wings, one on either side to connect the prootics. Immediately behind the wings, the bone is broader and gently curves upward. At the posterior end, the parasphenoid joins the basioccipital. The anterior end connects the posterior portion of the vomer. The portion of parasphenoid behind the tip of vomer up to the lateral wings forms the ventral margin of orbital cavity. The anterior end of parasphenoid is lanceolate in all the three genera, but in *Leiognathus* it is wide, standing in relation to the short posterior portion of vomer with which it articulates (in the other two genera, the posterior portion of vomer is narrow and

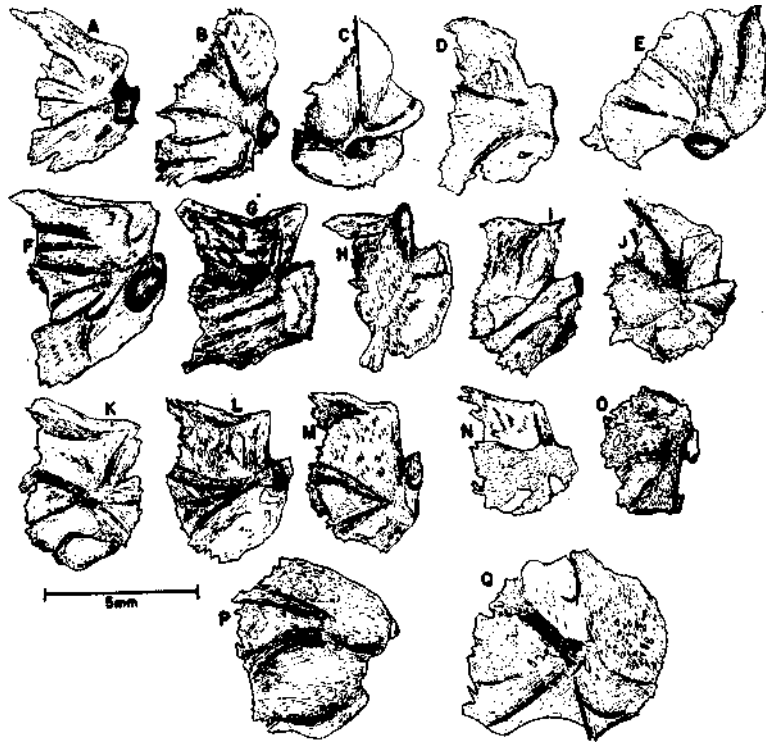


FIG. 22. Exoccipitals of A. *L. fasciatus*; B. *L. equulus*; G. *L. smithursti*; D. *L. splendens*; E. *L. jonesi*; F. *L. dussumieri*; G. *L. daura*; H. *L. blochi*; I. *L. brevirostris*; J. *L. leuciscus*; K. *L. berbis*; L. *L. Lineolatus*; M. *£. bindus*; N. *5. ruconius*; O. *5. insidiator*; P. *G. minuta*; Q. *G. achlamys*.

long). The middle portion (about one-third length) of parasphenoid in *Leiognathus* bears a broad fringe of bone on the ventral side which is narrower in *Gazza* and absent in *Secutor*. The anterior two-third length of the bone is strongly curved upwards in *Secutor* which is almost straight in the other two genera. The lateral wings are prominent in *Gazza* when compared to the other two genera, the wings pointing forwards in *Leiognathus*.

The *basisphenoid* (*bsph*) is a small median 'Y' shaped bone which unites the parasphenoid with the prootics and alisphenoids. The median vertical limb is compressed and the dorsal head-like portion is crescent shaped guarding the opening to the brain chamber. The basisphenoid is more prominent in *Leiognathus* than in the other two genera and its vertical limb is the longest. In *Secutor*/both the dorsal and ventral portions are smaller than in the other two genera. In *Gazza* the dorsal portion is larger than in the other two genera and

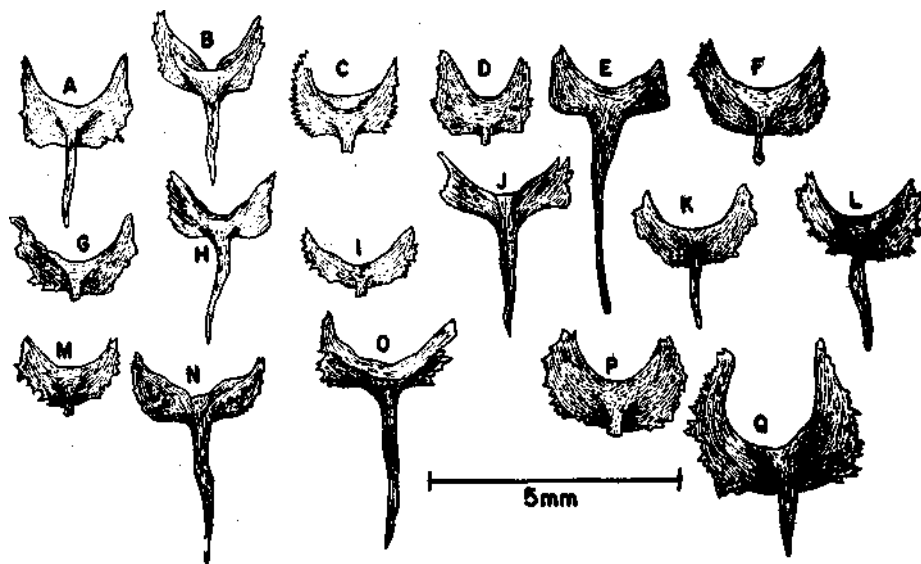


FIG. 23. Basisphenoid of A. *L. faciatus*; B. *L. equulus*; C. *L. smithursti*; D. *L. splendens*; E. *L. jonesi*; F. *L. dussumieri*; G. *L. daura*; H. *L. blochi*; I. *L. brevisrostris*; J. *L. leuciscus*; K. *X. berbis*; L. *Z. Lineolatus*; M. *L. bindus*; N. *5. ruconius*; O. *5. insidiator*; P. *G. minuta*; Q. *G. achlamys*.

the vertical portion smaller than that in *Leiognathus* and longer than that in *Secutor*. In *Secutor* the ventral part does not reach the parasphenoid but remains free.

The *basioccipital* (*boc*) (Fig. 24) is a small bone with two cavities separated by a median wall on dorsal side and on one cavity on the ventral side. It bears the concave, round occipital condyle that articulates with the atlas. The basioccipital supports dorsally the exoccipital of the corresponding side and is bounded ventrally by the parasphenoid and in front by the prootics. The forked end of parasphenoid fits on either side of the median process of the basioccipital, the latter fitting in the posterior end of parasphenoid. The vertebral or paraoccipital condyles of the exoccipitals to the atlas rest on **the hind** end of basioccipital. The dorsal cavities are deeper in *Gazza* than in *Leiognathus* where they extend only half way down resulting in a single wall on each side for the ventral cavity in *Leiognathus* whereas a double wall is formed in *Gazza*. In *Secutor* no dorsal and ventral cavities are formed but the median partition is confined to dorsal half.

BRANCHIOCRANIUM

Oromandibular region: The *premaxilla* (*pmx*) (Figs. 25, 26) has the form of number '7' the horizontal limb lying at the edge of mouth and the vertical limb

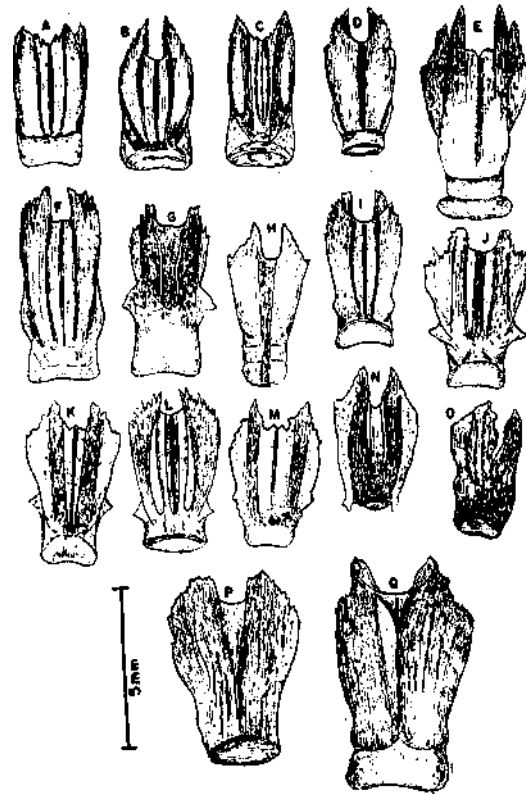


FIG. 24. Basioccipitals of A. *L. fasciatitis*; B. *L. equulus*; C. *L. smithursti*; D. *L. splendens*; E. *L. jonesi*; F. *L. dussumieri*; G. *L. daura*; H. *L. blochi*; I. *L. brevirostris*; J. *L. leuciscus*; K. *L. berbis*; L. *L. lineolatus*; M. *L. bindus*; N. *S. ruconius*; O. *S. insidiator*; P. *G. minuta*; Q. *G. achlamys*.

together with the one of the opposite side forms a shaft, working back and forth on the top of skull through an arch formed by the dorsal tips of the maxillae, constituting the chief mechanism for the protrusible mouth. The hind end of the shaft is free to facilitate this movement. The premaxilla bears teeth on the outer margin of the horizontal portion. Two short processes, outer blunt and inner sharp, directed backwards arise from the inner margin of the horizontal limb of the premaxilla. The vertical limb is almost straight in *Gazza* and *Secutor* but curved in *Leiognathus*. The horizontal limb makes an angle of 90° to vertical limb in *Gazza* and *Secutor*, but the angle is less than 90° in *Leiognathus* (the horizontal limb is directed backwards). The outer and inner processes from the horizontal limb are similar (small) in *Leiognathus* and *Gazza* but they are large and prominent in *Secutor*. Teeth are conspicuous in *Gazza* but inconspicuous in the other two genera.



FIG. 25. Premaxillae of A. *L. fasciatus*; B. *L. equulus*; C. *L. smithursti*; D. *L. splendens*; E. *L. fonesi*; F. *L. dussumieri*; G. *L. daura*; H. *L. blochi*; I. *L. brevirostris*; J. *L. leuciscus*; K. *L. berbis*.

The *maxilla* (*max*) (Fig. 27) consists of a short backwardly curved dorsal part and a long 's' shaped ventral part with a small flattened posterior extension, about 1/3 length from above. The dorsal part of each side forms half the arch through which the premaxillary shaft works back and forth. The maxilla of *Gazza* and *Secutor* resemble closely whereas that of *Leiognathus* is shorter and broader. The posterior extension is forked in *Gazza* but concave in the other two genera.

The *dentary* (*dn*) (Fig. 28) is somewhat triangular in shape bearing teeth along the inner surface for about half length of the bone that forms the border of the mouth. The dentary is convex outwards and concave inwards. The

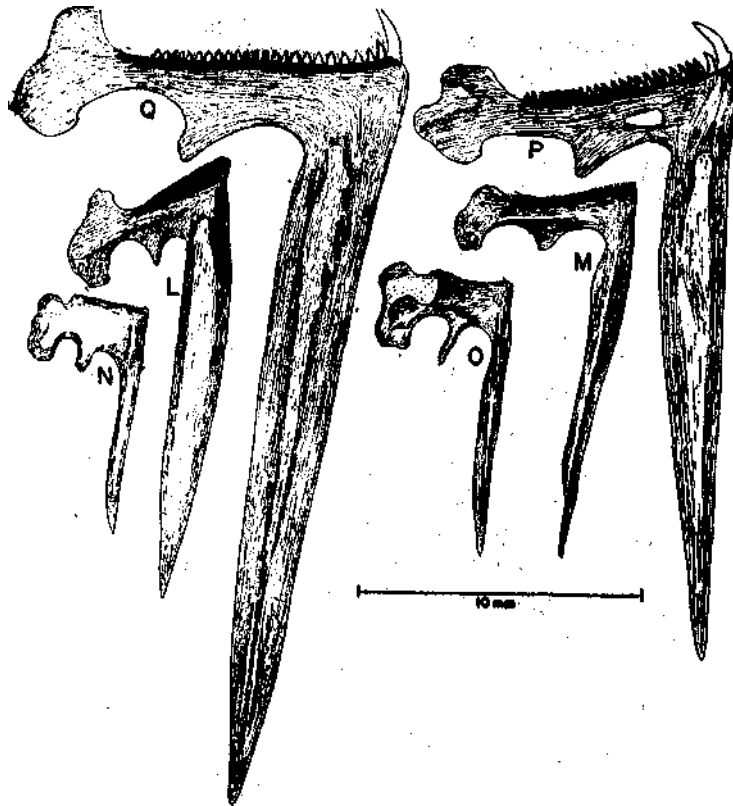


FIG. 26. Premaxillae of L. *L. lineotatus*; M. *L. bindus*; N. *S. ruconius*; O. *S. insidiator*; P. *G. minuta*; Q. *G. achlamys*.

dentaries of *Leiognathus* and *Gazza* resemble closely, whereas that of *Secutor* differs from the other two genera. Teeth are more prominent in *Gazza* than in the other two genera.

The *articular* (*art*) (Fig. 29) is a wing-like bone, convex outwards and concave inwards. The articular of the three genera is alike. No separate *angular* has been noticed in any of the genera.

The *metapterygoid* (*mty*) is broad below where it articulates with the dorsal margin of quadrate and narrow above. Along the anterior margin and base, it partly overlaps the entopterygoid. In *Leiognathus*, an anterior and a posterior fringe are present which are absent in the other two genera, except for a small indication of an anterior fringe in *Gazza*. The notches on the anterior and posterior margins of the bone in *Secutor* are absent in the other two genera.

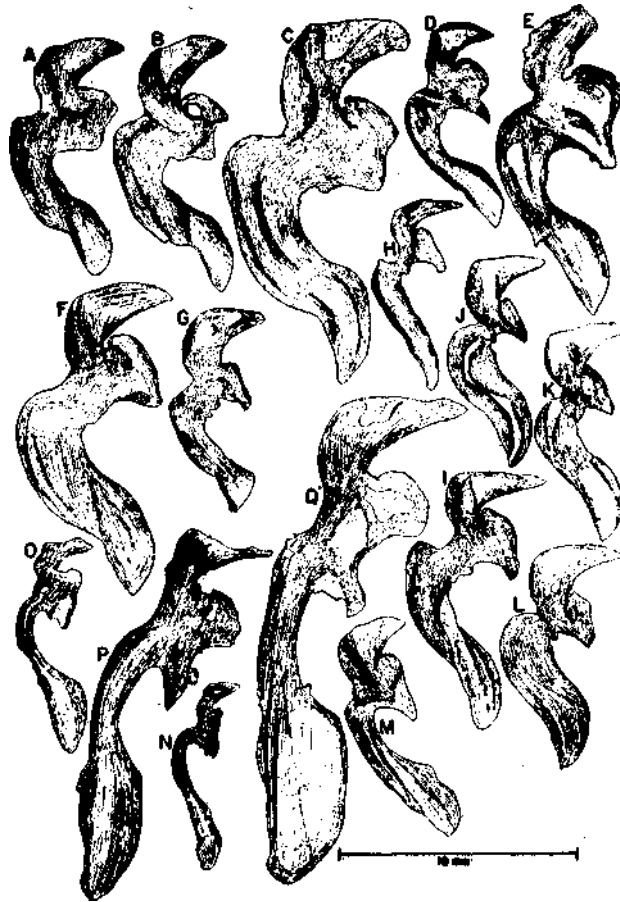


FIG. 27. Maxillae of A. *L. fasciatus*; B. *L. equulus*; C. *L. smithursti*; D. *L. splendens*; E. *L. jonesi*; F. *L. dussumieri*; G. *L. daura*; H. *L. blochi*; I. *L. brevirostris*; J. *i. leuciscus*; K. *Z. berbis*; L. *i. lineolatus*; M. *L. bindus*; N. *S. ruconius*; O. *S. insidiataf*; P. *G. minuta*; Q. *G. achlamys*.

Secutor and *Gazza* also resemble in that the base of metapterygoid occupies the posterior three-fourths of the dorsal margin of quadrate whereas in *Leiognathus* it occupies the entire margin.

The *ectopterygoid* (*ecpt*) is a bent bone, uniting with the palatine and entopterygoid anteriodorsally and with the quadrate postero-ventrally. It is broad and blunt at the anterior end and narrow and sharp at the posterior end. The ectopterygoid of *Gazza* and *Secutor* closely resemble in shape. In *Leiognathus* each both ends of the bone are sharp and the middle portion broad. The anterior half of the bone bears a prominent ridge.

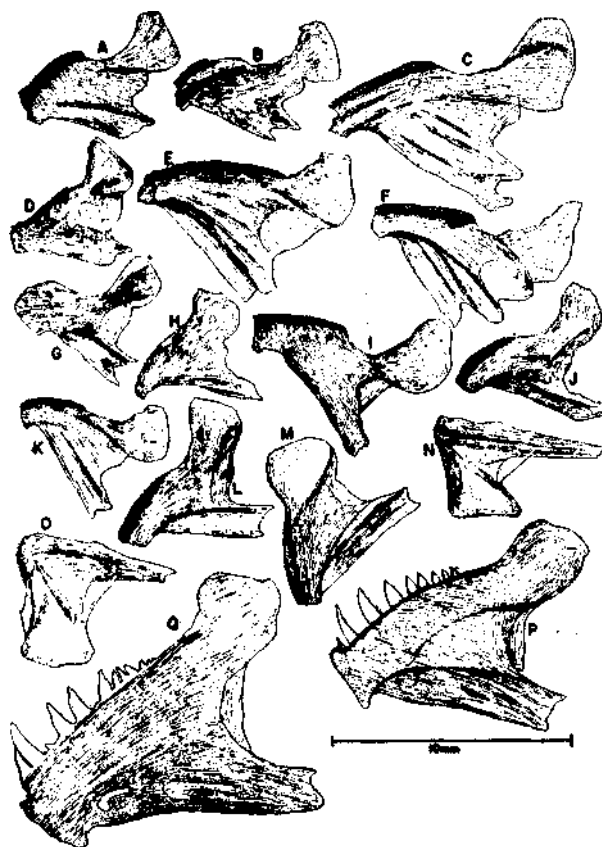


FIG. 28. Denlaries of A. *L. fasciatus*; B. *L. equulus*; C. *L. smithursti*; D. *L. splendens*; E. *L. jonesi*; F. *L. dussumieri*; G. *L. daura*; H. *L. blochi*; I. *L. brevirostris*; J. *L. leuciscus*; K. *L. berbis*; L. *L. lineolatus*; M. *L. birtus*; N. *S. ruconius*; O. *S. insidiator*; P. *G. minnta*; Q. *G. achlamys*.

The *entopterygoid* (*enpt*) (Fig. 30) is a long bone, the dorsal end being narrow and the ventral end broad. It is partly overlapped at the posterior margin and at the base by metapterygoid. At its anterior base, it is connected to the palatine and the ectopterygoid. The entopterygoid is somewhat triangular in *Secutor*, but oblong in *Leiognathus* and *Gazza*. In *Gazza*, a prominent triangular posterior fringe of bone is present, resting at upper anterior corner of quadrate and joining with it and the base of anterior portion of metapterygoid.

The *palatine* (*pi*) (Fig. 31) runs forwards on the external side of Vomer and connects in front the maxilla and behind the ecto- and entopterygoids. The

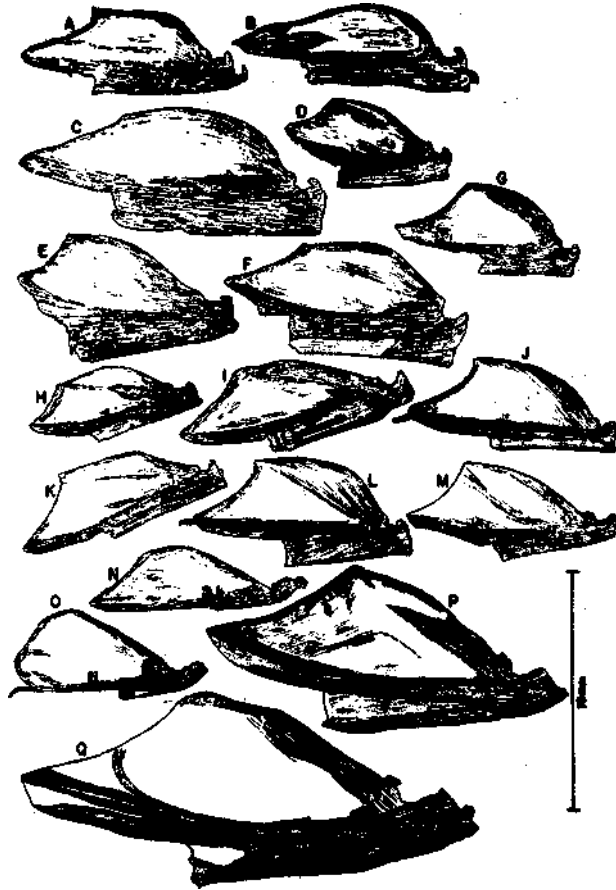


FIG. 29. Articulars of A. *L. fasciatus*; B. *L. equulus*; C. *L. smithursti*; D. *L. splendens*; E. *L. jonesi*; F. *L. dussumieri*; G. *L. daura*; H. *L. blochi*; I. *L. brevirostris*; J. *Z. leuciscus*; K. *L. berbis*; L. *i. lineolatus*; M. *L. bindus*; N. *S. ruconius*; O. *S. insidiator*; P. *G. minuta*; Q. *G. achlamys*.

palatine is devoid of teeth. The palatine of *Gazza* and *Secutor* resemble closely in that its front end is sharp whereas that of *Leiognathus* has a vertical bar at the front end.

The *quadrate* (*qu*) (Fig. 32) is a triangular bone uniting ventrally with the articular, anterodorsally with the ectopterygoid, dorsally with the metapterygoid, entopterygoid and the stem of the hyomandibular and posteriorly with the preopercle. It is broad above and narrow below, with a strong spiny ridge along the posterior margin. Unlike in the other two genera, in *Gazza* the spiny ridge

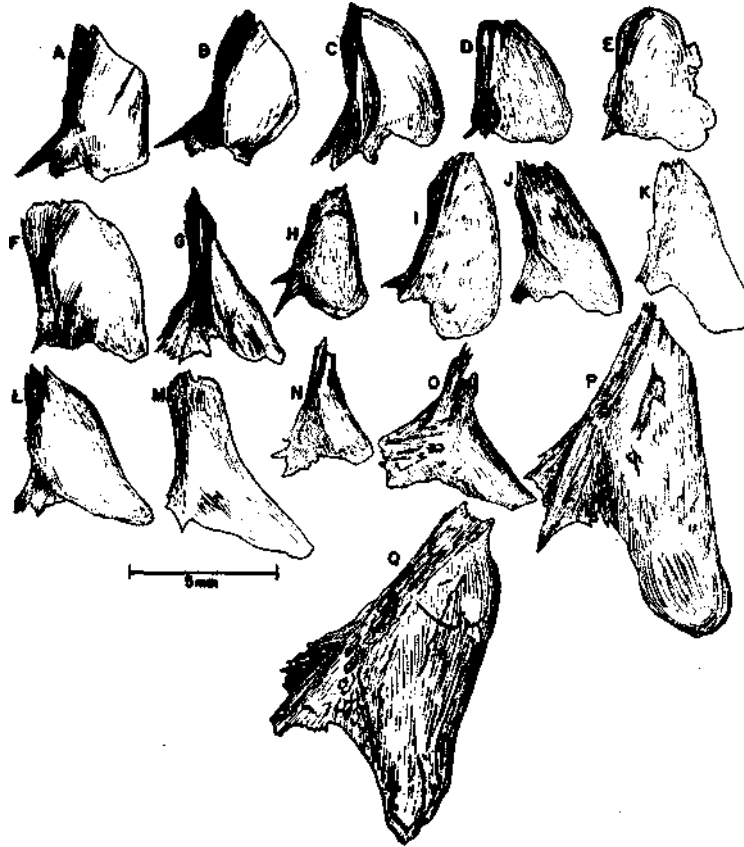


FIG. 30. Entopterygoids of A. *L. fasciatus*; B. *L. equulus*; C. *L. smithursti*; D. *L. splendens*; E. *L. jonesi*; F. *L. dussumieri*; G. *L. daura*; H. *L. blochi*; I. *L. brevirostris*; J. *L. leuciscus*; K. *L. berbis*; L. *L. lineolatus*; M. *L. bindus*; N. *S. ruconius*; O. *S. insidiator*; P. *G. minuta*; Q. *G. achlamys*.

does not extend fully along the posterior margin. The quadrate and metapterygoid are united by bony fibrous connections at mid point along the line of attachment in *Leiognathus*.

The *symplectic* (*sym*) is very small, spatulate in shape, located in a small cavity at the top of the posterior margin of quadrate. The bone is visible only from inside. No significant difference was noticed between the genera.

Hyoid-opercular region: The *opercle* (*op*) (Fig. 33) is a triangular bone, broad dorsally and narrow ventrally. A median process is present on the dorsal margin. The anterior margin of the bone is straight, overlapped by the hind edge of preopercle. It joins the subopercle posteroventrally. The opercle is convex externally and concave internally. The opercles of *Leiognathus* and *Secutor*

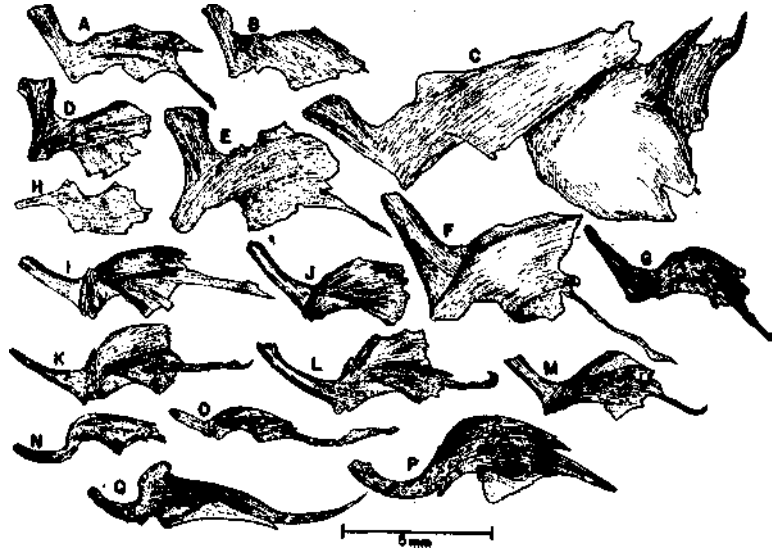


FIG. 31. Palatines of A. *L. fasciatus*; B. *L. equulus*; C. *L. smithursti*; D. *L. splendens*; E. *L. jonesi*; F. *L. dussumieri*; G. *L. daura*; H. *L. blochi*; I. *L. brevisrostris*; J. *L. leuciscus*; K. *L. berbis*; L. *L. lineolatus*; M. *L. bindus*; N. *S. ruconius*; O. *S. insidiator*; P. *G. minuta*; Q. *G. achlamys*.

resemble each other in that they are broad and short, whereas that of *Gazza* is narrow and elongated. The process on top is sharp in the former two genera but blunt in the latter genus.

The *subopercle* (*sop*) is a long narrow bone, pointed dorsally and broad ventrally, articulating with the opercle along its anterodorsal margin. Its posterior margin is free. Anteroventrally, it articulates with the interopercle. The subopercle is slightly convex externally and concave internally. A small process is present along the inner margin at the base. The subopercles of *Leiognathus* and *Secutor* resemble each other in shape and differ from that of *Gazza*. The process along the inner margin is very distinct and prominent in *Gazza* compared to that in the other two genera.

The *interopercle* (*iop*) joins in front with the articular, dorsally with preopercle and posteriorly with subopercle. By the midlength on the inner margin, it provides articulation for the hyoid arch (by ceratohyal). The interopercle forms the anterior and inferior margins of gill cover. It is narrow and long in *Leiognathus* and *Secutor* but broad in *Gazza*.

The *preopercle* (*pop*) (Fig. 34, 35) is a typical reversed 'L' shaped bone with an inner thickened ridge. The preopercles of *Secutor* and *Gazza*

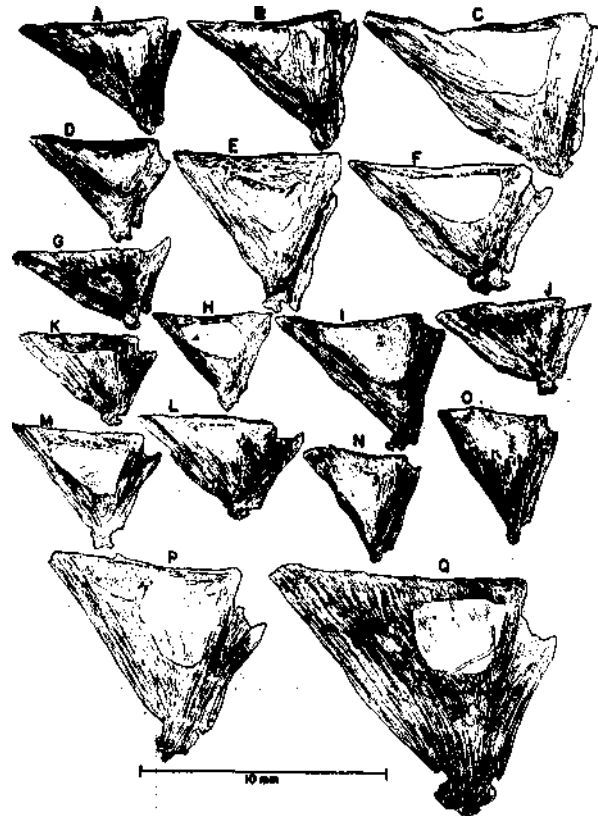


FIG. 32. Quadrate of A. *L. fasciatus*; B. *L. equulus*; C. *L. smithursti*; D. *L. splendens*; E. *L. jonesi*; F. *L. dussumieri*; G. *L. daura*; H. *L. blochi*; I. *L. brevirostris*; J. *L. leuciscus*; K. *L. berbis*; L. *Z. lineolatus*; M. *L. bindus*; N. *S. ruconius*; O. *S. insidiator*; P. *G. minuta*; Q. *G. achlamys*.

closely resemble each other in that at the inner angle of the vertical and horizontal limbs there is a fringe of bone which is absent in *Leiognathus*.

The dorsal part of the preopercle articulates with the stem of hyomandibular in front and opercle behind. The ventral part articulates with the quadrate and metapterygoid anterodorsally and the interopercle posteroventrally. The ventral edge of the preopercle is serrate, the serrations directed backwards. The ventral portion covers the greater part of interopercle. The angle of the preopercle is sculptured.

The *hyomandibular* (*hyom*) (Fig. 36) has a head and a stem, the head with three distinct articular condyles, two of them anterodorsal and one posteroventral. Of the two dorsal condyles, the anterior one articulates on the posterior

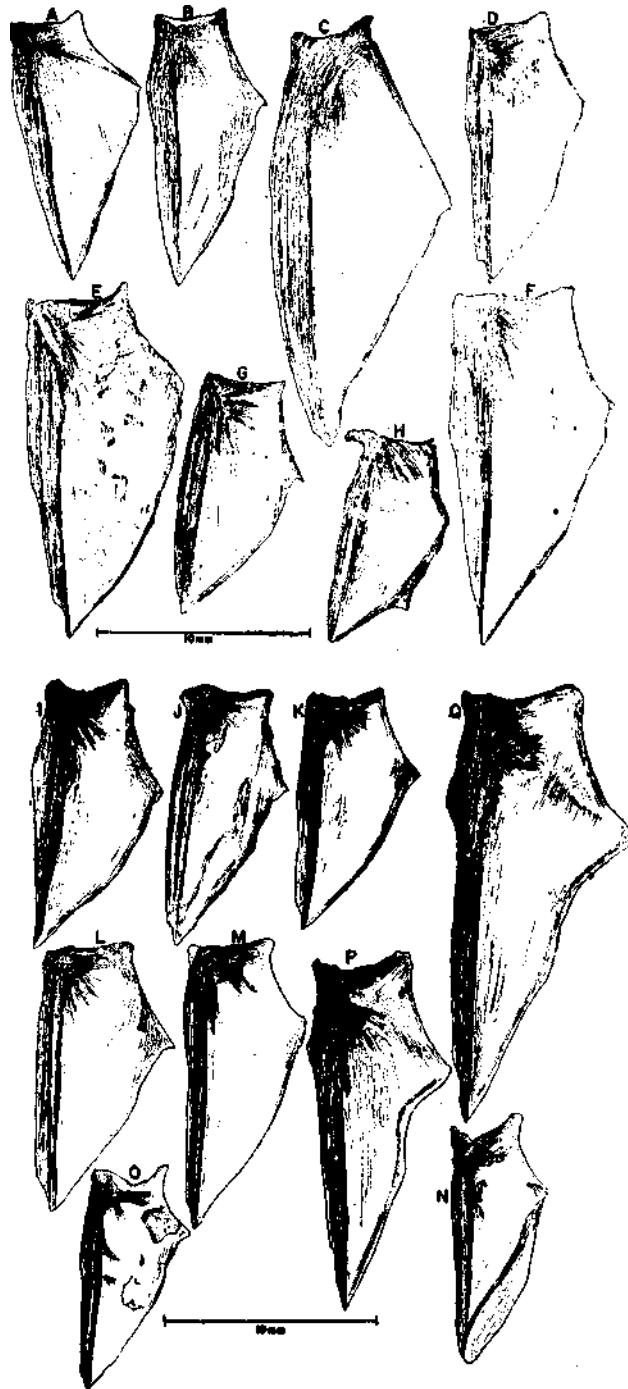


FIG. 33. Opercle of A. *L. fasciatus*; B. *L. equulus*; C. *L. smithursti*; D. *L. splendens*; E. *L. jonesi*; F. *L. dussumieri*; G. *L. daura*; H. *L. blochi*; I. *L. brevirostris*; J. *L. leuciscus*; K. *L. berbis*; L. *L. lineolatus*; M. *L. bindus*; N. *S. ruconius*; O. *S. insidiator*; P. *G. minuta*; Q. *G. achlamys*.

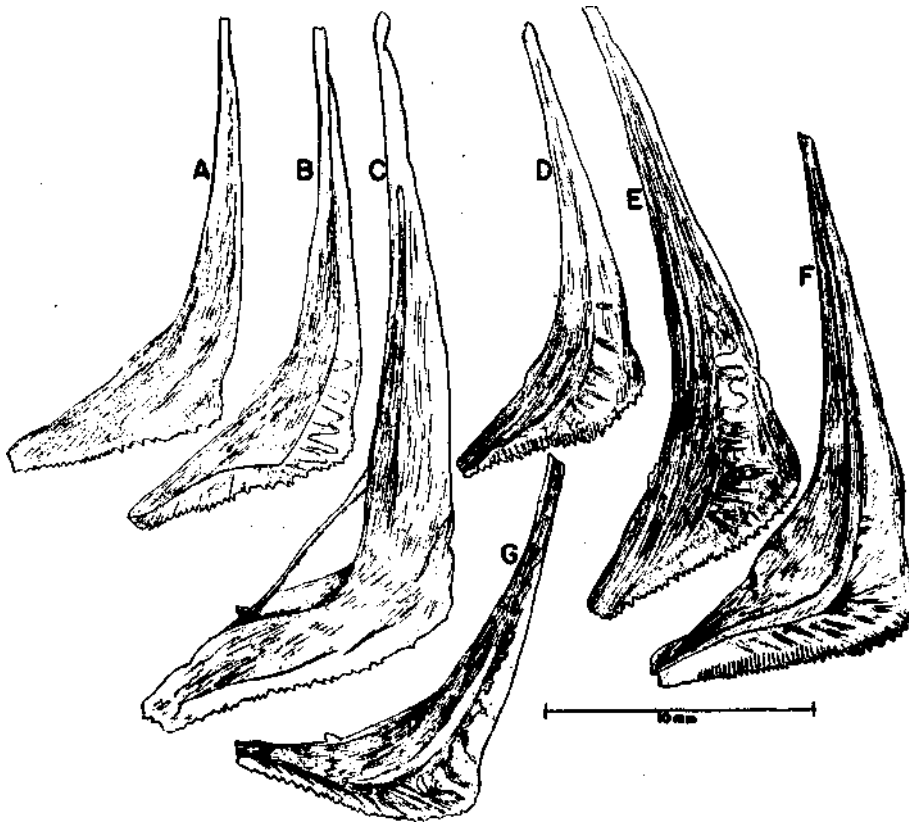


FIG. 34. Preopercles of A. *L. fasciatus*; B. *L. equulus*; C. *L. smithursti*; D. *L. splendens*; E. *L. Jonesi*; F. *L. dussumieri*; G. *L. daura*.

side of sphenotic and the other below the pterotic. The third condyle articulates with the opercle posteriorly. Below the head on either side of the stem there are bony lamellae. The lamella on the posterior side provides articulation to the preopercle by passing underneath the anterior edge of the latter. Anteroventrally, it articulates with the metapterygoid. The articular facet of hyomandibular on sphenotic is deeper than that on pterotic. The bone strikingly differs in structure in the three genera. In *Leiognathus*, the anterior fringe is much broader than the posterior fringe, both fringes terminating at the same point ventrally. In *Secutor*, both fringes are narrow and least developed, the posterior ending below the anterior fringe. In *Gazza*, the anterior fringe is narrow but the posterior fringe is best developed than in other two genera and ends below the anterior fringe as in *Secutor*.

The *hyoid arch*, or *cornu* (Figs. 37, 38) consists, in addition to glossohyal, of four pieces, the basihyal, ceratohyal, epihyal and interhyal. The interhyal



FIG. 35. Preopercle of H. *L. blochi*; I. *L. brevirostris*; J. *L. lenciscus*; K. *L. berbis*; L. *L. lineolatus*; M. *L. bindus*; N. *S. ruconius*; O. *S. insidiator*, P. *G. minuta*; Q. *G. achlamys*.

connects the arch to the opercular-complex at the junction of the metapterygoid, quadrate and preopercle on the inner side of the preopercle and posterior angle of metapterygoid and quadrate. In addition to this, the posterior end of the epihyal also articulates on a raised area of the ridge on the inner side of the interopercle. The four components of the arch are joined with each other by simple joints.

The *glossohyal* (*gloss*) is a club-shaped bone, broad anteriorly and narrow posteriorly. It articulates with a distinct base at the union of the two basi-hyals of each side. It is, not flat.

The *basihyal* (*bshy*) is triangular in shape, broad anteriorly and narrow posteriorly. The two basihyals of the two sides unite in the median line and articulate laterally with the anterior end of ceratohyal.

The *ceratohyal* (*cerhy*) is the largest bone in the arch, narrow anteriorly and broad posteriorly. It has a median, prominent articular head to unite with the basihyal.



FIG. 36. Hyomandibulars of A. *L. fasciatus*; B. *L. equulus*; C. *L. smithursti*; D. *L. splendens*; E. *L. jonesi*; F. *L. dussumieri*; G. *L. daura*; H. *L. blochi*; I. *L. brevirostris*; J. *L. leuciscus*; K. *L. berbis*; L. *i. lineolatus*; M. *L. bindus*; N. *S. riiconius*; O. *S. insidiator*; P. *G. minuta*; Q. *G. acMamys*.

The *epihyal* (*ephy*) is a triangular bone, broad anteriorly and narrow posteriorly. Posteriorly, it articulates with the interopercle and the interhyal.

The *interhyal* (*ihy*) is the smallest in the series, providing at the hind end attachment to opercular complex at the preopercular angle on the inner side. Anteriorly, it joins the epihyal. The bone lies almost at right angles to the hind end of epihyal.

Branchiostegal rays (*brstg*) are either four or five, attached on the inner side of the hyoid arch. All or most of the rays arise from the ceratohyal and one or two from the epihyal.

The *urohyal* (*urohy*) is narrow anteriorly and broad posteriorly, located between the basihyals. Middorsally, it bears a high bony lamella which is embedded free in the muscular mass of the throat.

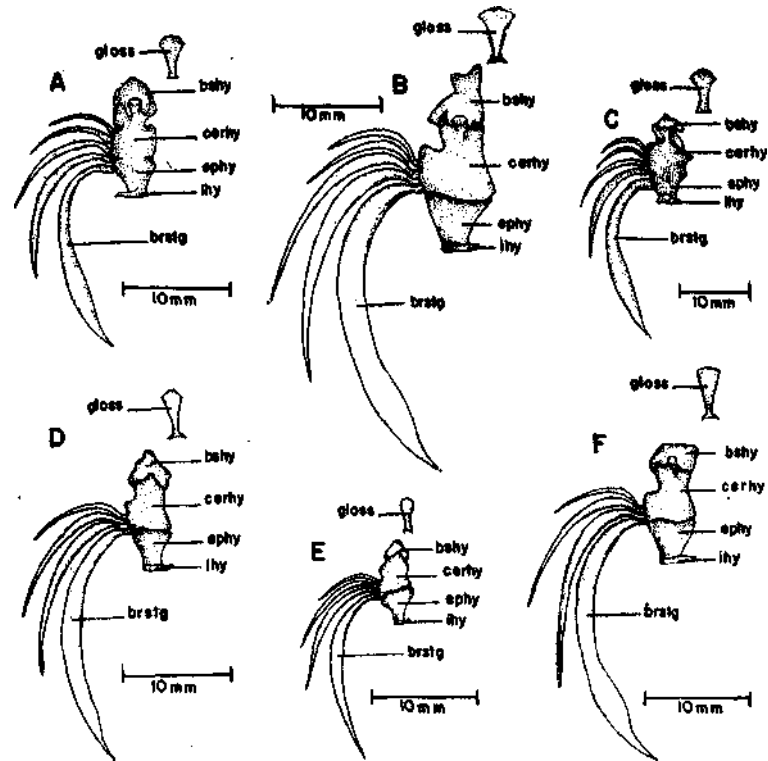


FIG. 37. Hyoid arch and glossohyal of A. *L. fasciatus*; B. *L. equulus*; C. *L. smithursti*; D. *L. splendens*; E. *L. jonesi*; F. *L. dussumieri*.

brstg: branchiostegal ray; bshy: basihyal; cerhy: ceratohyal; ephy: epihyal; gloss: glossohyal; ihy: interhyal.

Branchial region: The branchial arches (Figs. 39 to 41) are enclosed within the hyoid arch with which they are connected at the base. They form the support for the gills and are composed of smaller bones. The branchial skeleton in the three genera exhibits a similar pattern as described below:

The three *basibranchials* (*bbr*-*bbri*) form a linear series along the median line, giving support and attachment to the four branchial arches. The first basibranchial is arrow-head shaped and articulates immediately behind the base of glossohyal and in between inner corners of basihyals. Laterally, the second basibranchial articulates with the first hypobranchial which in turn articulates with their anterior margins with the posterior margins of basihyals. The second basibranchial is larger than the first and shorter than the third. The third basibranchial is the longest of the series, very narrow and thin. The second basibranchial gives origin to both the first and second hypobranchials. The first and

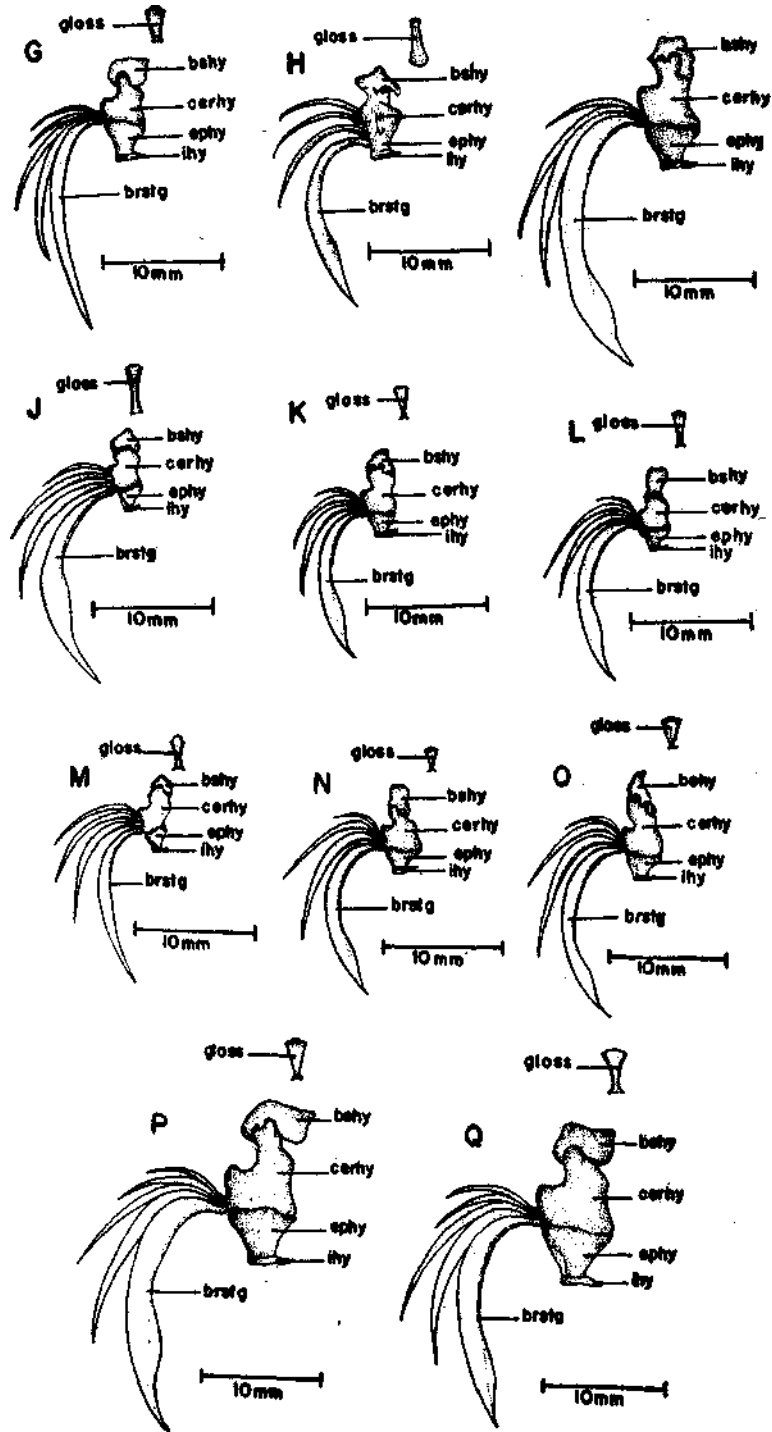


FIG. 38. Hyoid arches and glossohyals of G. *L. daura*; H. *L. blochii*; I. *L. brevirostris*; J. *L. leuciscus*; K. *L. berbis*; L. *L. lineolatus*; M. *L. bindus*; N. *S. ruconius*; O. *S. insidiator*; P. *G. minuta*; Q. *G. achlamys*.

brstg: branchiostegal ray; bshy: basihyal; cerhy: ceratohyal; ephy: epihyal; gloss: glossohyal; ihy: interhyal.

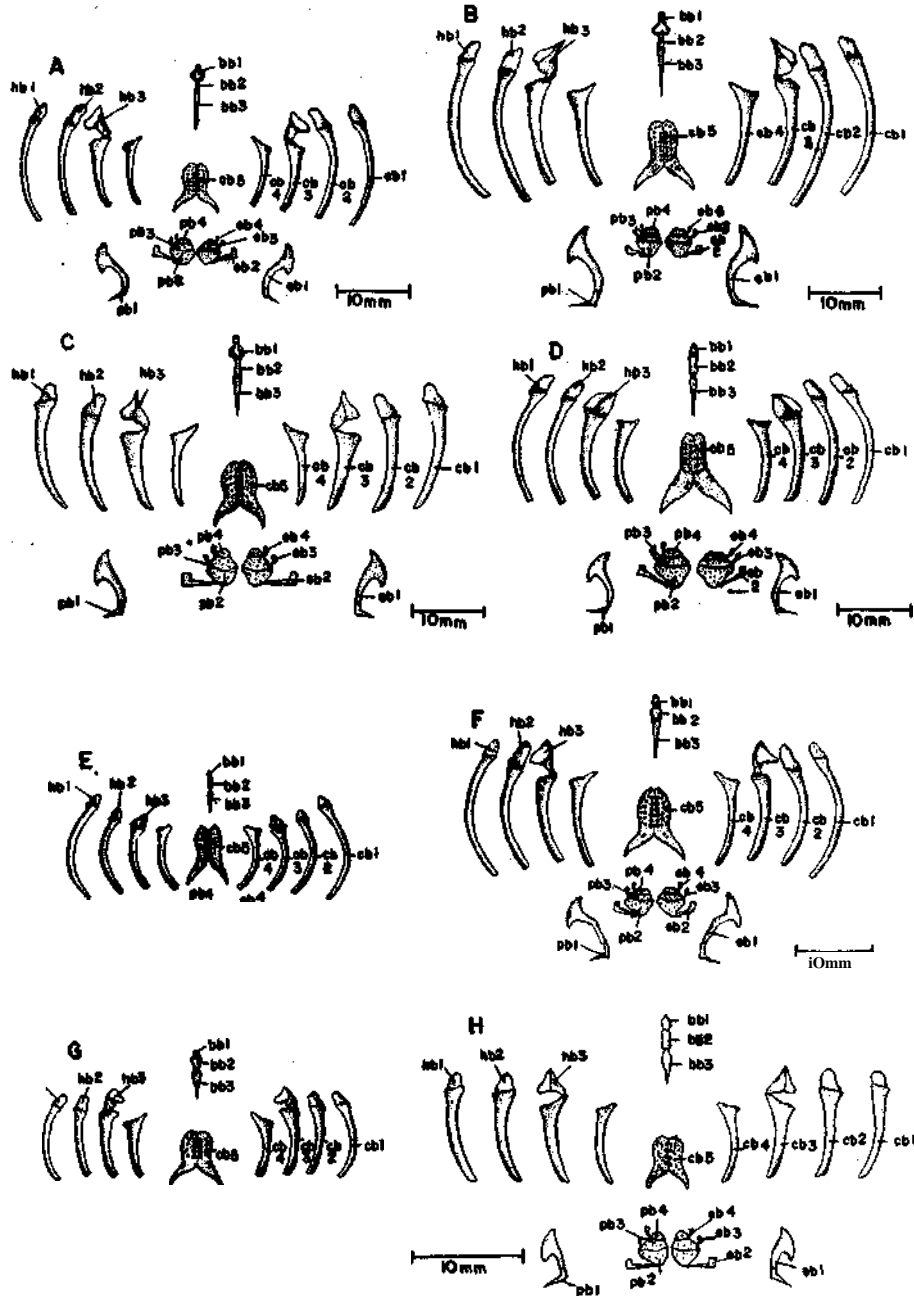


FIG. 39. Branchial arches of A. *L. fasciatus*; B. *L. eqimlus*; C. *L. smithursti*; D. *i. spfen dens*; E. *i. jonesi*; F. *Z. dussumieri*; G. *L. daura*; H. *i. blochi*.

bb1 to bb3: basibranchials 1-3; cb1 to cb5: ceratobranchials 1-5; eb1 to eb4 epibranchials 1-4; hb1 to hb3: hypobranchials 1-3; pb1 to pb4; pharyngobranchials 1-4 (ventral half above, dorsal half below).

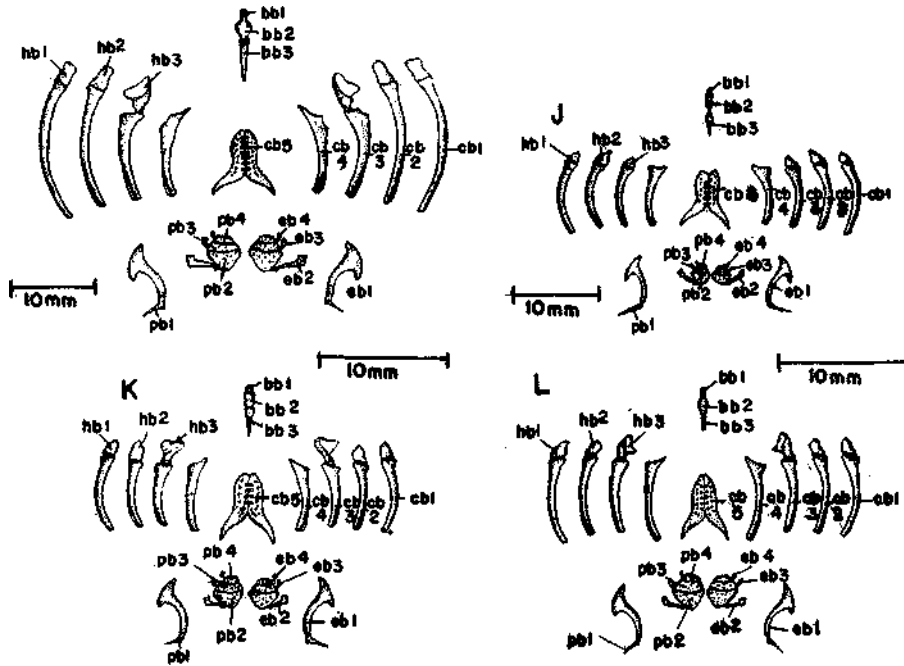


FIG. 40. Branchial arches of [I. *L. brevisrostris*; J. *L. leuciscus*; K. *L. berbis*; L. *L. lineolatus*.

bb1 to bb3: basibranchials 1-3; cb1 to cb5: ceratobranchials 1-5; eb1 to eb4: epibranchials 1-4; hb1 to hb3: hypobranchials 1-3; pb1 to pb4: pharyngobranchials 1-4 (ventral half above, dorsal half below).

second hypobranchials resemble each other in shape, being small and rectangular, whereas the third is large and conspicuous, triangular in shape, narrow anteriorly and broad posteriorly. It articulates at the anterior end of third basibranchial.

The ceratobranchials (*cb*1-*cb*5) are very long and curved, constituting the major support of the lower or ventral half of the branchial arches. The ceratobranchials decrease in length from the first to the last but are similar in shape except that the anterior ends of the third and fourth ceratobranchials are comparatively broader than others. The ventral surfaces of ceratobranchials are deeply grooved to their full length. The lower pharyngeals or modified fifth ceratobranchials are closely united along their inner surfaces and form a triangular structure on the floor of the pharynx. They bear large round denticles on the inner surface, mostly clustered in the central region and also possess stiff hair-like processes along the margins, presenting a roughened surface.

The epibranchials (*eb*1-*eb*4) form a series of irregularly curved and bent bones which are the main support to the upper or dorsal half of branchial arches.

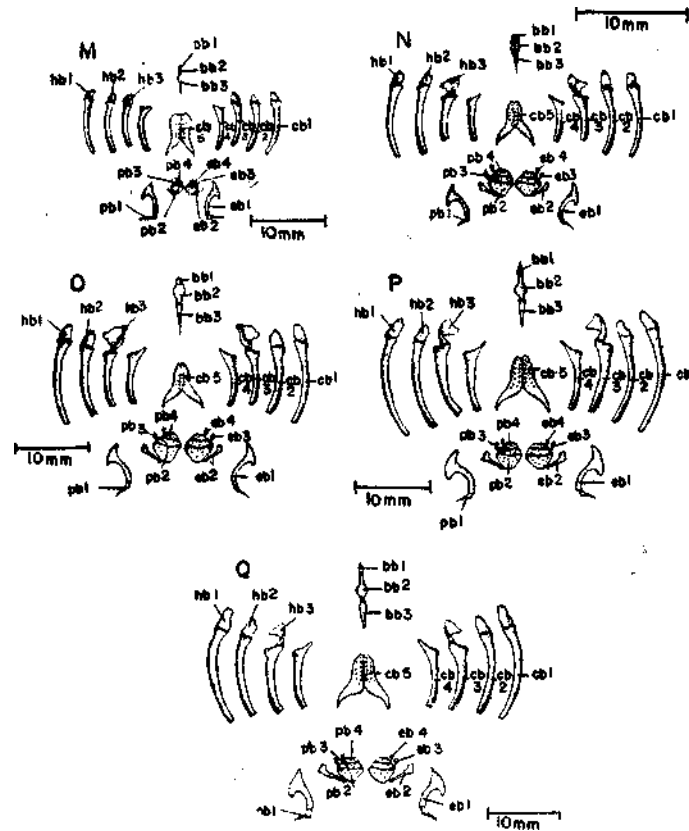


FIG. 41. Branchial arches of *M. L. bindus*; *N. S. ruconius*; *O. S. iisidiator*; *P. G. minula*; *Q. G. achlamys*.

bb1 to **bb3**: basibranchials 1-3; **cbl** to **cb5**: ceratobranchials 1-5; **eb1** to **eb4**: epibranchials 1-4; **hb1** to **hb3**: hypobranchials 1-3; **pb1** to **pb4**: pharyngobranchials 1-4 (ventral half above, dorsal half below).

The first epibranchial is the largest, with a prominent ventral head for attachment with the posterior end of the first ceratobranchial. It is strongly curved, giving articulation to the first pharyngobranchial (suspensory pharyngeal). The second, third and fourth epibranchials decrease in length from outside inwards, each with a ventral articulating surface with the corresponding ceratobranchial and a dorsal articulating surface with the respective pharyngobranchial.

The four upper pharyngeals or *pharyngobranchials* (**pb1**-**pb4***) are unequal in size and differ in shape. The first or the suspensory pharyngeal, is a tiny bent bone that articulates ventrally with the first epibranchial and connects dorsally the branchial arches to the neurocranium on its ventral side. The second,

third and fourth upper pharyngeals are closely united as a mass of bone and all of them bear villiform teeth (some ending bluntly and others ending in very sharp points) on the inner surface (facing mouth cavity) working against the lower pharyngeals, which are also bearing denticulations and stiff processes.

When separated, the second pharyngobranchial is the largest of the three bones and articulates with the dorsal end of second epibranchial. The third pharyngobranchial is crescent shaped uniting below with the dorsal end of the corresponding epibranchial. The fourth pharyngobranchial is the smallest, articulating with the fourth epibranchial.

On the surface facing the mouth cavity, the first epibranchial and the first four ceratobranchials bear gill rakers but they are better developed only on the first ceratobranchial. The number and size of gill rakers vary in the different species of the genera.

PECTORAL GIRDLE AND FIN

(Fig. 42 A to C)

The pectoral girdle is situated close behind the neurocranium and is connected with its upper part by the post-temporal.

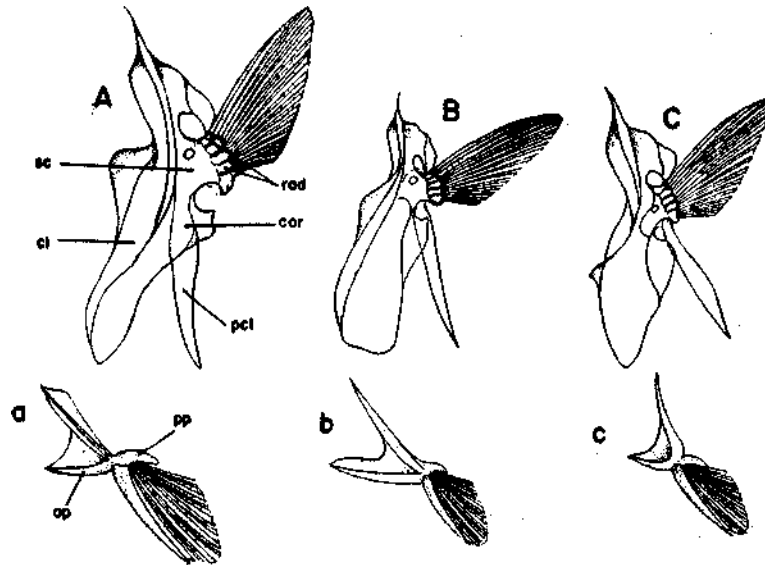


FIG. 42. Pectoral girdles and fins (A-C) and pelvic girdles and fins (a-c) of A. *L. jonesi*; B. *S. insidiator*; C. *G. minuta*.

cl: clavicle; cor: coracoid; pel: postcleithrum; rad: radial; s: scapula.
Pelvic girdle and fin of A. *L. jonesi*; B. *S. insidiator*; C. *G. minuta*.
ap: anterior process; pp: posterior process.

The post-temporal (ptm) is a forked bone which affords the principal articulation of the pectoral girdle to the neurocranium. The fork of the bone is directed anteriorly, the dorsal arm being longer and sharper than the ventral which is short and blunt, the former articulating with the epiotic and the latter with the pterotic. Posteroventrally the supracleithrum joins with the post-temporal.

The supracleithrum (supel) is a flat bone, thick anteriorly and thin posteriorly. Dorsally, it articulates with the post-temporal on its external side and ventrally overlaps the dorsal end of the cleithrum.

The cleithrum (cl) is the largest bone of the pectoral girdle with a small upper portion and a larger lower portion. The former has the external surface convex and internal surface concave and the reverse is true for the latter. The upper portion also ends in a sharp dorsal process with which it articulates with the supracleithrum.

The scapula (scap) is a small flat bone united to the cleithrum at its posterior margin at the level where the larger lower portion of cleithrum commences. It is pierced by the scapular foramen. Ventrally, it articulates with the dorsal end of the coracoid.

The posterior face of the scapula gives articulation to the four pterygials (ptryg) which support the pectoral fin, the ventral most one being the largest.

The coracoid (cor) joins above with the scapula and along the entire anterior face with the cleithrum. It is sharp at its ventral end.

The postcleithrum (pel) is a prominent bone-situated behind the cleithrum in an inclined manner, its dorsal end bracing behind the scapula and its ventral end resting between the pelvic girdles.

The pectoral fin consists of one spine and 12 rays.

PELVIC GIRDLE AND FIN

(Fig. 42 a to c)

The pelvic girdle consists of a flat plate, the dorsal arm of which is longer than the ventral arm, both directed anteriorly. The dorsal arm has an external low ridge. At the posterior corner, where the pelvic spine articulates with the pelvic girdle, it bears a curved bone on the external side. The pelvic girdle is located close to the ventral portion of pectoral girdle, the upper ends of the dorsal arms of the two girdles of the two sides resting in the concavity of the cleithra of the two sides, the lower end of the post-cleithrum resting on the inner side of pelvic girdle at the origin of the fin. The pelvic girdle is embedded free in the flesh of the abdominal wall.

The pelvic fin consists of a strong dagger-like spine and six rays. On the external side, an elongated scale is also present.

DORSAL FIN

(Fig. 43)

The dorsal fin commences immediately behind the supraoccipital crest and consists of 8 spines and 14 rays. The soft dorsal fin terminates a little in front of the origin of caudal fin.

Each radial of the dorsal fin consists of three pterygiophores, the proximal, middle and distal. The proximal or first pterygiophore (interneural) is by

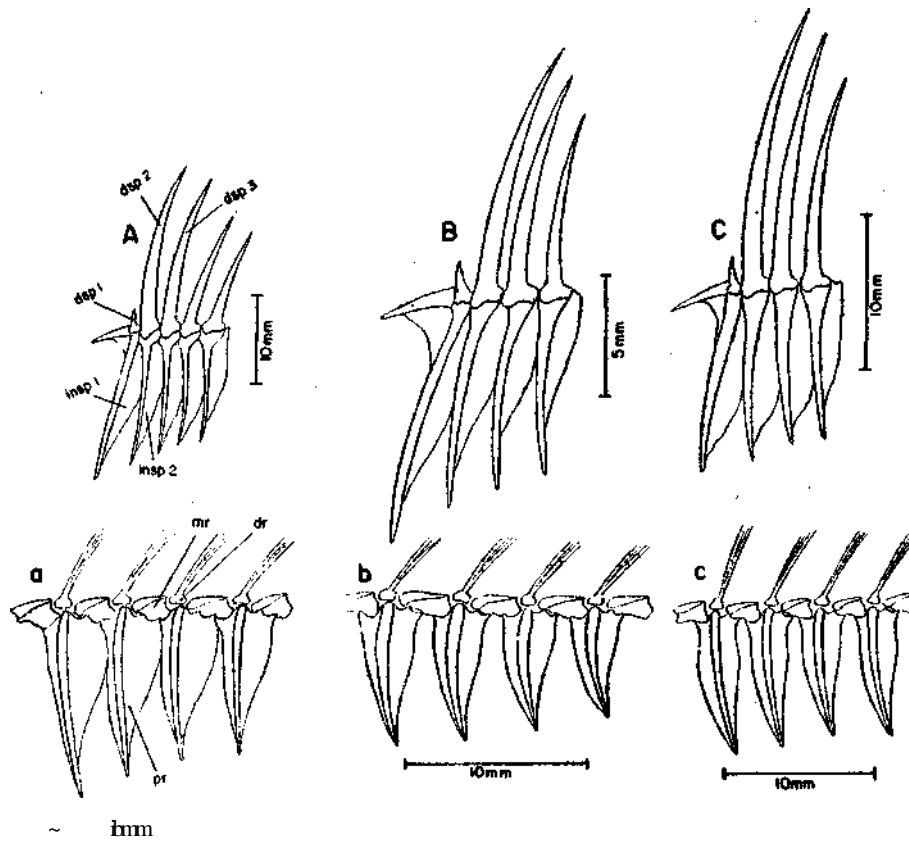


FIG. 43. Skeletal elements (shown in part) of (A-C) spinous dorsal fin and (a-c) soft dorsal fin of A. *L. jonesi*; B. *S. insidiators*; C. *G. minuta*.

dspl to dsp3: dirsal spines 1-3; inspl to insp2: interneural spines 1 and 2.
 dr: distal radial; mm: middle radial; pr: posterior radial.

far the largest and prominent of the series and forms the essential support of spines or rays. Each interneural is like a strong spine with a narrow anterior and a broad posterior wing-like extensions. In the case of dorsal fin spines, the corresponding interneurals articulate with them directly without the middle and distal pieces. However, a small anteriorly directed process is present on the top of the interneural. The first interneural has an additional antero-ventrally directed sharp spine in the angle of which is a wing-like bone. The first dorsal spine which is united on top of it shows limited movement in the antero-posterior plane. Other spines also have similar movement. The base of each spine is broad with lateral articulating surfaces and a median cavity, the former resting on the surface on top of the interneural and into the latter fits tightly the anteriorly directed process on top of the interneural.

The rays are supported by the three distinct pterygiophores. The top of the interneural provides a flat and wide articulating surface for the base of the middle piece, which is the next largest pterygiophore. The middle piece accommodates the proximal part of the distal piece. The distal part of the distal piece is bifurcated and tightly fits into corresponding cavities at the base of each ray which clasps the region. This ball and socket-like articulation affords a free movement of the fin ray. The three pterygiophores articulate consecutively, though not in a vertical line.

There is a uniform pattern of correspondence between the interneurals and the neural spines in the three genera and also between the species of the three genera.

The first dorsal spine is supported by first interneural arising in front of second neural spine. The second interneural spine (for second dorsal spine) arises between second and third neural spine: Thereafter, the order is 3/4, 4/5, 5/6, 6/7, 7/8, 8/9 of interneural spine|neural spine. The first three dorsal rays have independent interneural spines (9, 10, 11) corresponding to 10, 11, 12 neural spines. Thereafter, the order is 12, 13/13, 14/14, 15, 16/15, 17, 18/16, 19, 20/17, 21, 22/18, 23/19, 24/20 of interneurals|neural spines. Thus, a total of 24 interneural spines and 19 neural spines (excluding atlas) support the spinous and soft dorsal fin.

The interneural spines 9 to 22 are thick compared to others. The neural spines 2 to 6 are compressed. In some cases the interneural spines are compressed and plate-like, in certain others, they are swollen in the middle. The middle region may be solid and bony.

Each fin ray consists of a base and a long flexible hair-like filament, with the two lateral halves of the latter firmly united. The base of each ray is compressed laterally and more or less spherical in shape. Between the two halves of the base of the fin ray lies the distal portion of the third pterygiophore with which the fin ray articulates.

The structure of the dorsal fin is essentially the same in all the three genera.

ANAL FIN

(Fig. 44)

The anal fin begins slightly behind the vent and runs midventrally towards the posterior end and terminates opposite the posterior extremity of the dorsal fin. The spinous anal fin is represented by three spines, the first very small, the second the largest and the third sub-equal to the second.

The first interhaemal is very long, its dorsal end passing in between the haemal processes of the last precaudal vertebra and the first caudal vertebra (the first caudal vertebra with prominent haemal spine, last precaudal vertebra with wing-like haemal processes) to touch the vertebral column. Below, the first interhaemal spine gives articulation to the first two anal spines. These two spines have limited movement in the antero-posterior direction, swinging from an axis provided by the base of the interhaemal.

Articulation to the third spine is provided by the second interhaemal at its base on the anterior end. The base of the spine on the inner surface has

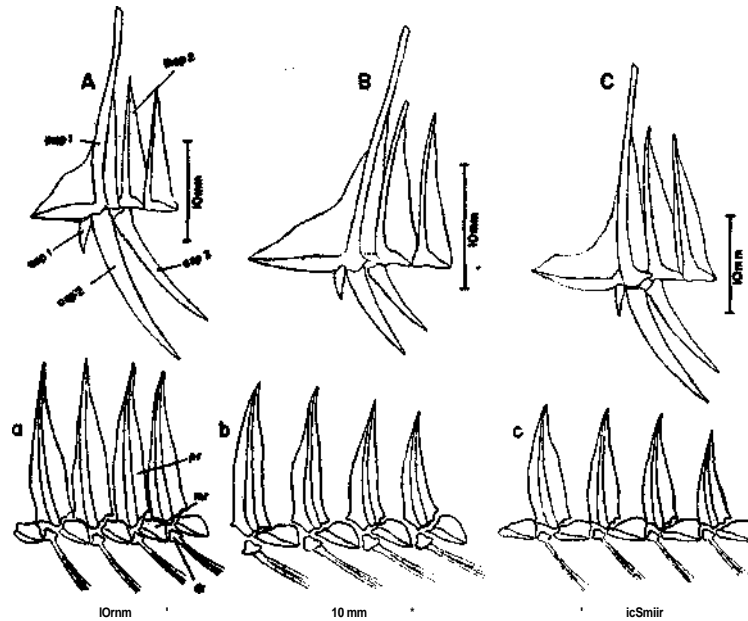


FIG. 44. Skeletal elements of (A-C) spinous anal and (a-c) soft anal fins of *L. jonesi*; *S. insidlator*; *G. minuta*.

aspl to asp3: anal spines 1-3; ihsp1 to ihsp2: interhaemal spine 1-2; dr: dorsal radial; mm: middle radial; pr: posterior radial.

two processes directed posteriorly which also help in its articulation with the base of the interhaemal. They restrict the movement of the spine upwards and backwards. The base of the third spine is serrated for about 1/3 length on the outer side. The other two spines do not bear any serration.

The first interhaemal has a narrow fringe of bone on the posterior side of stem from about 1/3 length down and a triangular piece on the anterior side for 1/3 length from below. The second interhaemal has only the fringe on posterior side throughout the length, broadening towards base. The first two interhaemals run on either side of the first haemal spine (1/1, 2) and thereafter the arrangement may be indicated as 2/3, 4, 3/5, 4/6, 7, 5/8, 6/9, 10, 7/11, 12, 8/13, 14, 9/15, 10/16 (number of haemal spine/number of interhaemal spines). Thus, 10 haemal spines and 16 interhaemal spines support the spinous and soft anal fin. The third to fifteenth interhaemals are thick compared to others. Sometimes, they are plate-like, central portion thick and opaque, rest of the region being transparent. The anal rays are attached from third to sixteenth interhaemals (total 14 rays).

The third interhaemal has bony fringe on both sides but more on the anterior side. When two interhaemals are obtained to a haemal spine, the fringe is more on opposite sides for the anterior one on the anterior side, for the posterior one on the posterior side. When only one interhaemal articulates with haemal spine, it has more on posterior side because the one in front (double) has also more on posterior side. The last interhaemal is a small piece of bone without any distinct stem. Its structure is peculiar in that it consists of two pieces united by ligaments and bony teeth-like processes. The lower piece is tipped with cartilage at the posterior end.

In the soft anal fin, each radial consists of the proximal, middle and distal pieces. At the base, the interhaemal provides articulation for the middle piece at a toothed surface. The anterior end of middle piece is also denticulate and narrow. Its distal end is broad providing articulation to distal piece ventrally. Its dorsal half of posterior end articulates with the succeeding interhaemal which also partly touches the distal piece of the preceding radial. The body of the distal piece articulates with the middle piece anteriorly and with the ray posteriorly. The bifid end is directed upwards and touches the anterior end of middle piece of the next radial.

CAUDAL FIN

(Fig. 45)

The neural and haemal spines of the 20th vertebra possess wing-like extensions. Those of 21st vertebra are elongate and strongly bent posteriorly to support the caudal skeleton. The neural spine ends in a sharp point, while the haemal spine ends in a blunt point. The neural spine of 22nd vertebra is very

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short and ends in a sharp point compared to its haemal spine which is blunt and flattened. The 23rd vertebra or urostyle is virtually a half centrum to which two triangular hypural plates are attached for giving origin to caudal fin rays.

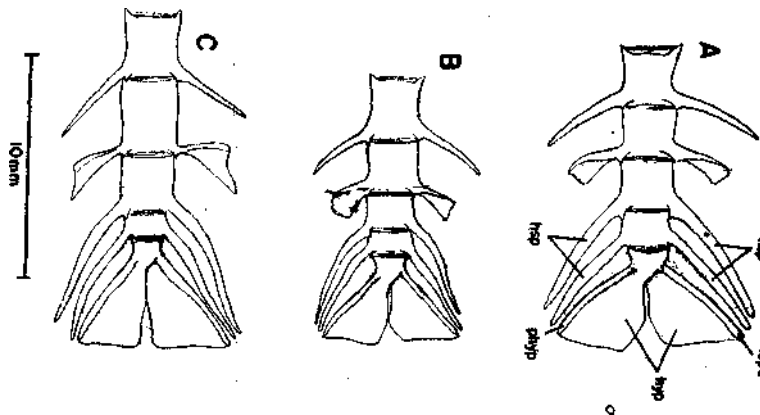


FIG. 45. Caudal skeleton of A. *L. jonesi*; B. *S. insidiator*; C. *G. minuta*.

epu: epiural; hsp; heamal spine; hyp: hypural; nsp: neural spine; phyp: parhypural.

VERTEBRAL COLUMN

(Plates I to IV)

The vertebral column is divisible into two distinct regions, the precaudal (abdominal) and caudal. The pre-caudal vertebrae are short, each with two lateral cavities and one ventral cavity. The parapophyses gradually increase in size from first to ninth vertebra. They also gradually descend from first to ninth vertebra, which in the ninth vertebra are very large and wing-like, separating the precaudal from caudal vertebrae.

The first six neural spines are compressed and gradually increase in size. They are also inclined backwards. The neural spines of seventh to ninth vertebrae are more or less vertical.

While the neural spine of first Caudal vertebra (10th) is longest, its haemal spine is shorter than that of 11th vertebra (having the longest haemal spine). From 11th vertebra onwards, both neural and haemal spines gradually decrease in size. The neural and haemal spines of 20th vertebra are short and compressed (wedge shaped). The vertebrae of caudal region are longer than those of thoracic region. The dorsal and anal rays terminate opposite the 19th vertebra.

The variations in the number of vertebrae are given in Table 1. There are 10 precaudal vertebrae, 12 to 14 caudal vertebrae and 22 to 24 total vertebrae. There are no intergeneric or interspecific variations in the number of vertebrae.

TABLE 1. *Vertebral variations in Leiognathidae.*

Species	No. of specimens	Size range (TL in mm)	No. of pre caudal vertebrae	No. of caudal vertebrae	Total No. of vertebrae
<i>Leiognathus fasciatus</i>	8	105-160	10	13	23
<i>L. equulus</i>	7	90-175	10	13	23
<i>L. smithursti</i>	10	130-180	10	13	23
<i>L. splendens</i>	10	60-117	10	13	23
<i>L. jonesi</i>	40	80-135	10	13	23
<i>L. dussumieri</i>	10	80-125	10	13	23
<i>L. daura</i>	10	90-125	10	13	23
<i>L. blochi</i>	10	62-85	10	13	23
<i>L. brevirostris</i>	10	90-120	10	12-13	22-23
<i>L. leuciscus</i>	10	98-120	10	13	23
<i>L. berbis</i>	20	65-100	10	13	23
<i>L. lineokttus</i>	10	60-120	10	13	23
<i>L. bindus</i>	20	50-110	10	13	23
<i>Secutor ruconius</i>	15	50-70	10	13-14	23-24
<i>S. insidiator</i>	10	75-105	10	13	23
<i>Gazza minuta</i>	10	80-135	10	13	23
<i>G. achlamys</i>	10	90-150	10	13	23

RIBS

The ribs are thin and fragile, lining the abdominal cavity. The seven pairs of ribs are loosely articulated to vertebrae 3 to 9. The first five pairs reach the base of anal fin with their tips embedded in the muscles. The sixth pair is shorter than the preceding, extending to about 2/3 distance ventrally. The seventh pair is much shorter, closely opposed to the basal elements of the anal fin. The epipleural ribs are attached to the first 12 to 14 vertebrae, including the atlas.

(For a synoptic comparison of the three genera as well as of the different species in each genera, see Part II of the article in Number 4 of the Volume).