COMPARATIVE OSTEOLOGY OF THE RIBBON FISHES OF THE FAMILY TRICHIURIDAE FROM INDIAN WATERS, WITH REMARKS ON THEIR PHYLOGENY*

By P. S. B. R. JAMES

Central Marine Fisheries Research Institute, Mandapam Camp

INTRODUCTION

THE ribbon fishes of the family Trichiuridae are represented by three genera and four species in Indian waters (James 1959) and are the subject of one of the important commercial fisheries. The genus *Eupleurogrammus* Gill is represented by two species namely *E. intermedius* (Gray) and *E. muticus* (Gray). The other two genera are monotypic, represented by *Trichiurus lepturus* Linnaeus and *Leputracanthus savala* (Cuvier). The most recent revision places the genus *Eupleurogrammus* under the subfamily Lepidopodinae and the latter two genera under the subfamily Trichiurinae, of the family Trichiuridae (Tucker, 1956).

Our present knowledge about the osteology of the ribbon fishes is very meagre. Gunther (1860) has outlined some general osteological characters of *Trichiurus lepturus* and Starks (1911) and Gregory (1933) have made some remarks on the skull of the same species, while the osteological characters of the other two genera have not been examined so far. Regan (1909) made reference to some general osteological features of Trichiuriformes, including the Trichiuridae and Gemyplidae.

Herein, an attempt is made to make a comprehensive and comparative study of the osteology of ribbon fishes from Indian waters. From this study, it is also aimed to draw a clear distinction between the different species based on osteological characters, as many similarities and differences have been noticed amongst the species under investigation. A brief discussion of these characters and their systematic significance is given, together with an osteological key.

In comparing the osteology of the four species it was noticed that while they have many features in common, two of them viz. *T. lepturus* and *L. savala* share certain characters and stand apart from the two species of *Eupleurogrammus*. Hence a detailed description of the osteology of *T. lepturus* which appears to be the most widely distributed of all four species is given below, and the characters in which other species differ from it are mentioned. A comparison of these with other genera of the family is made, to infer their possible phylogenetic relationship. For this purpose, the works of Allis (1903), De Sylva (1955), Francisco (1956), Gregory (1933), Gunther (1860), Starks (1910, 1911) and Kishinouye (1923) have been a valuable aid.

MATERIAL AND METHODS

The material for the study has been collected from different fish landing centres along the Indian coast and all the four species have been examined in different sizes. The majority of the fishes examined were obtained from local fish landing places on the Gulf of Mannar and Palk Bay, where three of the species occur together (James, 1959).

Skeletons were prepared for study by cooking the fresh fish in water. It has been found easy first to boil the water and then keep the specimen in it just long enough (about 5 minutes) to loosen the muscles from the bones. The bones of the skull of all species were disarticulated and studied. Alizarin staining technique as employed by Hollister (1934) referred to by Clothier (1950) was used with slight modifications to study the skeleton *in situ*.

The following procedure has been adopted for alizarin staining, which gave good results : For all preparations 4% KOH in distilled water was used. Staining solution was prepared by the following formula :—

Glacial Acetic acid	..	0.5 c.c.
Glycerine	..	3.0 c.c.
Chloral hydrate	..	10.0 c.c.
Alizarin Stain	..	0.1 gm.

Specimens were first hardened and kept straight in 5% formalin for 10-15 days. They were washed thoroughly under running tap water and then placed in 4% KOH. They take 2 to 4 weeks to become transparent, and ready for staining. The staining solution is added drop by drop to fresh KOH containing the specimens till it showed a violet-pink colour. The specimens take stain in 2 to 7 days depending on the size as well as the species. After they are stained, the used up solution was pippetted out, fresh KOH and increasing quantities of glycerine were added at regular intervals and preserved finally in pure glycerine. At each stage they were kept at least for 48 hours. Young individuals take less time to clear and the bones are much clearer than in older groups. Radiographs of a dozen specimens of each species ranging in size between 25-65 cm. S.L. were also examined.

In naming the various bones of the skeleton Clothier (1950), Ford (1937), Gregory (1933), Gunther (1860), Harrington (1955), Kishinouye (1923), Ramaswami (1952) and Starks (1901, 1910, 1911) were followed.

OSTEOLOGY

The very elongate, narrow shape of the skull (Figs. 1 and 2) reflects the highly carnivorous nature of these fishes. The bones of the skull are thin, except those of the jaws. Gunther (1860), and Starks (1911) have remarked that the skull of *T. lepturus* is very similar to that of *Lepidopus* Gouan and *Aphanopus* Lowe belonging to the two other sub families under Trichiuridae. Gregory (1933) has drawn attention to the close similarity of the skulls of *Trichiurus* Linnaeus and Gempylids. Except for minor details the skulls in the other two genera viz. *Eupleurogrammus* and *Lepturacanthus* also resemble those of *Lepidopus* and *Aphanopus*.
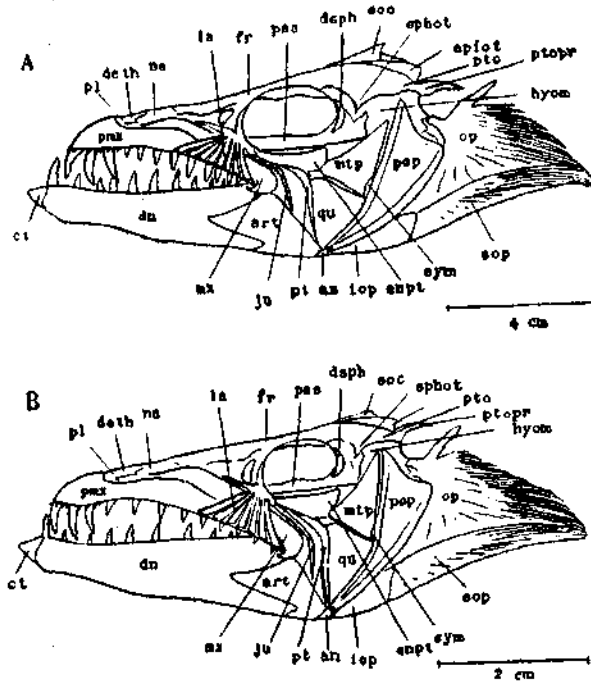
FIG. 1. Skull, lateral view. A. *Trichiurus lepturus*. B. *Lepturacanthus savala*.
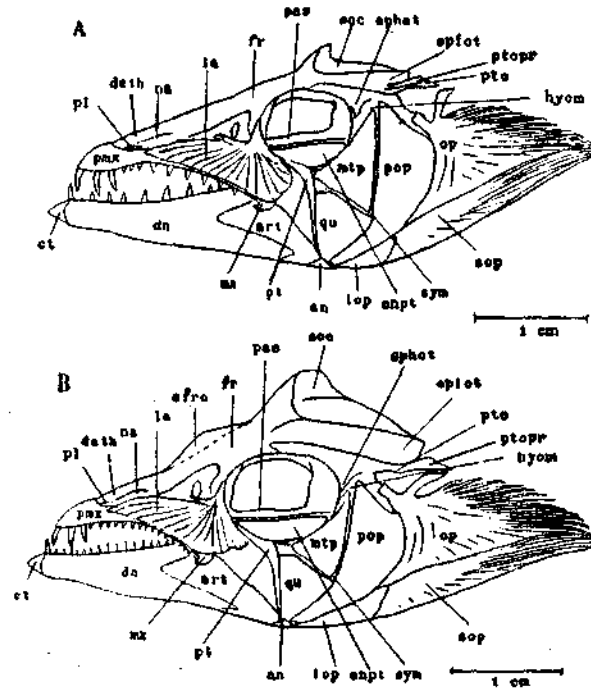

FIG. 2. Skull, lateral view. A. *Eupleurogrammus intermedius*. B. *Eupleurogrammus muticus*.

The main features of the skeleton may be summarized as follows : Bones thin and light ; neurocranium elongate and laterally compressed ; supraoccipital crest low ; posterior confluence of the frontals elevated to a median crest ; dorsal surface of the skull with grooves and ridges posteriorly ; dermethmoid cylindrical, forked posteriorly ; vomer devoid of teeth, broad at the anterior end and tapering to a sharp point posteriorly ; nasals long, and narrow ; maxilla broadest at the posterior end and premaxilla at the anterior end ; lower jaw tipped with a triangular piece of cartilage ; premaxilla and dentary forming upper and lower margins of the mouth cleft ; maximum of 3 canine-like barbed teeth anteriorly on each premaxilla and one on each dentary, the latter tooth remaining outside when the mouth is closed ; these followed by variable number of smaller and simpler teeth on both jaws ; palatine teeth in series or in villiform band ; suborbital ring incomplete, lacrymal most prominent, membranaceous and sculptured ; head of hyomandibular cruciform ; margins of opercle and subopercle fringed ; preopercle strong and bony with prominent ridges in the shape of ' Y ' ; pterotics produced posteriorly into spine-like processes ; alisphenoids, simple, triangular ; number of gill rakers variable and prominent on the outermost arch ; vertebrae numerous, extending to tip of tail ; ribs fragile ; interneurals and interhaemals usually correspond to neural and haemal spines ; pelvic girdle and fins absent or reduced ; dorsal and anal fin rays numerous.

NEUROCRANIUM

The neurocranium (Figs. 3-7) in the three genera is long and narrow, broadest at the posterior end. The dorsal surface is more or less flat in *T. lepturus* and *L. savala* while it is convex in *Eupleurogrammus*. The dorsal profile in a complete specimen is sharply declevous to the snout from nape in *E. muticus*. Along the dorsal surface, the median ridge is not prominent except at the supraoccipital region. On either side are three grooves, separated by 2 ridges of bone, viz. the dilator, temporal and supratemporal grooves extending from the outer to the inner regions of the skull
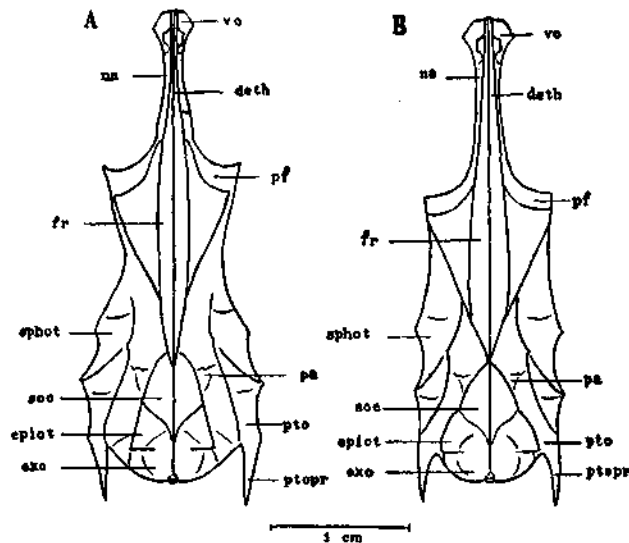

FIG. 3. Neurocranium, dorsal view. A. *T. lepturus*. B. *L. savala*.

respectively. Unlike in *E. intermedius* the median ridge is carried forward by the frontals to the dermethmoid (ethmofrontal crest) in *E. muticus*, such a prominent crest being absent in the other two species resulting in lesser height of the neurocranium and consequently of the head. The supraoccipital crest is very feeble in all the species.
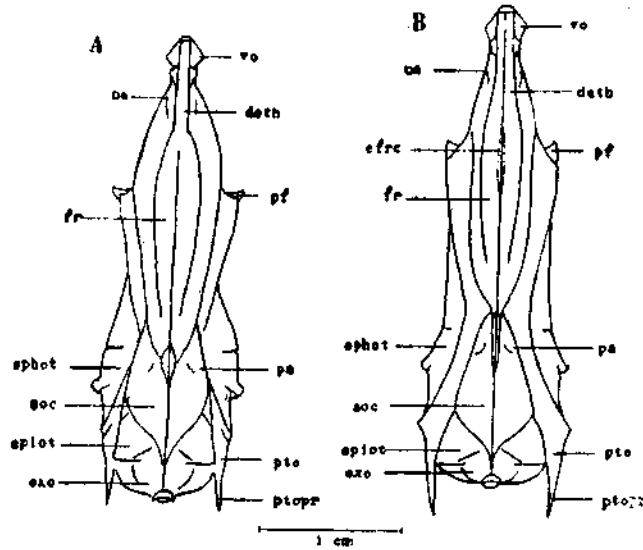

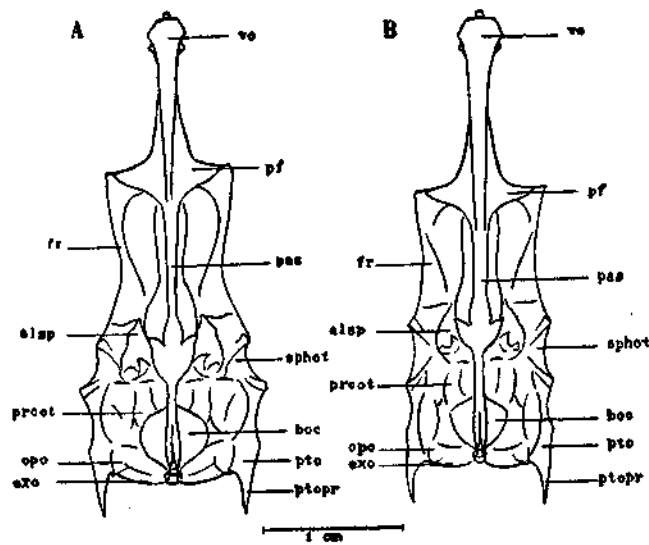FIG. 4. Neurocranium, dorsal view. A. *E. intermedius*. B. *E. muticus*.

FIG. 5. Neurocranium, ventral view. A. *T. lepturus*. B. *L. savala*.

The grooves and ridges present a variable pattern over the dorsal surface of the skull. They are well defined only in *T. lepturus*. The temporal and pterotic ridges

are quite distinct and run more or less parallel. The *temporal ridge* in *T. lepturus* stops short and fades into the general surface at about the posterior confluence of frontals. It presents posteriorly a flap-like projection whereas the outer terminates laterally and anterior to pterotic. In *L. savala* the ridge is much shorter and stops short anteriorly at the lateral mid-portion of supraoccipital presenting a flap-like
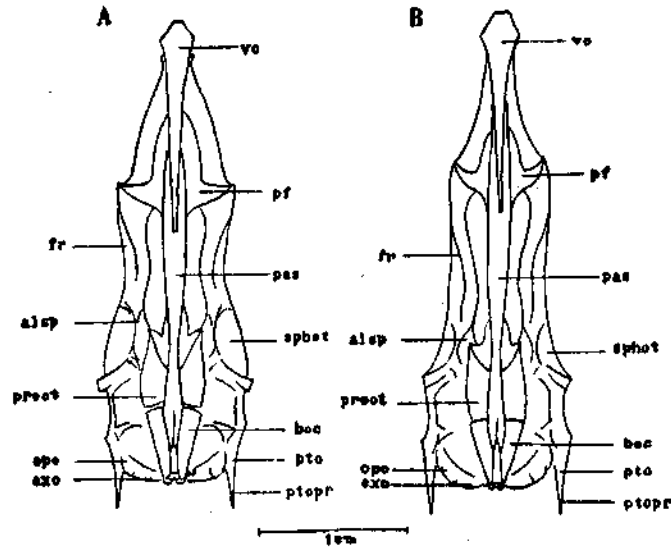

Fig. 6.   Neurocranium, ventral view.   A.   *E. intermedius*.   B.   *E. muticus*.

projection posteriorly as in *T. lepturus*. In *E. intermedius* this ridge runs forward and terminates at the posterior end of the nasal, while in *E. muticus* it curves laterally merging with the general surface about the middle region of the orbit. The external or *pterotic ridge* in *T. lepturus* extends forward to the mid-level of the orbit and fades into general surface. Posteriorly it merges with the lateral side of the pterotic bone. In its anterior course, it is deeply curved and runs parallel to the frontal ridge. In *L. savala* this ridge is very similar to that of *T. lepturus* but the anterior extremity is not parellel to the frontal ridge and being apparently approximated with the latter. The external ridge is very short in *E. intermedius* and it unites with the internal ridge at the level of supraoccipital to continue forward to the nasal. A similar condition is seen in *E. muticus* where it joins the internal ridge but terminates above the mid-level of the orbit. The *dilator groove* is much deeper and wider in *T. lepturus* and *L. savala* than in the species of *Eupleurogrammus*. The middle or *temporal groove* is broad in *T. lepturus* and very narrow and short in *L. savala* and *Eupleurogrammus*. It is relatively shorter in *E. intermedius* than in *E. muticus*. The groove is the biggest and broadest in *T. lepturus*, but shortest and narrowest in *L. savala* among the four species. The *supratemporal groove* is the widest of the grooves. It is comparatively shallower in *L. savala* than in the other forms.

The orbits are large in *T. lepturus* about 1/3 length of neurocranium while they are small in *L. savala* measuring less than 1/3 of the neurocranium. They are nearly equal in size in *Eupleurogrammus* species but less than 1/3 the length of neurocranium.
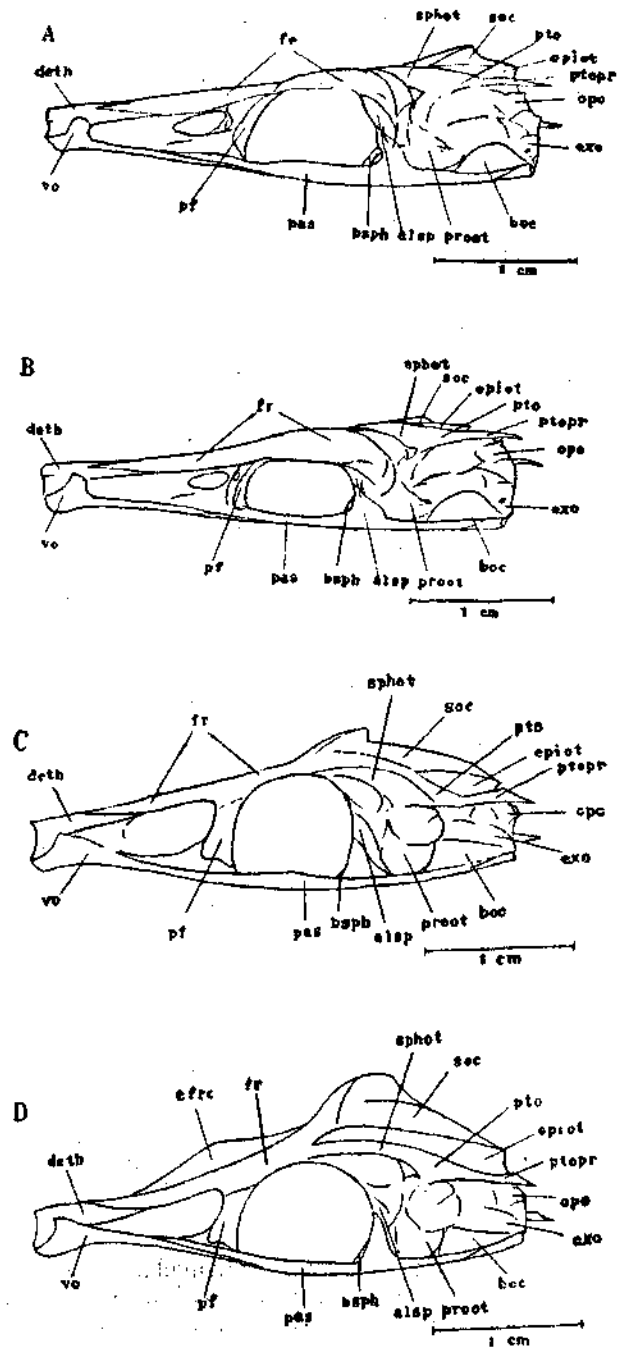
Fig. 7. Neurocranium, lateral view. A. *T. lepturus*. B. *L. savala*. C. *E. intermedius*. D. *E. muticus*.

INDIVIDUAL BONES OF THE SKULL

(Figs. 8-11)

Olfactory Region : The *dermethmoid* (*deth*) is median and forked posteriorly. It is more or less cylindrical enclosing a cavity. Anteriorly it rests over three protruberances of the vomer, and posteriorly overlapped by the anterior ends of frontals. Posterolaterally it is bounded by the prefrontals. At the anterolateral portion the dermethmoid supports the nasals. The anterior tip of the dermethmoid is blunt in *T. lepturus* and *L. savala* while it is sharp in *Eupleurogrammus*.

The *prefrontals* (*pf*) are two irregular bones, forming the anterior wall of the orbit and the posterior mesial walls of the nasal cavity. The bones meet along the median line and articulate above with the frontals, anteriorly with the lateral extensions of the dermethmoid and posteroventrally with the parasphenoid. The anteroventral extension of the bone found in *T. lepturus* and *L. savala* is absent in *Eupleurogrammus*. On the other hand there is a sharp anterodorsal process in *E. intermedius* and *E. muticus* which is absent in *T. lepturus* and *L. savala*.

The *nasals* (*na*) are elongate, flat bones, cemented along their entire length to the anterolateral sides of the dermethmoid. The nasals of *T. lepturus* and *L. savala* are alike and those of *E. intermedius* and *E. muticus* resemble each other. The nasals of the former two species differ from the latter two in that they are longer and slightly bent anteriorly.

The *vomer* (*vo*) is broad at the anterior end and narrows down to a long process posteriorly which ends in a sharp point. Anteriorly it articulates with the maxilla and posteriorly it lies in the groove on the external side of parasphenoid. It presents three protruberances at the anterior inner extremity, on which the dermethmoid rests. The vomer is devoid of teeth in all species. In *T. lepturus* and *L. savala* the anterior articulatory facet is short and straight while in *Eupleurogrammus* it is long and upturned.

Orbital Region : The paired *frontals* (*fr*) from the largest portion, approximately 2/3 of the dorsal roof of the skull. The bones are pointed anteriorly and cover the bifurcated posterior end of dermethmoid. Posteriorly they are broad. The frontals are closely approximated over their entire length, except at their anterior tips which diverge and partly cover the dermethmoid. The posterior confluence of the frontals is elevated in *T. lepturus* to a low crest which is least developed in *L. savala*, highest in *E. muticus*. The frontal crest in *E. intermedius* resembles that of *T. lepturus*.

Anteriorly the frontals lie over the posterior end of dermethmoid and the dorsal ends of the parethmoids. Laterally they contribute to the roof of the orbit and posteriorly they are connected with the supraoccipital, sphenotics, parietals, alisphenoids and pterotics.

The *alisphenoids* (*alsp*) are paired, small, triangular bones. They form the posterodorsal angle of the orbit wall and articulate with the sphenotics, prootics and basisphenoid. As in all scombroids, they do not articulate with parethmoids.

The brain chamber opens between the alisphenoids. Its aperture is wider in *T. lepturus* than in *L. savala* and is much deeper in *E. muticus* than in *E. intermedius*.

Figs. 8 and 9. Disarticulated bones. *T. lepturus.*

1. opercle, 2. preopercle, 3. subopercle, 4. premaxilla, 5. interopercle, 6. maxilla, 7. dentary, 8. articular, 9. ectopterygoid, 10. entopterygoid, 11. palatine, 12. metapterygoid, 13. parasphenoid, 14. hyomandibular, 15. frontal, 16. vomer, 17. dermethmoid, 18. quadrate, 19. lacrymal, 20. dermosphenotic, 21. supraoccipital, 22. symplectic, 23. prefrontal, 24. alisphenoid, 25. parietal, 26. sphenotic, 27. nasal, 28. pterotic, 29. basisphenoid, 30. opisthotic, 31. basioccipital, 32. epiotic, 33. jugal, 34. prootic, 35. exoccipital, 36. urohyal.

The parasphenoid (pas) is more or less similar in shape in all the genera and species. The part of the parasphenoid opposite the orbital cavity (when the neurocranium is viewed ventrally) is slightly broader in *Eupleurogrammus* than in the other two genera.

The *lacrymal (la)* is the largest bone of the suborbital ring and is characterized by the sculpture which decorates it. It consists of a dorsal bony rod and a membranous fringed flap. A curved dorsal process from the bony rod binds the anterior margin of the eye. The membranous part hides from view the major portion of the maxilla and the premaxilla on each side. The lacrymal differs strikingly in shape and relative size, in the two sub-families. In *Trichiuris* and *Lepturacanthus* it is short, high and fan-like covering only about one-third of premaxilla and maxilla while in *Eupleurogrammus* it is comparatively large covering a greater portion (about two-thirds the length) of premaxilla and maxilla.

The second element of the suborbital ring is represented by a delicate bent bone, the *jugal (ju)* in *T. lepturus* and *L. savala* and unrepresented in *Eupleurogrammus.* It is situated immediately behind the lacrymal.

A third ossicle, the *dermosphenotic (dsph)* is crescent-shaped, freely suspended, small bone with an inward wing-like extension situated centrally at the posterior margin of the orbit, apparently forming the suborbital shelf. This bone is also not represented in *Eupleurogrammus.*

Otic Region : The *parietals (pa)* 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 the frontals and posteriorly with the epiotics. The parietals do not take part in the formation of the roof of the brain cavity, and are similar in all the genera.

The *supraoccipital (soc)* forms dorsally the median portion of the posterior end of the neurocranium. It is convex above, broadest in the middle and narrower at either ends. The posterior blunt end of it extends between the epiotics. The supraoccipital bears a ridge middorsally, its ridge separating the supratemporal grooves of the two sides. The supraoccipital is bounded anteriorly by the frontals, anterolaterally by the parietals and laterally by the epiotics. The posterior confluence of the frontals is elevated to a dorsomedian crest, more conspicuously in *Eupleurogrammus.* The posterior end of supraoccipital is somewhat blunt in *T. lepturus* and *L. savala* while it ends in a sharp point in *Eupleurogrammus.* In the latter the ridge is confined to the anterior end of supraoccipital in continuation with the posterior confluence of frontals. It is low in *E. intermedius* but high in *E. muticus,* in which it is more strikingly seen in a lateral view of the skull.

The supraoccipital in several specimens of *T. lepturus* of various sizes from different localities was found to be subject to excessive thickening while the absence of this phenomenon in the other three species appears significant, as shown in a recent study (James, 1960).*

The *pterotics (pto)* form the posterolateral corners of the skull and are produced into short spine-like processes on either side. They also contribute to the formation of the temporal and dilator grooves and to the main portion of the pterotic ridge.

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* Bhatt and Murthi have referred to this subject in a recent paper. (*J. Univ. Bombay,* vol. 28 (5) : 84-89, 1960).

The pterotics bear anterior processes in *Eupleurogrammus* which are absent in the other two genera.

The *prootics (proot)* are irregular bones prominent on the ventral side of the neurocranium. The prootics in all the species are alike in shape and disposition and articulate with the parasphenoid, sphenotics, pterotics and basioccipital.

The *epiotics (epiot)* are two small bones, each with a dorso-lateral and a posterior surface intervened by a thin transparent area. Dorsally a process receives the upper branch of the post-temporal, thus forming a connection between the pectoral girdle and neurocranium. This process at the posterior end of the temporal ridge is equally prominent in all the species.

Anteriorly and along the median line the epiotics join the supraoccipital, posteriorly they unite with the exoccipitals and laterally with the pterotics.

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 *T. lepturus* and *L. savala* the sphenotic bears a prominent dorsal ridge which is lacking in *Eupleurogrammus* species. The lateral margin of sphenotic presents a concavity in the two former species while it is entire in the latter forms. In all cases there is an inward extension of this bone overlapped by the posterior end of the frontals. The sphenotics are flattened bones and bear a postero-lateral projection in all species.

The *opisthotics (opo)* are small scale-like bones interposed between the pterotics and the exoccipitals.

The *exoccipitals (exo)* are fan-shaped bones which enclose the foramen magnum and articulate with the basioccipital along the median line. Anteriorly they join the prootics, and laterally the pterotics. Their vertebral or paraoccipital condyles to the atlas are concave, and project beyond the basioccipital. The ventral surface is slightly concave and bears a prominent aperture or the foramen for the passage of the vagus nerve.

Basicranial Region : The *parasphenoid (pas)* is a long rod-like bone that forms 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. The parasphenoid is long and bears posteriorly two small lateral ascending wings, one on either side to connect the prootics. Behind these wings the parasphenoid is constricted and gradually broadens with a gentle curvature upwards. At the sharp posterior bifurcated end the parasphenoid is embraced by the ventral sides of the basioccipital, and the median spine-like process of the latter fits into its forked end. The anterior end is simple and grooved externally for a distance, where it is overlapped ventrally by the posterior portion of the vomer. The portion between this point and the point of origin of lateral wings is the narrowest part of parasphenoid and forms the ventral margin of orbital cavity. The middle portion of the parasphenoid (ventral margin of orbital cavity) is narrow in *Trichiurus* and *Lepturacanthus* but broad in *Eupleurogrammus*. In *E. muticus* it is relatively broader than in *E. intermedius*.

The *basisphenoid (bsph)* is a small median Y-shaped bone, which unites the parasphenoid with the prootics and alisphenoids. The median vertical process is

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laterally compressed. The basisphenoid is very much alike in all the species, but greatly exposed in *T. lepturus* in a lateral view of neurocranium than in the other species.

The *basioccipital* (*boc*) is a short narrow bone with two wing-like extensions. It bears the concave rounded occipital condyle that articulates with the atlas. The median portion which is spine-like, fits into the forked posterior end of parasphenoid. The anterior end is broader than the solid posterior end.

The basioccipital supports dorsally the exoccipital of the corresponding side of the neurocranium and is bounded ventrally by the parasphenoid and in front by the prootics. The vertebral or paraoccipital condyles of the exoccipitals to the atlas rest on the hind end of basioccipital.

The shape and size of basioccipital varies in the different genera. In *Trichiurus* and *Lepturacanthus* it is short and broad especially at the anterior end. In *Eupleurogrammus* it is long and narrow, with the lateral wings less expanded at their anterior ends.

Except for the differences mentioned above, the basicranial bones are much similar in structure in all the three genera of ribbon fishes.

BRANCHIOCRANIUM

Oromandibular Region : The *premaxilla* (*pmx*) is a long curved bone tapering anteriorly and posteriorly. The bone is thickest at the anterior end, with an ascending process. The ascending process is more pointed in *Eupleurogrammus* than in *Trichiurus* and *Lepturacanthus*. The nasal process of the premaxilla projects into the concavity in front of and over the dermethmoid.

The number of premaxillary teeth is variable in the species. Of the four species, *Eupleurogrammus muticus* bears the maximum number of teeth and *Lepturusanthus savala* the minimum. A detailed study of the oral armature in the Indian Trichiurids in correlation with their feeding habits will be published elsewhere. However, brief details are given in Table I for comparison.

In the angle between the posterior margin of the ascending nasal process of the premaxilla and the dorsal edge of the shank of the bone there is a small backwardly directed process or projecting edge which has two depressions or articular facets, one on either side. The edge fits into the anterior forked cartilaginous part of the maxilla, while the two cartilaginous pieces of the latter lie firm in the two facets.

The *maxilla* (*mx*) is also a long, curved bone, the inferior surface of which lies over the superior surface of premaxilla behind the ascending process of the latter and extends beyond its posterior end. The head of the maxilla ends in a bifurcated cartilaginous piece, the two portions of which embrace the backwardly directed process of the premaxilla, while the cartilaginous pieces lie in depressions on either side. The maxilla is laterally compressed and is relatively broader at its posterior end.

The *dentary* (*dn*) is a large posteriorly forked bone, which forms the basis of the lower jaw, and like the premaxilla and maxilla it is laterally flattened. It bears a single row of triangular, sharp teeth on the dorsal arm. The ventral arm is relatively
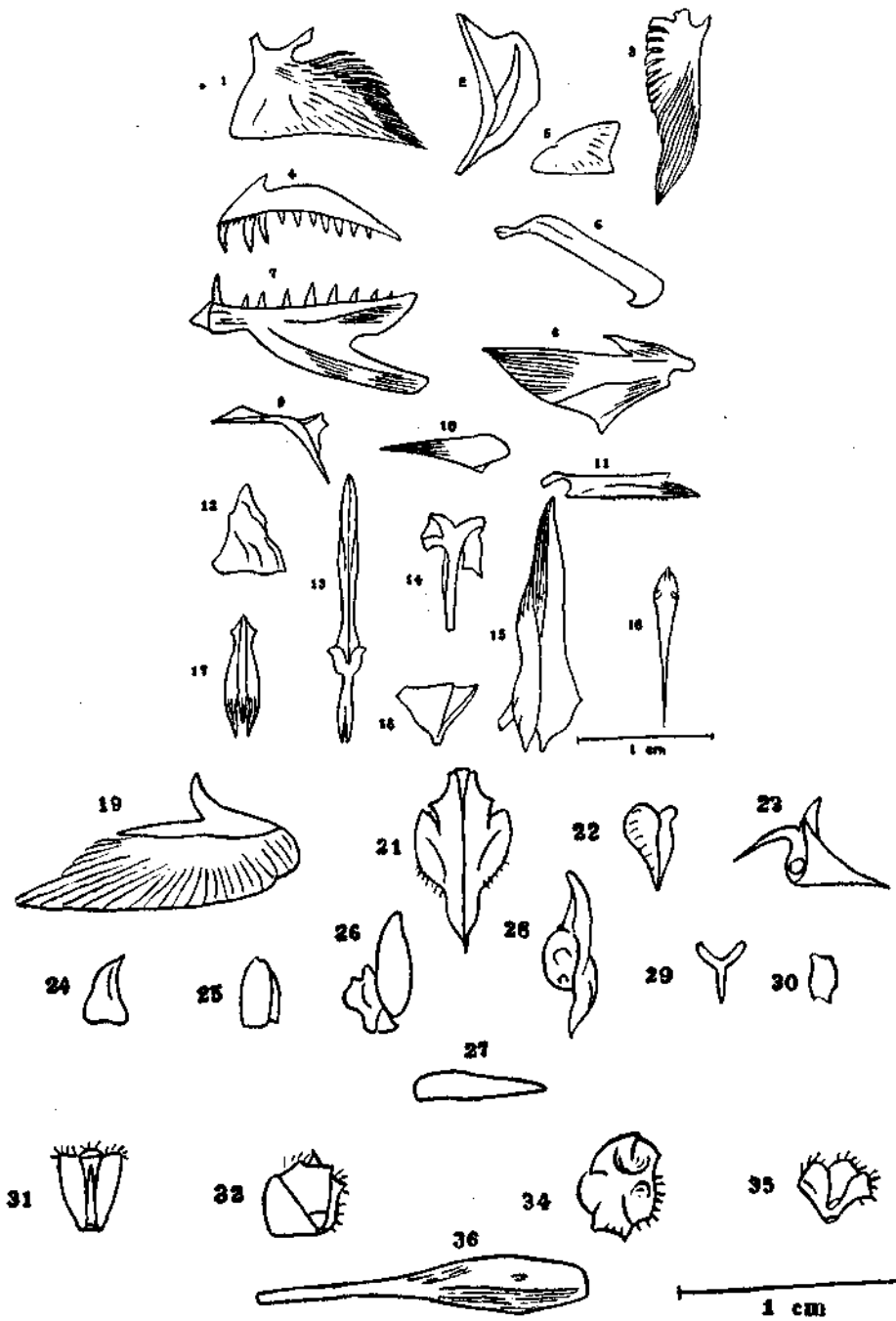
FIGS. 10 and 11. Disarticulated bones. *E. intermedius.* Order of numbers as in Figs. 8 and 9. Numbers 20 and 33 absent.

narrower but longer than the dorsal one and both arms are covered by the anterior end of articular. The anterior end of dentary is joined with its fellow of opposite side by means of a symphysis. At the symphysial region, the lower jaw is tipped with a small conical piece of cartilage. The dentary is very much alike and the lower jaw is uniformly tipped with cartilage in all four species. The jaws are subequal the lower being longer.

The *articular* (*art*) is more or less a spear-shaped bone, which is concave internally and convex externally, its concavity corresponding to the convexity of the dentary partly overlapped by the former. The posterior end of the articular bears 3 processes, the uppermost directed antero-dorsally, the lower directed antero-ventrally and the third directed posteriorly the last of which articulates with the head of quadrate. The articular is similar in general shape in all the species, except in *Eupleurogrammus* where it is broader with the dorsal process diverging less distinctly from it.

The *angular* (*an*) is a small bone attached to the posterior end of articular.

The *metapterygoid* (*mtp*) is a flat bone, triangular in shape. Its postero-dorsal margin presents a fringe or appendage of bone for the articulation of the stem of the hyomandibular, its anterior margin being entire. The ventral margin is also straight and borders the quadrate and symplectic. The dorsal narrow portion of the meta-pterygoid articulates firmly with the anterior lower angle of hyomandibular. The stem of the hyomandibular runs adjoined with the posterior margin of the metaptery-goid. The metapterygoid is similar in all the species, but in *T. lepturus* and *L. savala* the posterior margin is more convex than in *Eupleurogrammus.*

The *ectopterygoid* (*pt*) is a T-shaped bone, the top of ' T ' forming its posterior end. The ectopterygoid is joined with the entopterygoid dorsally, with the palatine laterally and anteriorly and with the quadrate and metapterygoid posteriorly. The shank of the ' T ' is grooved anteriorly, with concavity situated dorsally and convexity ventrally opposing a concave narrow fringed anterior portion of the entopterygoid. The ventral convexity of the anterior end of ectopterygoid forms part of the roof of buccal cavity. The ectopterygoid is alike in all the species.

The *entopterygoid* (*enpt*) is a long typically thin papery bone which connects with the palatine, metapterygoid and ectopterygoid and lies on the parasphenoid with its mesial and posterior edges free. The dorsal surface is concave. The entoptery-goid differs slightly in shape in the different species. In *Trichiurus* and *Lepturacanthus* the broadest portion of the entopterygoid lies about the mid length of the bone where-as its anterior end is much sharper and posterior end broader in *Eupleurogrammus.* The ventral surface is smooth in all species.

The *palatine* (*pl*) runs forward on the external side of the vomer and hooks over the anterior end of the maxilla, immediately ventral to the nasal. Along the ventral edge, the palatine is armed with fine teeth. At the anterior end the palatine presents a hook-like process, strongly curved down in *T. lepturus* and *L. savala*, while it is just bent down in *Eupleurogrammus.* Posteriorly the palatine is broader and connects with the entopterygoid and ectopterygoid. The arrangement of the teeth on pala-tines varies with the genera. In *Trichiurus* and *Lepturacanthus* they are in the form of a villiform band, teeth being more prominent in *L. savala*, while in *Eupleuro-grammus* they are arranged in irregular series.

The *quadrate* (*qu*) is a triangular bone with two prominent V-shaped ridges on the inner side. It is more or less a central bone, articulating dorsally (by its broadest side) with the metapterygoid and the stem of hyomandibular, posteriorly with the preopercle and ventrally with the articular and angular, the last two presenting a depression for the articular head of quadrate. Antero-dorsally, the quadrate is connected with ectopterygoid. Along the posterior margin, there is a thickened portion, grooved on its inner surface appearing as a strong spine-like process, directed upwards. This ridge or process provides articulation for the preopercle. The quadrate is broader than high in *Eupleurogrammus* and the reverse holds good, in *T. lepturus* and *L. savala*.

The groove on the inner surface of the quadrate lodges the *symplectic* (*sym*) a small, narrow bone which is scarcely visible externally and can be seen clearly when the quadrate is viewed from inside. The dorsal projecting portion of symplectic articulates with the lower end of hyomandibular.

Hyoid-Opercular Region : The *opercle* (*op*) is a thin bone, roughly triangular in shape. The anterior superior and middle portions are thicker than the rest of the opercle. Dorsally and anteriorly there are two processes, the shorter directed anteriorly to articulate with the opercular process of hyomandibular and the longer directed posteriorly. The superior and posterior free margins of opercle are finely fringed. Its anterior margin is plain, overlapped by the hind edge of preopercle and its ventral margin joins the dorsal border of subopercle.

The *subopercle* (*sop*) is a long, narrow, thin bone, broad anteriorly and narrow posteriorly. It is fringed along the posterior and inferior margins. Anteriorly it bears a small process, directed forward and upward to articulate with the preopercle. The bone is longer and narrower and inferior margin of the subopercle is concave in *Trichiurus* and *Lepturacanthus* while it is broader and the inferior margin convex in *Eupleurogrammus*.

The *interopercle* (*iop*) is triangular in shape and thin like the opercle and the subopercle, but very much smaller than the two. It forms the anterior and inferior free margin of the gill cover and along its inner surface it articulates with the ceratohyal. The dorsal margin of interopercle is overlapped by the ventral posterior margin of the preopercle and the posterior margin joins the subopercle and partly the opercle (at its posterior dorsal corner). The bone is essentially similar in all species except for the more convex dorsal margin in *Eupleurogrammus*.

The *preopercle* (*pop*) is a characteristic wing shaped bone, differing strikingly from all the other bones of the opercular complex. It is very bony and strongest of all the opercular bones, broad above and narrow ventrally. There are two strong bony ridges in the shape of ' Y ' along anterior and posterior margins which are highly prominent on the inner surface. The posterior edge of preopercle overlaps the opercle and the subopercle, while its anterior margin with the ridge and a groove lies in juxtaposition with a similar ridge of the hyomandibular, articulating with the latter and also with the symplectic and the quadrate. The preopercle is similar in general shape in all the species, but is somewhat broader and shorter in *Eupleurogrammus* than in the other two genera.

The *hyomandibular* (*hyom*) is typically cruciform with three condyles, two of them for articulating with the neurocranium by means of two facets, one in

the postero-inferior face of the sphenotic and the other on the ventral surface of the pterotic. The third condyle articulates with the opercle posteriorly. There is a fringe of bone in the angle of the posterior process and the stem of hyomandibular. The fringe is small in *T. lepturus* and *L. savalà* while it is large and directed postero-ventrally ending in a sharp point in *Eupleurogrammus*.

Anteriorly, the ventral surface of the hyomandibular connects the metapterygoid, the symplectic and the interhyal, the last of which is orientated along the axis of the stem. The posterior portion of the stem presents a deep groove which articulates with the anterior surface of the vertical limb of the preopercle.

The stem of the hyomandibular is separated into anterior and posterior portions by a strong ridge which extends from the ventral end upward and forward in a slightly curved line. Between the ventral margin of the anteriormost condyle and the anterior margin of the stem of the hyomandibular below it, there is a narrow bony lamella.

The *hyoid arch* or *cornu* (Fig. 12, A-D) in all the four species contains in addition to the glossohyal, which is embedded in the tissues of the tongue, four separate bones, the basihyal, ceratohyal, epihyal, and interhyal. These pieces are connected by plain joints and fibrous connections. The interhyal articulates the complex posteriorly with the hyomandibular and symplectic, while the basihyal connects the anterior end to its fellow of the opposite side and to the anterior extremity of the first basi-branchial of the branchial arch.
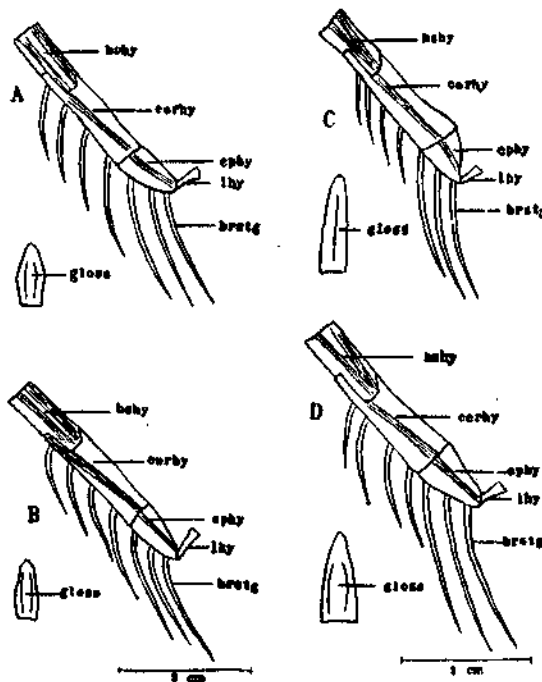

Fig. 12.   Hyoid arch and glossohyal.   A.   *T. lepturus*.   B.   *L. savala*.   C.   *E. intermedius*, D.   *E. muticus*.

The *glossohyal* (*gloss*) is a flat bone, broad at the base and tapers anteriorly. The glossohyal in *T. lepturus* and *L. savala* is short and broad, while it is very long and gradually tapers in *E. intermedius* but is broader at the base and pointed at the tip, in *E. muticus*.

The *basihyal* (*bshy*) is composed of two centres of ossifications firmly united in a straight line. The two halves are nearly of the same size. The ventral ossification at its posterior end rests over a narrow process of ceratohyal, while a dorsal smaller process of the latter binds the posterior corner of the dorsal half of basihyal.

The *ceratohyal* (*cerhy*) is the largest piece of the complex. It is broader at the posterior portion and slightly concave along its dorsal margin. Four of the *branchiostegal rays* (*brstg*) are attached to respective articular surfaces along its ventral margin. The anterior end of ceratohyal bears two processes, a longer ventral and a shorter dorsal, which articulate with the basihyal. The posterior end of ceratohyal is firmly articulated with the epihyal.

The *epihyal* (*ephy*) is triangular in shape, broad anteriorly and narrow posteriorly where it articulates with the interhyal. The three remaining branchiostegal rays take origin from the ventral margin of epihyal.

The *interhyal* (*ihy*) is a small, narrow bone, which articulates the hyoid complex with the hyomandibular and symplectic and is directed obliquely upward.

The three posterior branchiostegal rays are shorter in *T. lepturus* and *L. savala* while they are comparatively longer in *Eupleurogrammus*.

The *urohyal* (*urohy*) is enlongated and medially located between the basihyals. Its posterior end is laterally compressed, blade-like and embedded free in the muscular mass of the throat. In *Trichiurus* and *Lepturacanthus* the urohyal is much broadened specially the posterior portion, which ends in a sharp point while in *Eupleurogrammus* the urohyal is rod-like and the posterior end is broad but truncated.

Except for the relative length of the posterior branchiostegal rays and the shape of urohyal, the bones of the hyoid complex are very similar in the four species.

Branchial Region : The *branchial arches* (Fig. 13, A-D) 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 four species exhibits a similar general pattern as described below :

The three *basibranchials* (bb_1-bb_3) form a linear series along the median line, giving support and attachment to the four branchial arches. The first basibranchial fits into a depression on the posterior face of the glossohyal and laterally it is joined to the basihyals through intervening cartilage. The second and third basibranchials bear deep oblique grooves on each side to receive the first and second hypobranchials, respectively. All the basibranchials are narrowest in the middle region and broader at either end. The first basibranchial articulates with the second by a broad piece of cartilage and the second with the third by a narrow cartilage. The posterior half of the third basibranchial is much broader but narrows down into a process at the extremity. The third basibranchial is slightly larger than the other two.

The *first hypobranchial* (hb_1) arises from the posterior end of first basibranchial. The *second hypobranchial* (hb_2) is articulated at the posterior end of second basibranchial. Both first and second hypobranchials are narrow bones, the latter shorter
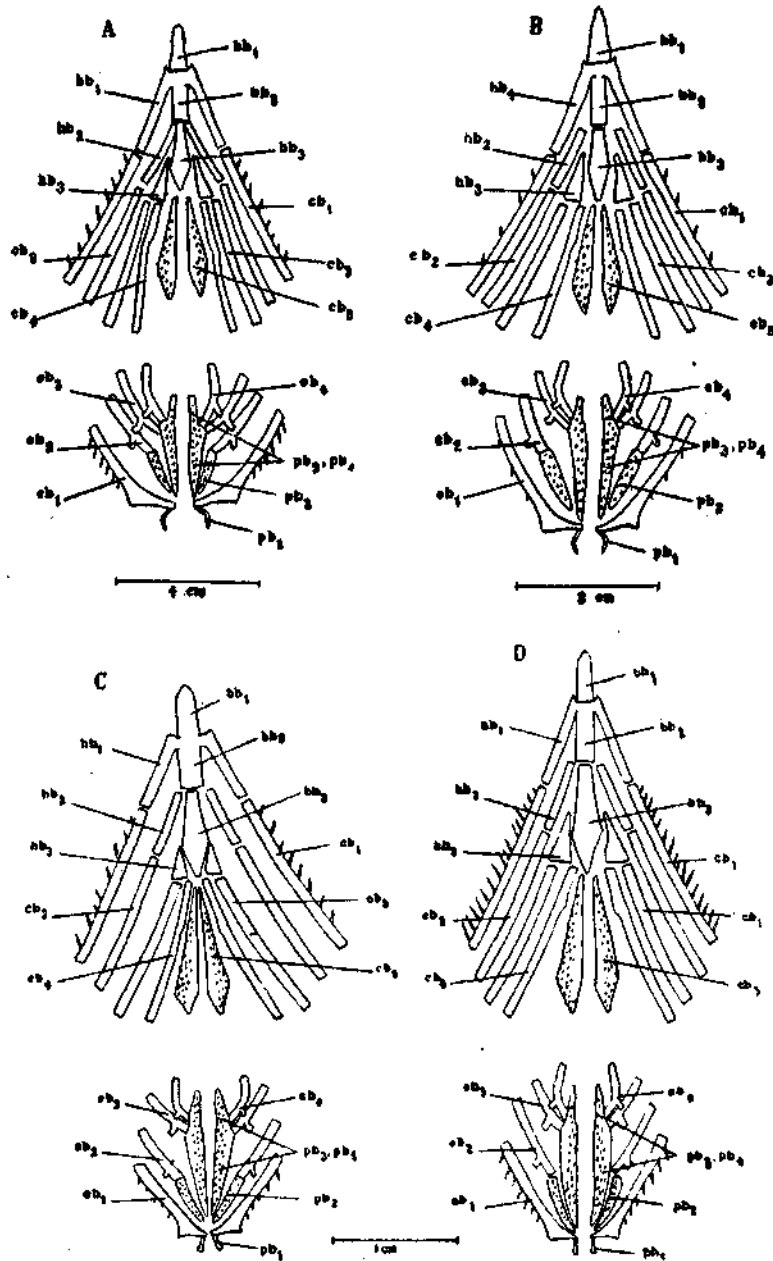

Fig. 13. Branchial arches, ventral half shown above, gill rakers indicated only on the outermost arch. A. *T. lepturus*. B. *L. savala*. C. *E. intermedius*. D. *E. muticus*.

than the former. The *third hypobranchial* (hb_3) is a short triangular bone and differs strikingly, being flat and not rod-like as the other two. They lie adjacent to the posterior end of third basibranchial.

The *ceratobranchials* (cb_1-cb_3) are very long, narrow, gently 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 the fourth which is slightly twisted at its anterior end. The ventral surfaces of ceratobranchials are deeply grooved to their full length.

The *epibranchials* (eb_1-eb_4) form a series of four irregular curved pieces of bone, which are the main support to the upper or dorsal half of branchial arches. The fourth piece is the most internal, very narrow and bent while the other three are gently curved. All four elements are forked at their anterior ends.

The lower pharyngeals or modified *fifth ceratobranchials* (cb_5) bear villiform teeth in a patch along the outer margin.

The four upper pharyngeals or *pharyngobranchials* (pb_1-pb_4) are unequal in size and also bear fine teeth, except the first (suspensory pharyngeal) which is a tiny rod-like bone. This suspensory pharyngeal connects posteriorly the branchial arches to the neurocranium on its ventral side. The second upper pharyngeal is a flat wing-like bone articulating with the second epibranchial. The third and fourth upper pharyngeals are more or less united to form a single long piece on each side, and they articulate posteriorly with the last two of the epibranchials.

At their external margin the first epibranchial and all the ceratobranchials except the innermost bear a series of gill rakers, prominent and better developed only on the outermost arch. It may, however, be mentioned here that they are least developed in *L. savala* and best developed in *E. muticus*. The gill rakers are teeth-like, sharp and pointed, more or less straight sometimes with smaller, accessory spines. The number of gill rakers is quite variable among the species as shown in Table I. The surface of the extremities of the branchial arches is denticulated.

PECTORAL GIRDLE AND FIN

The *pectoral girdle* (Fig. 14, A-D) is situated close behind the neurocranium, and is connected with its upper part by the post-temporal.

The *post-temporal* (*ptm*) is a forked bone which affords the principal articulation of the pectoral girdle to the neurocranium. Its anterior end is divided into a long and sharp dorsal process and a short and blunt ventral process. The dorsal branch articulates with the epiotic, and the ventral lies over the pterotic. The posterior portion of the post-temporal is broader than either of its anterior processes. The post-temporal is alike in all the four species.

The *supracleithrum* (*supcl*) is a rod-like bone, broad and rounded at its anterior end, where it articulates with the posterior end of the post-temporal. Its posterior end rests on the dorsal part of the cleithrum. The supracleithrum is similar in *T. lepturus* and *L. savala*. In *E. intermedius*, it is straight and rod-like with a blunt

posterior end, while in *E. muticus* it is slightly bent medially broader and sharper at the posterior end.

The *cleithrum* (*clt*) is a strong bent bone, being the largest of the bones of the pectoral girdle. Its ventral portion is broader and is folded back to present a concavity on the inner side. The cleithrum is similar in all the species, except that it is slightly broader at its upper portion, over the bent, in *E. muticus*.

The *scapula* (*scap*) is a small bone, articulating with the cleithrum on its inner side about the angle of the bent. It is pierced by a foramen, which is oblong in *T. lepturus* and *L. savala*, and roughly triangular in *Eupleurogrammus*.

The upper part of the scapula is thickened to receive the four *pterygials* (*ptryg*) which support the pectoral fin, the one at the base of the pectoral spine, being the largest.

The *coracoid* (*cor*) joins the scapula above, and ventrally articulates with the tip of the cleithrum. The dorsal portion is expanded and the ventral portion is rod-like. The shape of the coracoid is much alike in all except *E. muticus* in which it strikingly differs, the ventral portion being blade-like and flattened, instead of being rod-like.

The *postcleithrum* (*pcl*) is a fine rib-like process arising from the inner side of the cleithrum. It is directed posterior and downwards. It is more abruptly bent at its middle in *T. lepturus* and *L. savala* than in *Eupleurogrammus* species. Its posterior end surpasses vertical below 9th dorsal fin ray in *T. lepturus*, extends to or surpasses vertical below 8th dorsal fin ray in *L. savala*, extends to below 8th dorsal fin ray in *E. intermedius* and surpasses vertical below 8th dorsal fin ray in *E. muticus*.

Significantly enough the pectoral fin consists of one spine (*psp*) and ten branched rays (*ptr*) in all the four species. The pectoral spine is often serrated (Fig. 14, A) along its outer margin the serrations pointing downwards in some individuals of *T. lepturus* and *L. savala*, a condition, not met with in innumerable specimens of both species of *Eupleurogrammus* examined. It was also found that it has no relation with sex. The entire length of the spine except the base, bears the serrations which are more pronounced at the base than at the tip. The pectoral fins characteristically stand vertical and so close to the operculum that they are partly overlapped by it in all the species.

The pectoral fin differs in shape and height in the different species. The fin is relatively longer and reaches nearly the dorsal margin of the body in *T. lepturus* and *L. savala*, while it is much shorter in *Eupleurogrammus*. In the former two species the difference in height between the anteriormost and posteriormost rays (uppermost and lower-most rays) is not significant while in *Eupleurogrammus* species it is very striking, the rays falling rapidly in height. This difference in height of the rays gives the fin a characteristic shape in each of the groups (Fig. 14, A-D).

PELVIC GIRDLE AND FIN

Pelvic girdle and fins are lacking in *T. lepturus* and *L. savala*. In *Eupleurogrammus* species the *pelvic girdle* (Fig. 15, A,B) is a much modified and rudimentary structure represented by a bony rod (*pelv*) equivalent to the pelvic bones, and the fins by

two reduced scale-like structures. The pelvic girdle is embedded free in the flesh of the abdominal wall and it consists of two halves. The anterior half is much shorter than the posterior. The basal portion of the anterior half is flattened out and the sides are folded back to enclose a groove and two lateral projections. The anterior end of the posterior half is broader and at this level are suspended the pelvic fins. Both extremities of the pelvic girdle end in fine points. The girdle appears long in *E. muticus* than in *E. intermedius*.
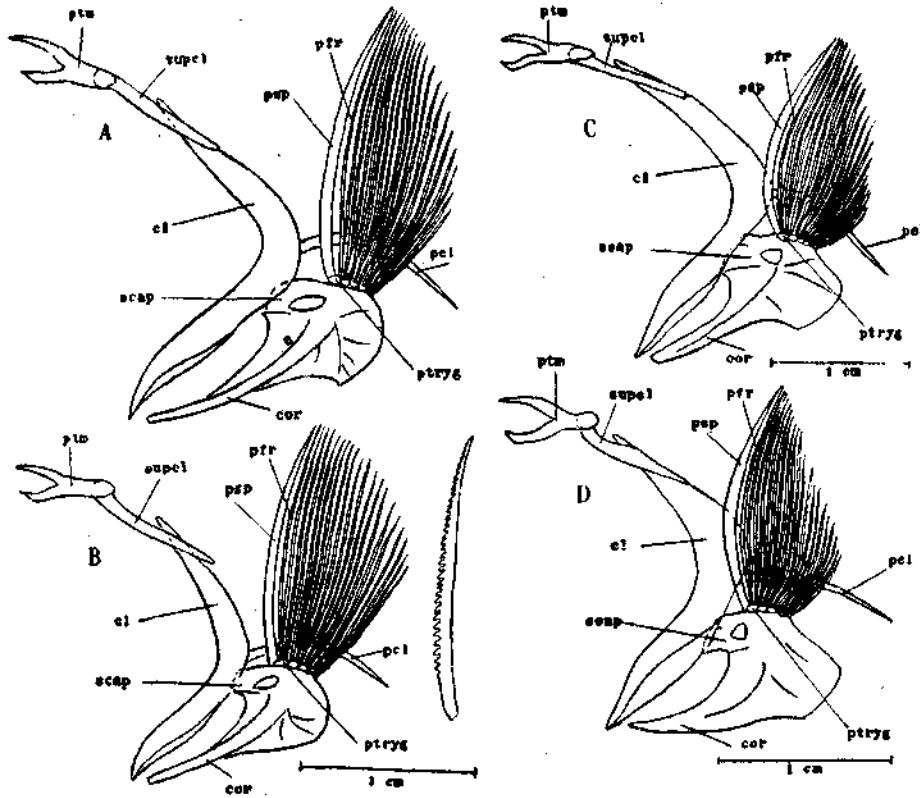

FIG. 14. Pectoral girdle and fin. A. *T. lepturus*. Serrated pectoral spine shown separate. B. *L. savala*. C. *E. intermedius*. D. *E. muticus*.

The pelvic fins are two scale-like structures, directed posteriorly and situated about midway between tip of lower jaw and vent. They lie flush with the abdominal wall. The fins are comparatively bigger and triangular in *E. intermedius*, whereas they are oval and small in *E. muticus*. In general, the degree of reduction and rudimentary nature of the pelvic girdle and fins seems to be greater in the latter than in the former species.

DORSAL FIN

The *dorsal fin* (Pl. I, 1-4) is characteristically long in all the four species origi-nating immediately behind the occipital crest and extending for a greater length along the dorsal margin of the body, towards the tip of the tail. It is low at the anterior

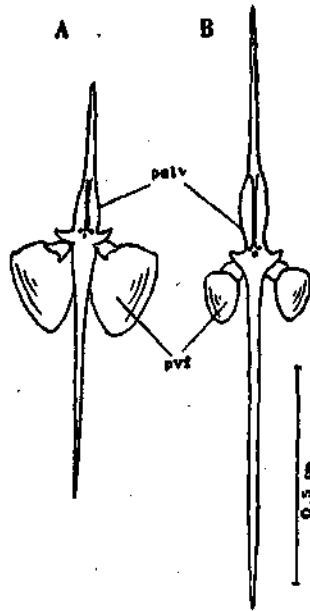and posterior ends, reaching its maximum height at a point opposite or slightly behind the anal region.

FIG. 15. Pelvic girdle and fins.
A. *E. intermedius.* B. *E. muticus.*

The fin consists of 3 anterior spines in *T. lepturus* and *Eupleurogrammus* while they are 4 in *L. savala* followed by simple rays.   Table I gives the range in variation of the rays, in the species.   The posteriormost few rays are usually very small and not easily detectable in fresh specimens.   They are accurately enumerable only by help of radiographs or by alizarin staining.

Each radial of the dorsal fin consists of three pterygiophores, the proximal, middle and distal.   The proximal or the first pterygiophore (interneural) is by far the largest and prominent of the series and forms the essential support of the fin ray. Each interneural is a long stiff spine, the distal portion of which, along the dorsal margin of the body, is compressed from side to side with a short horizontal portion and provides articulation for the one preceding and succeeding it.   Each interneural bears a transparent lamellar portion connecting the horizontal and vertical portions, on the anterior side.   A large oval foramen perforates the lamellar portion, close to the angle of the horizontal and vertical limbs.   The interneurals articulate below with the neural spines.   Certain interneurals in some specimens of *T. lepturus* were occasionally thickened and give the appearance of ' stones'.   Their occurrence, nature and significance have been discussed elsewhere (James 1960).

The middle pterygiophore is a small piece of bone, more or less triangular in shape and lies in line with the horizontal limb of the first.   It fits in tightly over the posterior portion of the horizontal limb of the interneural with which it lies in a line and the anterior portion of the horizontal limb of the succeeding interneural.

The distal pterygiophore is equal in size with the middle and for the greater portion concealed by the two halves of the clasping base of the fin ray, except for its

condylar basal (proximal) portion which abutts on the little concavity at the posterior end of the middle piece. This ball and socket like articulation affords a free movement of the fin ray. The distal portion of this pterygiophore (which is clasped in between the two halves of the base of the fin ray) is flattened antero-posteriorly, and is distinctly seen in an anter or view of the fin ray. It still retains its supporting function and as stated above, provides for free motion of the fin ray, although it is known to have lost its function in most of the scombroidae. The three pterygiophores articulate consecutively, though not in a vertical line.

There is usually a regular correspondence between the number of interneurals and the neural spines (hence indirectly with the number of vertebrae) excluding the first or atlas vertebra. Certain irregularities in this relation between the vertebrae and the neural spines and dorsal fin rays are mentioned elsewhere in the text.

Each fin ray consists of a base and along 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 four species of ribbon fishes.

ANAL FIN

The *anal fin* (Pl. I, 1-4) commences slightly behind the vent and runs midventrally towards the tip of the tail. The anal fin extends beyond the point of termination of the dorsal fin, in all the species.

The species differ in the structure of their anal fins. In all the species, the spinous anal is represented by two anterior spines (the 2nd spine variously modified) and the soft anal by a varying number of modified fin rays, in the form of spinules, which may or may not break through the mid ventral line of the body.

The first anal spine is very rudimentary in all the species, and appears only as an appendage of the second. The second anal spine in *T. lepturus* is less developed than in *L. savala* where it is usually a strong, dagger-shaped and more conspicuous in the juveniles. In *E. intermedius* and *E. muticus* the second anal spine is a dorso-ventrally compressed triangular scale rather than a typical spine of the type seen in the other two species. The former also have a great likeness to their rudimentary ventrals which are· scale-like.

The soft anal rays are represented by modified spinules which scarcely break through midventrally in *T. lepturus*, but distinctly break through as small curved sharp spines, directed posteriorly in *L. savala*. In *E. intermedius* and *E. muticus*, the external fin is entirely suppressed with the blunt protuberances of the basal elements slightly projecting out along the midventral line of the body in the former, while the ventral profile is very smooth in the latter.

Each radial is represented by the proximal piece or interhaemal spine, consisting of a long vertical proximal limb and a distal short horizontal limb. The horizontal limb articulates firmly with the one preceding and the other succeeding it, so that along the ventral margin of the body is formed a continuous rigid bony support

or keel. The basal element is fused with the distal portion of the interhaemal at its middle point. The interhaemals articulate proximally with the corresponding haemal spines. The first interhaemal spine is usually thickened in all the species and is also the largest of the series, to the base of which are attached the two anal spines. There is a gap of one or sometimes none, in the series of interhaemal spines behind the first in *T. lepturus, E. intermedius* and *E. muticus* and invariably one or two similar gaps in *L. savala.*

Several interhaemal spines were found to show excessive thickening in individuals of *T. lepturus,* collected from different parts of the Indian coast, as has been discussed elsewhere (James, 1960).

The range in variation of the anal fin elements in the different species is summarised in Table I.

VERTEBRAL COLUMN

The *vertebral column* (Pls. I and II) of the ribbon fishes exhibits a remarkable simplicity when compared to many scombroid fishes.

The vertebrae are more or less short in the anterior region and progressively long posteriorly to tip of the tail. This is specially so in *L. savala,* in which the tail is more filamentous and hair-like, when compared to the other three species. The vertebral column is very long and flexible in these fishes, in conformity with the ribbon-shaped body. But the length of the column is contributed more to by the increased number of vertebrae than by the length of each vertebra. The vertebral column is arched in the course of its length and the arched portion seems to be confined to pre-anal region in *T. lepturus* while it appears to be about midway between anus and tip of tail in the other three species. The bent however, appears more prominent in *E. intermedius.*

The neural and haemal spines are long, slender terminating in sharp points. The spines are stiff and strong in the anterior vertebrae, while posteriorly they become very fine and fragile. The neural and haemal spines are grooved on their anterior and posterior faces. From the anterior end the neural spines gradually increase in height and they decrease in size towards the tip of tail behind the anal point. The anteriormost haemal spines are the longest, and they fall in height towards the tip of tail. The neural arch is shorter and smaller than the haemal, corresponding to the size of canals enclosed. The haemal canal is big in the anterior caudal vertebrae, decreasing in size towards the tail end.

Each vertebra has six longitudinal grooves, ventral median, dorsal median and two pairs of laterals. This feature was also observed in many scombroid fishes (Kishinouye, 1923). The neural pre- and post-zygapophyses are well developed, specially the pre-zygapophyses with which successive vertebrae articulate. The haemal pre- and post-zygapophyses are well developed from the first caudal vertebra onwards. They are only minute processes in the precaudal region and towards the tail end they are reduced.

In all four species, the vertebral column presents a characteristic ridge on either side contributed to by small perpendicular lateral projections or apophyses on each individual vertebra. This lateral ridge appears from the vent or slightly in front of

it. Each vertebra from this point bears a sharp, lateral conical projection at its anterior end on either side, with the anterior margin of the lateral process at right angles to the vertebra. The successive processes are clearly separated from one another but appear with wider interspaces at right angles in *Trichiurus* and *Lepturacanthus*, whereas they are closer and inclined anteriorly in *Eupleurogrammus*. At either end the processes are shorter, the highest being about the middle region of their course. About 71 such prominent processes may be counted in *T. lepturus*, 62 in *L. savala*, 82 in *E. intermedius* and 75 in *E. muticus*. The lateral ridges appear more highly developed in *E. intermedius* than in the other three species.

The vertebral number shows both interspecific and intraspecific variation in the species. It may, however, be stated here that due to the extremely fragile nature of the tip of the tail in all the species this region is continually susceptible to breaking and hence there is every possibility that the maximum number of vertebrae in each of the species may be slightly greater than what is stated in the present study. This may be more true in case of *L. savala*, in which, as already noted above, the tail is excessively fragile. To overcome this difficulty, the numbers of vertebrae corresponding to the termination of dorsal and anal fins is given for all species (Table I). In a true end of the tail the urostyle is just a rod-like bone, without the neural or haemal processes. The morphology of the most posterior vertebrae which show interesting differences in the species, is described in greater detail below.

The vertebral column may be divided conveniently into precaudal (abdominal) and caudal portions. The first caudal vertebra is the one with a long haemal spine that articulates with the first interhaemal spine. In all the four species it was found that the range in variation of the number of precaudal vertebrae is less than that in the caudal vertebrae. The details of the variation are presented in Table I. The vertebrae in each of the two regions are more or less uniform in structure, except for minor differences. The first or atlas vertebra is the smallest, anchylosed to the neurocranium and bears ribs. As in many scombroid fishes (Kishinouye, 1923) the neural spines of first few vertebrae are laterally compressed. Such spines are fewer in *Trichiurus* and *Lepturacanthus* than in *Eupleurogrammus*. The rest of the trunk vertebrae bear simple neural spines. The 2nd to the 11th vertebrae in *T. lepturus* bear each a median ridge ventrally, separating the median ventral groove into two lateral halves. A similar partition is seen in the case of *L. savala* from the 2nd to the 8th vertebrae but it divides the groove rather imperfectly. In both *E. intermedius* and *E. muticus* the 2nd to 8th vertebrae exhibit this character, and are similar to those in *L. savala* in the less pronounced nature of their ridges.

The parapophyses make their appearance on the 3rd vertebra, as two small projections on the two sides. They retain the same structure to a considerable length of the vertebral column and suddenly lengthen to form the first haemal arch. The posterior few precaudal vertebrae bear more pronounced paraphyses in *Eupleurogrammus* than in *T. lepturus* and *L. savala*. The relative position of the first closed haemal arch is given in Table I.

The *ribs* in all the four species are very fragile and thin, lining the abdominal cavity, but not forming a complete basket. The more anterior ribs are attached to the centra along their ventro-lateral sides while the posterior ones are articulated in the notch between the haemal pre-zygapophyses and parapophyses of each vertebra at its anterior end. All the ribs are loosely articulated to the vertebrae. The *epipleural ribs* are few, 4-6 in number, present on the first to sixth vartebrae in *T. lepturus*,

and the *pleural ribs* appear from 3rd vertebra onwards and extend upto 36-39th vertebra ; in *L. savala* epipleural ribs are 4-5, present on the first to fifth vertebrae, and the pleural ribs appear from the 4th vertebra and extend upto 31-35th vertebra ; in *E. intermedius* epipleural ribs are 3-5, present on the first to fifth vertebra, and the pleural ribs appear from the 3rd vertebra and extend upto 29-32nd vertebra and in *E. muticus* epipleural ribs are 6, present on the first six vertebrae, and the pleural ribs appear from the 1st vertebra extending upto 30-35th vertebra. All the epipleurals are directed dorsally and posteriorly in all the species. The epipleurals are short and stiff in all except in *E. muticus*, where the first two are short, and the last four are very long and stout and more stiff.

In *Trichiurus* and *Lepturacanthus* the ribs are more or less similar extending the full distance of the trunk, while in *Eupleurogrammus* the basket is confined to the anterior end of the trunk with the ribs in this region long and thin while the posterior ribs are strikingly short and blunt.

Morphology of the posteriormost vertebrae : In *T. lepturus* and *L. savala* the most posterior vertebrae have the neural spines and zygapophyses almost reduced (Plate II). This reduction is very great in *L. savalva* when compared to *T. lepturus*. The vertebral column at this region is more in line with the dorsal profile in the former than in the latter. Each vertebra is a simple almost cylindrical rod with a very long, curved, fragile haemal spine, that lends supports to the ventral side of the tip of the tail in *L. savala*, while in *T. Lepturus* the vertebrae are long but dumbel-shaped and distinctly narrower at the mid portion than at either end, the haemal spine being cylindrical, broad at the base and sharp at the tip as in the former.

In *E. intermedius* and *E. muticus* the vertebrae are short, thick and bear distinct neural spines and zygapophyses till the last vertebra (Pl. II). The vertebral column is above the mid lateral line in both *E. intermedius* and *E. muticus*, with the short stumpy neural spines directed posteriorly. The haemal spines are very long and highly curved (more so in *E. intermedius*), with their distal halves laterally compressed (unlike the pointed ends as in *T. lepturus* and *L. savala*). Occasionally a double haemal spine may be present as in *E. muticus* (Pl. II).

The last vertebra in all the species very frequently assumes a bizarre appearance due to extra growths on all sides, much due to the continual loss and rounding off of the tip of the tail (Pl. II).

The dotted line below and parallel to vertebral column in the figures (Pl. II) indicates the course of the lateral line at this region of the body.

RELATIONSHIP BETWEEN THE SUBFAMILIES TRICHIURINAE AND LEPIDOPODINAE

As stated earlier, the four species dealt with in the present paper fall into two natural groups, *T. lepturus* and *L. savala* to the subfamily Trichiurinae, and *E. intermedius* and *E. muticus* to the subfamily Lepidopodinae, in which four other genera are also included. Of these, *Lepidopus* Gouan and *Assurger* Whitley are reported from the Indo-Pacific, while the general *Evoxymetopon* (Poey) Gill and *Tentoriceps* Whitley are so far not reported from this region.

TABLE I

Meristic counts*

No.	Character	T. lepturus	L. savala	E. intermedius	E. muticus
1.	Total number of vertebrae ..	13 : 167-175 (170)	12 : 167-187 (177)	12 : 158-163 (160)	12 : 189-201 (192)
2.	Precaudal vertebrae ..	13 : 38-40 (39)	12 : 33-37 (35)	12 : 31-32 (31)	12 : 39-42 (40)
3.	Caudal vertebrae ..	13 : 127-137 (131)	12 : 131-152 (141)	12 : 126-131 (129)	12 : 150-159 (152)
4.	First closed haemal arch at vertebra number ..	13 : 36-39 (38)	16 : 31-36 (33)	11 : 29-32 (30)	11 : 30-35 (33)
5.	Dorsal fin ray count ..	13 : III, 131-136 (132)	14 : IV, 108-123 (116)	12 : III, 123-129 (126)	12 : III, 139-147 (142)
6.	Dorsal extending upto vertebra number ..	13 : 135-140 (136)	14 : 113-128 (121)	12 : 127-132 (130)	12 : 143-151 (146)
7.	Anal fin ray count ..	13 : i+I, 103-109 (105)	14 : i+I, 77-93 (85)	12 : i+I, 113-121 (117)	12 : i+I, 113-122 (116)
8.	Anal extending upto vertebra number ..	13 : 143-148 (144)	14 : 116-130 (122)	12 : 146-153 (149)	11 : 154-163 (158)
9.	Teeth, upper jaw half, main series only ..	8 : 9-14 (11)	24 : 7-15 (10)	25 : 7-12 (10)	8 : 12-25 (19)
10.	Teeth, lower jaw half, main series only ..	8 : 9-14 (10)	24 : 7-15 (10)	25 : 7-12 (10)	8 : 16-23 (19)
11.	Gill rakers, upper limb, main series only ..	8 : 4-8 (6)	24 : 2-5 (4)	25 : 2-8 (5)	8 : 2-6 (4)
12.	Gill rakers, lower limb, main series only ..	8 : 6-13 (8)	24 : 1-8 (6)	25 : 8-15 (11)	8 : 11-16 (14)
13.	Gill rakers, total, main series only ..	8 : 10-21 (14)	24 : 3-13 (10)	25 : 10-23 (17)	8 : 13-22 (19)

*For each character the number of specimens examined is followed by the count, and the mean for each indicated in parentheses.
Teeth and gill rakers counted on the left side.

TABLE II

A synopsis of differential characteristics for *T. lepturus*, *L. savala*, *E. intermedius* and *E. muticus*.

No. character	*T. lepturus*	*L. savala*	*E. intermedius*	*E. muticus*
1. Occipital region of neuro-cranium.	Convex.	Flat. Dorsoventrally compressed	Convex.	Convex.
2. Ethmofrontal crest.	Absent.	Absent.	Absent.	Present.
3. Orbital ring composed of	Three ossicles.	Three ossicles.	One ossicle.	One ossicle.
4. Lacrymal.	Covers only 1/3 length of maxilla and pre-maxilla.	As in *T. lepturus*.	Covers 2/3 length of maxilla and premaxilla.	As in *E. intermedius*.
5. Orbital cavity.	Huge. About 1/3 length of neuro-cranium.	Small. Less than 1/3 length of neurocra-nium.	Less than 1/3 length of neurocranium, situated more towards dorsal profile.	Less than 1/3 length of neurocranium central-ly situated.
6. Palatines.	Bear teeth in villiform band.	As in *T. lepturus*.	Bear teeth in irregular linear series.	As in *E. intermedius*..
7. Posterior three branchio-stegal rays.	Little longer than the preceding, about ½ their own length.	As in *T. lepturus*.	Strikingly longer than the preceding, about ½ their own length.	As in *E. intermedius*.
8. Ventral portion of coracoid.	Rod-like.	Rod-like.	Rod-like.	Blade-like.
9. Pelvic girdle and fins.	Absent.	Absent.	Present, fins scale-like.	Present, fins scale-like.
10. Second Anal spine.	Rudimentary.	Dagger-like.	Scale-like.	Scale-like.
11. Posterior few vertebrae.	With reduced or no neural spines.	As in *T. lepturus*.	With prominent neural spines.	As in *E. intermedius*.

Tucker (1956) distinguishes these two subfamilies on the presence or absence of pelvic fins, the disposition of the lateral line and the shape of the hind margin of operculum. The present osteological study on three genera of these two subfamilies shows that the following additional characters also constitute a basis for their differentiation : (1) number of elements constituting the orbital ring, (ii) the relative extent of the lacrymal, (iii) relative length of the posterior three branchiostegal rays and (iv) the structure of the posterior caudal vertebrae. Besides these, it was found that the nature and arrangement of the palatine teeth is very distinct in the two subfamilies, as also the second anal spine.

While these characters constitute differences of some magnitude, the osteology of the other genera of the subfamily Lepidopodinae is expected to differ, especially as the genera show greater diversity. For instance, unlike *Eupleurogrammus*, the genera *Lepidopus*, *Assurger* and *Evoxymetopon* have a distinct caudal fin, which is also absent in *Tentoriceps*.

The osteological features of the members of the subfamily Aphanopodinae are not yet fully studied, as also of the other genera of the subfamily Lepidopodinae. In the light of this study, it is now possible to give a more comprehensive key based on the osteology of the genera and species studied here.

OSTEOLOGICAL KEY

I. Pelvic girdle and fins absent ; orbital ring represented by three elements, the lacrymal, jugal and the dermosphenotic. Lacrymal bone small, covering hardly one-third the length of premaxilla and maxilla. Palatine teeth villiform in a broad band. Inferior margin of suboperculum concave. Second anal spine typically spine-like. Last three branchiostegal rays are very slightly longer (about $\frac{1}{4}$ their own length) than the preceding. Posterior vertebrae with reduced or no neural spines (Subfamily Trichiurinae).

A. Orbital cavity large, about one-third the length of the neurocranium. Dorsal surface of neurocranium convex and occipital region elevated. Precaudal vertebrae 38-40 . . . . *T. lepturus.*

B. Orbital cavity small, less than one-third length of neurocranium. Neurocranium dorsoventrally compressed. Precaudal vertebrae 33-37 . . . . *L. savala.*

II. Pelvic girdle and fins present. Orbital ring, represented by one element only, the lacrymal. Lacrymal large, covering two-thirds of premaxilla and maxilla. Palatine teeth small, slightly recurved, arranged in irregular series. Inferior margin of sub-operculum convex. Second anal spine scale-like ; last three branchiostegal rays about half their own length larger than the preceding. Posterior vertebrae with distinct neural spines. (Genus *Eupleurogrammus* of subfamily Lepidopodinae).

A. Precaudal vertebrae 31-32. Median crest on ethmofrontal region absent. Posterior end of maxilla extends to or surpasses vertical below front border of orbital cavity . . . . *E. intermedius.*

B. Precaudal vertebrae 39-42. Median crest on ethmofrontal region present. Posterior end of maxilla falls short of vertical below front border of orbital cavity . . . . *E. muticus.*

It has also been found that *T. lepturus* and *L. savala* attain bigger sizes than species of *Eupleurogrammus*, the former exceeding even one metre, while the latter has not been reported to exceed 625 mm. (De Beaufort and Chapman, 1951). The author's examination of a large series of samples of these species also indicates the same trend.

RELATIONSHIPS OF THE GENERA OF THE FAMILY TRICHIURIDAE

Regan (1909) allied the Trichiuridae and the Gempylidae to form the first division, Trichiuriformes of his suborder Scombroidei, of the order Percomorphi. His suborder includes three other divisions namely, Scombriformes, Luvariformes and Xiphiformes. However, to have any understanding of the phylogenetic relationships of the genera studied here a reference to osteological work on the various groups indicated above seems necessary. Important contributions to the osteology of the true Scombroid fishes have been made by Allis (1903), De Sylva (1955), Gregory (1933), Gunther (1860), Kishinouye (1923), Leccia (1956), Starks (1910, 1911) and others.

Regan's definition of the division Trichiuriformes includes the following osteological features ' caudal fin rays not deeply forked at the base, the hypural in great part exposed. Premaxillaries beak like, free from the nasals. Epiotics separated by supraoccipital. In his generalised definition of the family Trichiuridae, attention is drawn to several important osteological characters which the author is able to corroborate with slight modifications. These are as follows :—

(i) ' Maxillary sheathed by the preorbital.' The preorbital or lacrymal covers not only a part of maxillary (maxilla) but also the premaxilla in *T. lepturus, L. savala* and *Eupleurogrammus.*

(ii) ' Anal with numerous short spines.' The anal rays are represented by reduced spinules, more prominent in *L. savala* than in *T. lepturus.* In *E. intermedius* the basal elements can still be noticed as.blunt protuberances along the mid-ventral line of the body, while the ventral profile is very smooth in *E. muticus.*

(iii) ' Pelvic fins reduced to a pair of scale-like appendages or absent.' The pelvic fins consist each only of a scale-like spine in *Eupleurogrammus.*

(iv) ' Dorsal and anal rays corresponding to the vertebrae, each interneural or interhaemal attached to a neural or haemal spine.' Usually the dorsal rays and their basals and interneurals always correspond to the trunk vertebrae. A similar condition is also seen for dorsal and anal rays in the caudal region but for occasional irregularities, such as three interhaemals with basal elements being related to a single vertebra ; two interhaemals articulating with a single basal element ; a haemal spine lacking an interhaemal, its basal element remaining free ; and two interneurals and two interhaemals articulating with a single vertebra with double neural and haemal spines. These irregularities are seen in all the four species, and appear to be common on the haemal than neural side. Since their occurrence is sporadic, it is likely that they represent a teratological condition.

(v) ' Pelvic bones, if present, united to form a slender spicular bone connected with the cleithra by a ligament.' The pelvic bones form a fused fenestrated structure, elongated in *Eupleurogrammus.*

(vi) ' Vertebrae numerous 100 (43+57) to 159 (39+120) or more.' Vertebral counts are much higher than hitherto noticed, details of which are presented in Table I.

In addition to these, the osteological characters of the family Trichiuridae have been studied for the following forms, genus *Aphanopus* by Gunther (1860), genus *Lepidopus* by Gregory (1933) and Starks (1911). On the basis of this, as well as the present study, it is possible to draw up a Table showing the common and differential osteological characters of the genera hitherto studied, thereby drawing attention to their affinities.

The close affinity between various members of the family Trichiuridae was drawn attention to in the above table. However, in the last five characters, very interesting differences are seen from genus to genus while at the same time, some which are otherwise distinct, show similarities. The phylogenetic tree presented by Tucker (p. 126), appears to represent this trend well for the different genera studied here. However, on the basis of the present study it is also possible to add that the differences between *T. lepturus* and *L. savala* are relatively smaller than those between the two species of *Eupleurogrammus*, *E. intermedius* showing convergence towards the condition seen in *Trichiurus*. Preliminary investigations on the food and feeding habits of these fishes indicate that *E. intermedius*, like *Trichiurus* is a more predaceous form when compared to *E. muticus*. In *L. savala* this trend is seen to attain the maximum development while *E. muticus* shows least specialisation in this direction. Perhaps this functional divergence has been responsible for bringing out wider differences between the two species of *Eupleurogrammus*, as *E. muticus* appears to subsist on smaller organisms of the same type.

SUMMARY

Comparative osteology of the four Indian species of ribbon fishes, *Trichiurus lepturus*, *Lepturacanthus savala*, *Eupleurogrammus intermedius* and *Eupleurogrammus muticus* is described.

The elongation of the bones, specially those of the preorbital region of the skull in all the four species illustrates the extremely predaceous habits of the members of this family. The preorbital region of the skull of *L. savala* shows a maximum elongation, and that of *E. muticus* minimum. This feature and the arrangement of teeth and gill rakers indicates *L. savala* as extremely carnivorous and *E. muticus* less predaceous of the four species. This view is corroborated by the studies on food of these fishes, to be published elsewhere.

The study, while substantiates the affinity between them, draws a distinction between two groups, one represented by *T. lepturus* and *L. savala* and the other by *Eupleurogrammus*. The basic skull pattern in the four species is comparable to other genera of the family.

The convergence or divergence between the four species, as evidenced by the structure of the skull and other parts of the skeleton may be explained as a result of function.

TABLE III

Character	Aphanopus	Lepidopus	Eupleurogrammus	Lepturacanthus	Trichiurus
1. Preorbital portion of skull..	Elongated	Elongated	Elongated	Elongated	Elongated
2. Longitudinal grooves and ridges on the skull ..	Present	Present	Present	Present	Present
3. Occipital crest ...	Low	Low	Low	Low	Low
4. Operculum and suboperculum ..	Fringed	Fringed	Fringed	Fringed	Fringed
5. Vomerine teeth ..	Absent	Absent	Absent	Absent	Absent
6. Lacrymal ..	Covers the space between orbit and jaw bones	Covers the space between orbit and jaw bones	Covers the space between orbit and jaw bones	Covers the space between orbit and jaw bones	Covers the space between orbit and jaw bones
7. Vertebrae ..	Numerous	Numerous	Numerous	Numerous	Numerous
8. Canine-like teeth ..	Slightly barbed	Slightly barbed	Slightly barbed	Slightly barbed	Slightly barbed

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LIST OF ABBREVIATIONS

alsp., alisphenoid ; an., angular ; art., articular ; bb_1-bb_3., basibranchials 1-3 ; boc., basioccipital ; brstg., branchiostegal ray ; bshy., basihyal ; bshp., basisphenoid ; cb_1-cb_5., ceratobranchials 1-5 ; cerhy., ceratohyal ; clt., cleithrum ; cor., coracoid ;* ct., cartilage ; deth., dermethmoid ; dn., dentary ; dsph., dermosphenotic ; eb_1-eb_4., epibranchials 1-4 ; * efrc., ethmofrontal crest ; enpt., entopterygoid ; ephy., epihyal ; epiot., epiotic ; exo., exoccipital ; fr., frontal ; glass., glassohyal ; hb_1-hb_3., hypobranchials 1-3 ; hyom., hyomandibular ; ihy., interhyal ; iop. interopercle ; ju., jugal ; la., lacrymal ; mtp. metapterygoid ; mx., maxilla ; na., nasal ; op., opercle ; opo., opisthotic ; pa., parietal ; pas., parasphenoid ; pb_1-pb_4., pharyngobranchials 1-4 ; pcl., postcleithrum ; pelv., pelvis ; pf., prefrontal ; pfr., pectoral fin ray ; pl., palatine ; pmx., premaxilla ; pop., preopercle ; proot., prootic ; psp., pectoral spine ; ptm., post-temporal ; pto., pterotic ; ptopr., pterotic process ; ptr., ectopterygoid ; ptryg.,pterygial ; pvf.,pelvic fin ; qu., quadrate ; scap., scapula ; soc., supraoccipital ; sop., subopercle ; sphot., sphenotic ; supcl., supracleithrum ; sym., symplecitic ; urohy., urohyal ; vo., vomer.
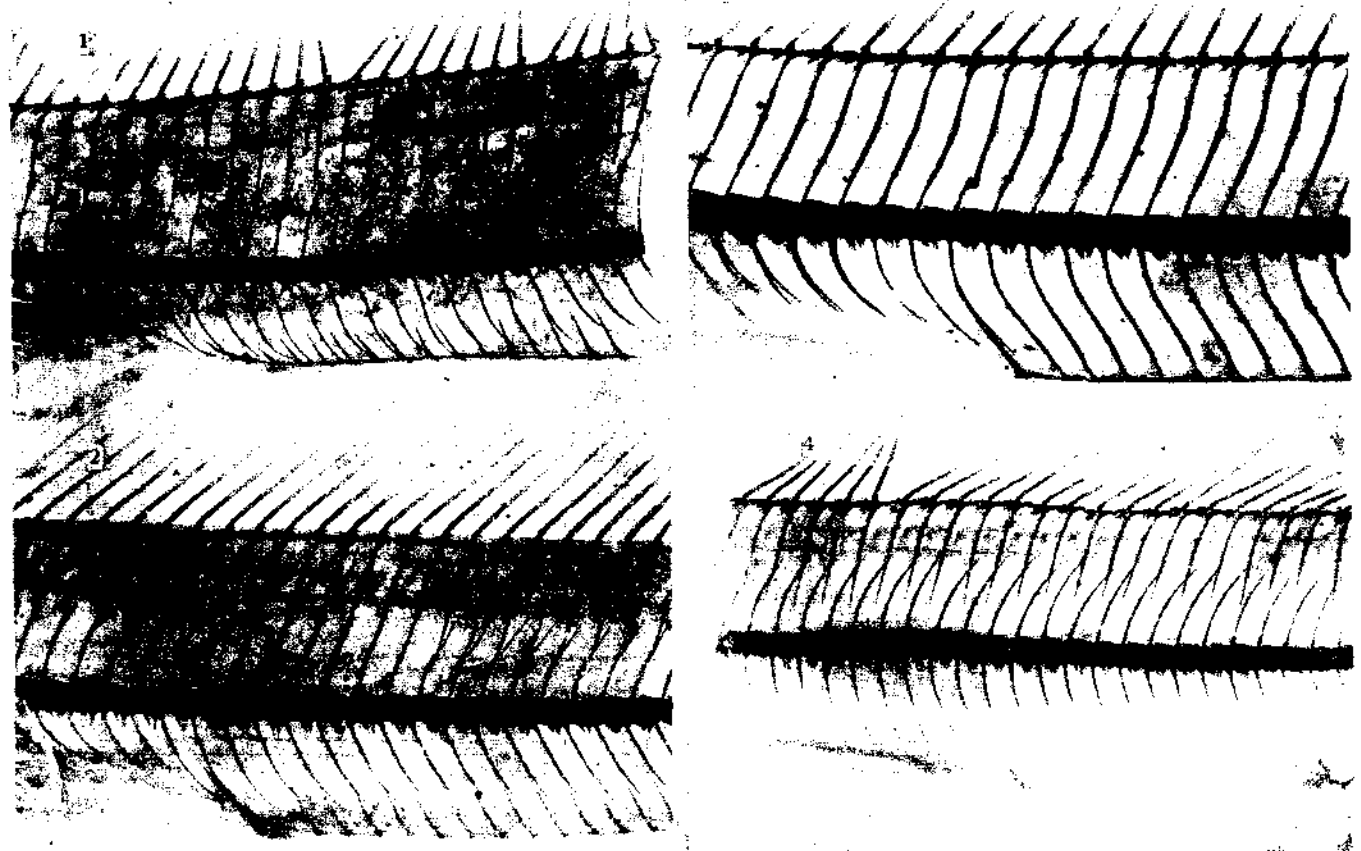
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*New abbreviations.

PLATE I. Comparative osteology of anal region, showing dorsal and anal fins and vertebral column (alizarin stained). 1. *T. lepturus* (S.L., 32.5 ; S.V., 10.8 cm.). 2. *L. savala* (S.L., 37.1 ; S-V. 11.8 em.). 3. *E. intermedius* (S. L., 45.7 ; S-V., 14.0 cm.). 4. *E. muticus* (S.L., 42.9 ; S-V. 11.9 cm.)
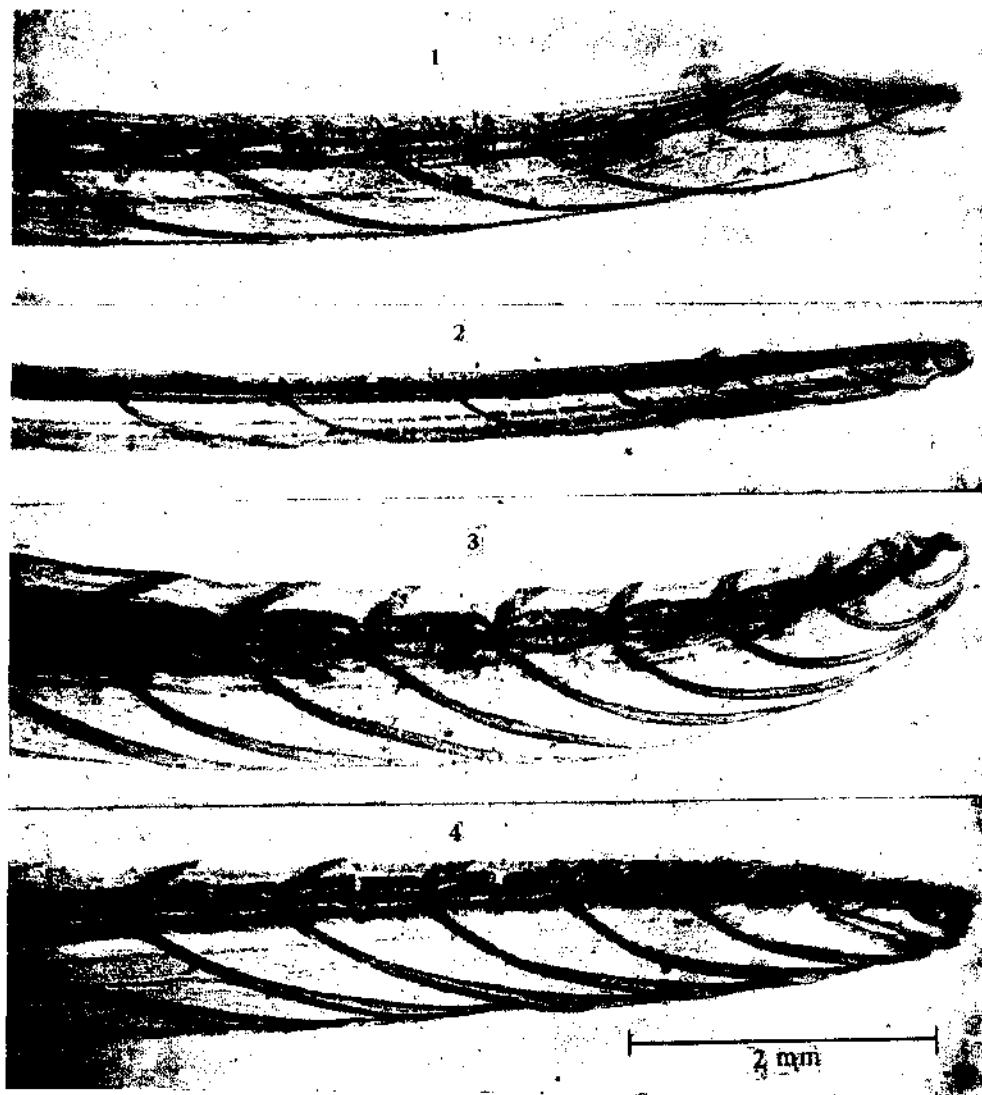
Plate II. Photomicrographs of posterior vertebrae (alizarin stained.) 1. *T. lepturus*. 2. *L. savala*. 3. *E. intermedius*. 4. *E. muticus*.