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The Internal Morphology and Systematic Position of *Leptobrama mülleri*, Formerly Included in the Family Pempheridae

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When STEINDACHNER (1878, p. 388) described the monotypic genus *Leptobrama* (type: *Leptobrama mülleri* STEINDACHNER), he discussed its taxonomic position as follows: "In der Körperform nähert diese Art ausfallender Weise manchen *Chorinemus*- oder *Lichia*-Arten, nach der Flossenbildung und Beschuppungsweise aber glaube ich sie in die Nähe der Gattung *Brama* reihen zu müssen." On the other hand, MACLEAY (1881, p. 151) placed his monotypic genus *Neopempheris* (type: *Neopempheris ramsayi* MACLEAY) in the family Kurtidae together with the genus *Pempheris*. Later, STEINDACHNER (1883, p. 1108) pointed out that *Neopempheris ramsayi* is the same as *Leptobrama mülleri*. MACLEAY might have followed GÜNTHER (1860, p. 508) who had assigned *Kurtus* and *Pempheris* to the Kurtina, a subdivision of the Carangidae*. These two forms do not form a natural group, as has been discussed by CUVIER and VALENCIENNES (1831, pp. 296 and 303) and by BEAUFORT (1914).

On the sole basis of differences in scale characters between *Pempheris multiradiata* and *Neopempheris ramsayi*, the subfamily Neopempherinae was suggested by COCKERELL (1913, p. 54). After a careful and elaborate study of *Leptobrama*, OGILBY (1913) proposed the subfamily Leptobraminae for this genus and the subfamily Pempherinae for the remaining genera of the Pempheridae. He was correct in evaluating the differences between the two subfamilies, but he did not go so far as to show that to assemble *Pempheris* and *Leptobrama* in a single family is not a natural grouping at all. Subsequent authors followed him until a new definition of the Pempheridae, excluding *Leptobrama*, was proposed by the author (TOMINAGA, 1963).

This paper gives an account of the internal morphology of *Leptobrama* and attempts to find its reasonable relatives by comparing its various external and internal characters with those of other forms.

Stating the conclusion first, the family Pempheridae (*Pempheris* and *Parapriacanthus*) and the genus *Leptobrama* have no more characters in common than any

* Later, he raised Kurtina to family rank 'the Kurtidae', which family alone represents one of the major division of the Acanthopterygii, 'the Kurtiformes' (GÜNTHER, 1861).

other two arbitrarily chosen acanthopterygian forms might be expected to have. Although the coincidence of *Chorinemus* (Carangidae) and *Leptobrama* in various structures is striking and hardly ascribable to the result of convcrgence alone, *Leptobrama* cannot be placed in the family Carangidae and it is necessary to erect a distinct family, Leptobramidae, for it.

I wish to express my hearty thanks to Prof. Itiro TOMIYAMA for his criticism and encouragement. I am very grateful to Dr. Giles P. WHITLEY and Dr. Tokiharu ABE for the opportunity to examine an excellent and invaluable specimen of *Leptobrama mülleri*, and their assistance in many ways during the study. I am much obliged to Mr. Richard L. HAEDRICH, Woods Hole Oceanographic Institution and MCZ, Harvard for valuable advice and reading of the manuscript; and to Dr. J. C. DAN, Ochanomizu University, for her kindness in correcting the English of the manuscript.

Material

Leptobrama mülleri STEINDACHNER: One specimen; Austral. Mus. J-12904, 265 mm in standard length; collected at Port Hedland, Western Australia (20°18′ S. lat., 118°35′ E. long.), in about the year 1912 and 1913.

Dorsal IV, 16; anal III, 25; branched caudal rays 8+7; pectoral ii, 14; pelvic I, 5; pored scales in lateral line 73 to caudal base, 6 on caudal fin; scales between origin of dorsal and lateral line 10 or 11; a black blotch at anterior top of dorsal fin*.

Internal Morphology

In *Leptobrama*, the components of the skeleton and their arrangement are essentially the same as those of typical Acanthopterygii, so that it is considered unnecessary to describe below the characters which are constant or usually seen in the great majority of spiny-rayed fishes.

Cranium (Fig. 1)

The length of the cranium is 41.5 mm (16% of the standard length). The greatest width of the cranium (the distance between the latero-posterior ends of the pterotics) is 48% of the length of the cranium, and the greatest depth of the cranium (near the posterior end of the supraoccipital crest) is 53%.

A median and two paired longitudinal crests on the dorsal surface of the cranium are well developed. The median or *supraoccipital crest* (SOC) is thin, blade-like and restricted on the supraoccipital bone for its full length, and extends anteriorly to the ethmoid; the frontals do not take part in forming the anterior portion of this crest. The *temporal crest* (TC) is thin, formed by the parietal and frontal, and extends anteriorly to the lateral edge of the cranium where the frontal meets the lateral

* Assumed to be the male character by OGILBY (1913, p. 65).

ethmoid; its posterior part ends in front of the epiotic. The *pterotic crest* (POC) is more massive than the other crests; anteriorly it reaches the anterior end of the temporal crest, and ends posteriorly at the latero-posterior corner of the pterotic.

The preorbital portion of the cranium is very short and scarcely projects forward beyond the frontals. The myodome is well developed and opens at the ventro-posterior end of the cranium through a breadthwise elliptical foramen. The auditory swelling is inconspicuous. The sensory canal system of the cranium is poorly developed.

The ventral anterior portion of the *vomer* (v) bears a produced rhomboid patch of pointed and close-set teeth. The posterior end of the *ethmoid* (e) is in contact with the supraoccipital; the dorsal part of the ethmoid is flat, horizontal, wedge-

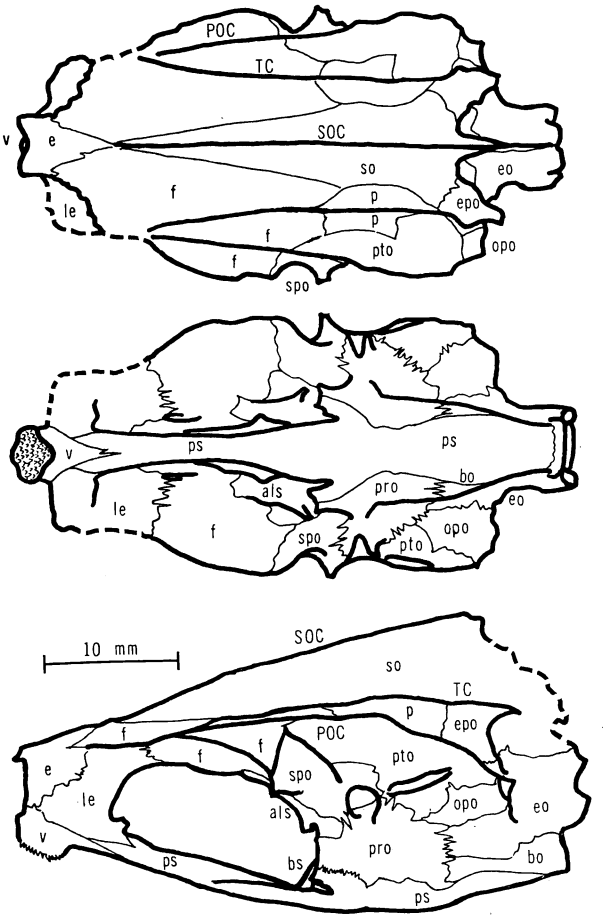

Fig. 1. Dorsal, ventral and lateral views of cranium of *Leptobrama mülleri*. **als**, alisphenoid; **bo**, basioccipital; **bs**, basisphenoid; **e**, ethmoid; **eo**, exoccipital; **epo**, epiotic; **f**, frontal; **le**, lateral ethmoid; **opo**, opisthotic; **p**, parietal; **POC**, pterotic crest; **pro**, prootic; **ps**, parasphenoid; **pto**, pterotic; **so**, supraoccipital; **SOC**, supraoccipital crest; **spo**, sphenotic; **TC**, temporal crest; **v**, vomer.

shaped, and bends abruptly vertically downward to the vomer; the vertical portion has a median ridge which is contiguous to the vomer. The *lateral ethmoids* (ecteth-moids or prefrontals) (le) meet broadly behind the ethmoid in front of the orbital cavity. The foramen for the olfactory nerve is large and passes through the lateral ethmoid. The *frontals* (f) are medially overlain for their full length by the supra-occipital. The *alisphenoids* (als) are remote from each other. The depression between the *prootic* (pro) and *sphenotic* (spo) for the anterior hyomandibular condyle is deep and round; another depression for the posterior hyomandibular condyle is elliptical and situated on the pterotic. The *epiotics* (epo) are completely separated from each other by the supraoccipital. The *opisthotic* (opo) completely separates the pterotic and exoccipital in ventral view, and interposes halfway between the two bones in dorsal view. The *supraoccipital* (so) is very long and extends to above the anterior-most part of the orbital cavity to make contact with the ethmoid; this bone is almost equal in length to the parasphenoid and as long as 87% of the length of the cranium. The *parietals* (p) are widely separated from each other by the supra-occipital. There is no prominent process at the latero-posterior end of the *pterotic* (pto). An unossified space is surrounded by the epiotic, parietal and pterotic. The *exoccipitals* (eo) meet each other above and below for their full length; the paired exoccipital condyles are narrowly in contact with each other above the foramen magnum. The ventral surface of the *parasphenoid* (ps) is not sharply keeled along the median line; on each side of the mouth of the myodome, the basal part of the ascending wing of the parasphenoid is deeply notched from the front. The descending process of the *basisphenoid* (bs) is tightly connected with the parasphenoid. The *orbitosphenoid* is absent. The *otoliths* are probably absent.

Lateral head bones (Figs. 2 and 3)

The bones of the suspensorium and opercular apparatus are set tightly together; there is no opening between the hyomandibular and metapterygoid. The *hyomandi-bular* (hm) sends off posteriorly a markedly developed protuberance with a condyle on its tip for articulation of the opercle; two condyles on the dorsal margin of the hyomandibular for the cranium are well separated from each other. The palatine, mesopterygoid and pterygoid are toothed; the patches of teeth on these bones are contiguous, in consequence the roof of the mouth is almost entirely toothed (Fig. 3). The teeth on the *mesopterygoid* (msp) are very minute, granular and densely distrib-uted on the whole ventral surface of the bone except along the medial margin. The teeth on the horizontal arm of the *pterygoid* (pt) resemble those on the meso-pterygoid in size and shape, except the anterior ones which are slightly larger; the short vertical arm of the pterygoid in front of the quadrate is devoid of teeth. The teeth on the *palatine* (pa) are pointed, smaller than those on both jaws but very much larger than those on the mesopterygoid and pterygoid, and arranged irregularly in about eight rows.

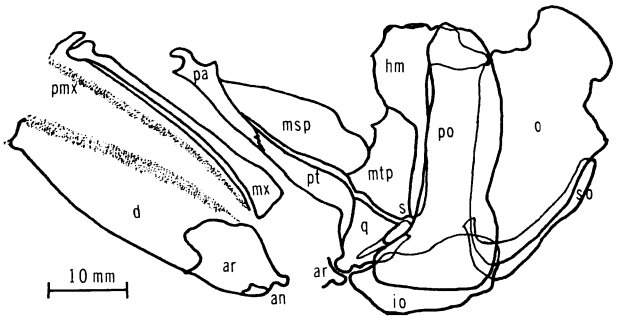

Fig. 2. Suspensorium, jaw and opercular bones of *Leptobrama mülleri*. **an**, angular; **ar**, articular; **d**, dentary; **hm**, hyomandibular; **io**, interopercle; **msp**, mesopterygoid; **mtp**, metapterygoid; **mx**, maxillary; **o**, opercle; **pa**, palatine; **pmx**, premaxillary; **po**, preopercle; **pt**, pterygoid; **q**, quadrate; **s**, symplectic; **so**, subopercle.

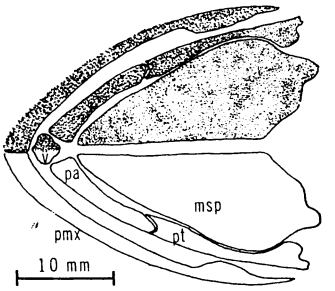

Fig. 3. Ventral view of oral roof of *Leptobrama mülleri*, showing patches of teeth of mesopterygoid (**msp**), palatine (**pa**), premaxillary (**pmx**), pterygoid (**pt**) and vomer (**v**).

The *preopercle* (po), *opercle* (o), *interopercle* (io) and *subopercle* (so) are membraneous, fragile and lacking spines or bony processes on their margins. The vertical arm of the preopercle is of nearly the same width throughout.

The *maxillary* (mx) and *premaxillary* (pmx) are long and slender; the former is tightly set in a long inner fold of the latter. The anterior ascending process of the premaxillary is very short and blunt; there is no dorsal triangular prominence near the center of the bone; the band of close-set, pointed teeth is composed of five or six irregular tooth rows anteriorly. The *supramaxillary* (supplemental maxillary) is absent. The teeth on the *dentary* (d) are like those on the premaxillary in shape and size, and arranged in eight to ten irregular rows throughout, except at the anterior and posterior ends of the band. The *articular* (ar) completely occupies the ∨-shaped space between the two posterior arms of the dentary.

The *nasal* and *orbital bones* are membraneous, fragile and imbedded in the cartilage around the eye; the boundaries between these bones are often indistinct in this formalin-fixed material. The orbitals, including the preorbital and dermatosphenoid, are probably six in number; the broad suborbital shelf extends inward from the second or third element. The first suborbital (preorbital) is not serrulate, contrary to OGILBY's description (1913, p. 62, key). The suborbital sensory canal is complete.

Hyoid arch (Fig. 4)

The *basihyal* (glossohyal) (bh) is ovoid in shape; its whole dorsal surface is provided with pointed teeth which are curved backward and nearly the same size as those on the vomer. The dorsal and ventral *hypohyals* (dhh and vhh) are present. There is a foramen slightly anterior to the middle of the *ceratohyal* (ch); a longitudinal canal runs across the foramen and opens externally near the posterior end of the bone into a narrow groove which extends posteriorly along the upper margin

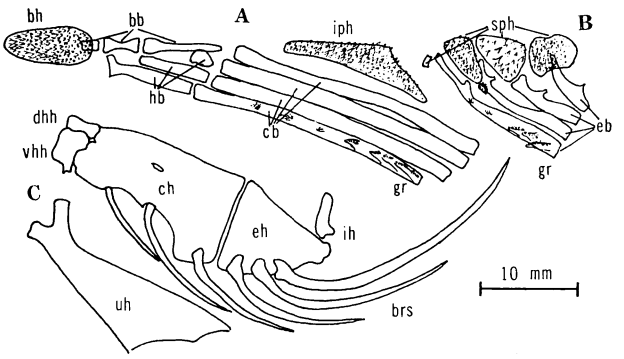

Fig. 4. Branchial arch (**A**, dorsal view of left side; **B**, ventral view of right side) and hyoid arch (**C**, lateral view) of *Leptobrama müllleri*. **bb**, basibranchials; **bh**, basihyal; **brs**, branchiostegals; **cb**, ceratobranchials; **ch**, ceratohyal; **dhh**, dorsal hypohyal; **eb**, epibranchials; **eh**, epihyal; **gr**, gill rakers; **hb**, hypobranchials; **ih**, interhyal; **iph**, inferior pharyngeal; **sph**, superior pharyngeals; **uh**, urohyal; **vhh**, ventral hypohyal.

of the *epihyal* (eh). The *urohyal* (uh) is scarcely expanded laterally at the ventral margin.

The *branchiostegals* (brs) are six in number; the posterior ones are larger than the anteriors ones, but scarcely wider. The first two branchiostegals are attached to the ventral edge of the ceratohyal, the third to the lower external surface of the same bone; and the succeeding three to the lower external surface of the epihyal.

Branchial arches (Fig. 4)

The *basibranchials* (bb) consist of three ossicles which increase in length posteriorly; the first element is in contact with the lower surface of the basihyal. The *hypobranchials* (hb) of the first and second arches are rod-like and attached to the second basibranchial; that of the third is a small triangular ossicle with a long descending process and is attached at the middle of the third basibranchial; the fourth branchial arch lacks the hypobranchial. The *ceratobranchials* (cb) of all the arches are of nearly the same length; the fourth originates from the end of the third basibranchial. The *epibranchials* (eb) decrease in length posteriorly. The lateral and latero-ventral surfaces of each of the hypo-, cerato- and epibranchials are covered with finely prickled bony plates; the ventral surface of each of these bones is grooved to hold the gill filaments.

The external *gill-rakers* (gr) of the first branchial arch are short and seven in number excluding the vestigial ones; none is present on the hypobrachial, three on the ceratobranchial, one at the junction between the cerato- and epibranchial, and three on the epibranchial. The internal gill-rakers of this arch are absent. There are no gill-rakers on the succeeding three arches.

The anteriormost *superior pharyngeal* (sph) is small, rod-like and edentate. The succeeding ones are toothed; the teeth on the patch of the third superior pharyngeal

are larger, more pointed and less densely set than those of the second and fourth. The second superior pharyngeal is divided into antero-medial larger and postero-distal smaller components. The teeth of the fourth (posteriormost) superior pharyngeal decrease in size posteriorly. The teeth on the *inferior pharyngeal* (iph) are like those on the second superior pharyngeal in size.

Shoulder and pelvic girdles (Fig. 5)

The *supratemporal* is no more than a three-forked bony tube of the sensory canal system; its anterior arm is the longest.

The *posttemporal* (pt) is forked; the dorsal arm is thin, long, wide and its anterior part covers the dorsal surface of the epiotic; the ventral arm is rod-shaped and attached to the dorso-posterior depression of the opisthotic. The dorsal anterior corner of the *cleithrum* (cl) is a sharp process attached to the inner surface of the *supracleithrum* (scl); the dorsal posterior part is a round, broad wing for the support of the dorsal postcleithrum. The scapular foramen is bordered anteriorly by the cleithrum in external view, but it is contained entirely in the *scapula* (sc) in internal view. The *coracoid* (cr) arches away from the cleithrum, extending nearly to the ventral extremity of the cleithrum, but not rejoining it. A projection from the dorsal and posterior part of the coracoid is in contact with the ventral margin of the fourth actinost. The *actinosts* (pterygiophores of pectoral fin) (ac) are four in number; the dorsal two are attached to the scapula, the next one is at the suture between the scapula and coracoid, and the ventral-most one rests on the coracoid. Three small foramina are present between each two actinosts; the bones and foramina increase in size ventrally. A foramen which is slightly smaller than the scapular one is surrounded by the coracoid and ventralmost actinosts. A thin lamellar wing is expanded posteriorly from the slender shaft of the *dorsal postcleithrum* (dpc); the *ventral postcleithrum* (vpc) is merely a slender rod attached dorsally to the internal surface of the dorsal one.

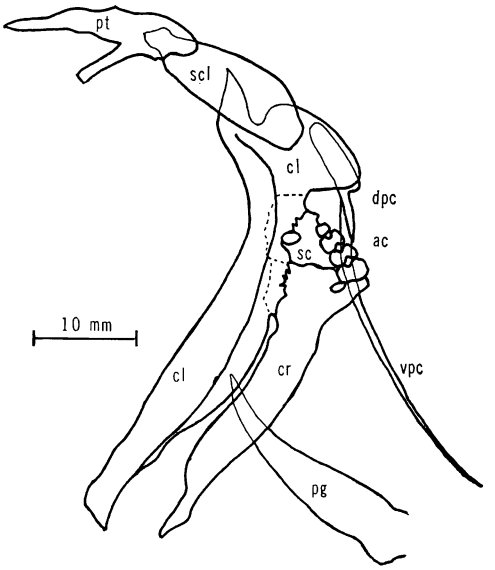

Fig. 5. Shoulder and pelvic girdles of *Leptobrama mülleri*. **ac**, actinosts; **cl**, cleithrum; **cr**, coracoid; **dpc**, dorsal postcleithrum; **pg**, pelvic girdle; **pt**, posttemporal; **sc**, scapula; **scl**, supracleithrum; **vpc**, ventral postcleithrum. Broken lines between each two of the cleithrum, scapula and coracoid show boundaries of these bones in internal view.

The *pelvic bone* (pg) is thin, tightly joined and probably ankylosed posteriorly with its counterpart. There are three longitudinal ridges along the lateral margin; the posterior process above the pelvic fin is short and not well ossified.

Vertebrae and ribs (Figs. 6 and 9A)

The number of vertebrae is 24; 10 are abdominal and 14 are caudal, including the urostylar vertebra*. The length of the abdominal vertebral column is 94 mm (37% of the standard length); that of the caudal one to the tip of the urostylar vertebra is 143 mm (54% of the standard length). All of the vertebrae are of nearly the same length.

The *neural spines* are 22 in number; the urostylar vertebra and the penultimate one are devoid of neural spines. The first neural spine is not coalesced to the first centrum.

The *haemal spines* are 13 in number; the urostylar vertebra is without a haemal spine; the last two haemal spines are tightly joined but not ankylosed with the centra. The origin of the haemal spine is slightly anterior to that of the neural spine in each vertebra.

The distinct *parapophyses* begin on the third centrum. In each of the eighth to tenth vertebrae, the parapophyses are connected with each other by a bony bridge to form a haemal canal above. The connected parapophyses can be distinguished from the succeeding haemal spines by their forked tips.

There are eight pairs of *ribs* beginning on the third vertebra. They are attached high on the centra anteriorly; the position of the attachement is gradually lowered down to the last pair (of the tenth vertebra), which originate from the extremities of the parapophyses.

The *neural prezygapophyses* are notched; the dorsal arms are crooked over the ventral arms; the ventral arms are small spurs and are absent or rudimentary in several anterior and posterior centra. The *neural postzygapophyses* are simple and inserted into the notches of the neural prezygapophyses of the succeeding centra.

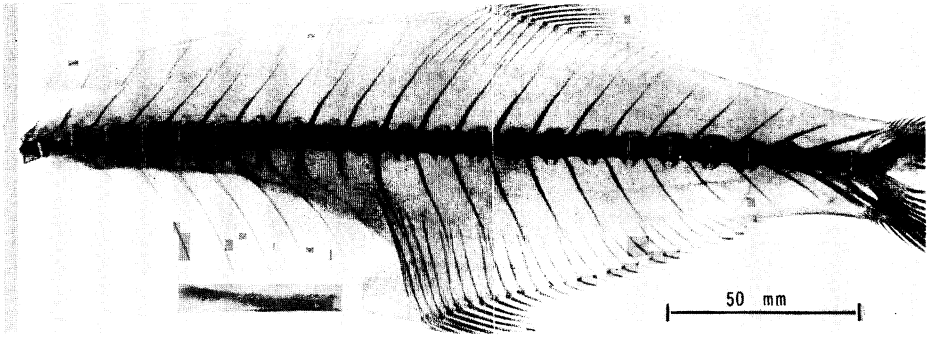

Fig. 6. Axial skeleton, ribs, vertical fins and their supporting elements of *Leptobrama mülleri* (radiograph).

* The terminology follows GOSLINE (1961, p. 265).

The *haemal pre-* and *postzygapophyses* are no more than simple short processes.

Median fin-ray supporting elements (Figs. 6, 7 and 9A)

The *rayless predorsal pterygiophores* are nine in number. The first one is inserted just in front of the neural spine of the first vertebra; each of the space between the neural spines of the abdominal vertebrae has a single rayless predorsal pterygiophore, except the space without a pterygiophore between the neural spines of the fourth and fifth vertebrae. The *pterygiophore* which bears the first dorsal spine is in front of the neural spine of the 11th (first caudal) vertebra and the next one with the second spine is behind the same neural spine. The last pterygiophore of the dorsal fin is inserted between the neural spines of the 17th and 18th vertebrae.

The first *pterygiophore of the anal fin*, bearing the first two anal spines, is slightly wider and longer than the succeeding ones, and inserted in front of and detached from the first haemal spine (of the 11th vertebra). The second one, with the third anal spine, is inserted just behind the first haemal spine. Each of the spaces between each two haemal spines of the 12th to 19th vertebrae has three pterygiophores; the last four are inserted between the haemal spines of the 18th and 19th vertebrae (Fig. 9A).

The *caudal-fin skeleton* is made up of the urostylar vertebra, three epurals, two pairs of uroneurals, five hypurals and two (or two pairs of) ossicles along the distal parts of the last two (autogenous) haemal spines (Fig. 7). The first hypural bears a thin, weakly developed hypuropophysis. The reduction in number of the hypurals

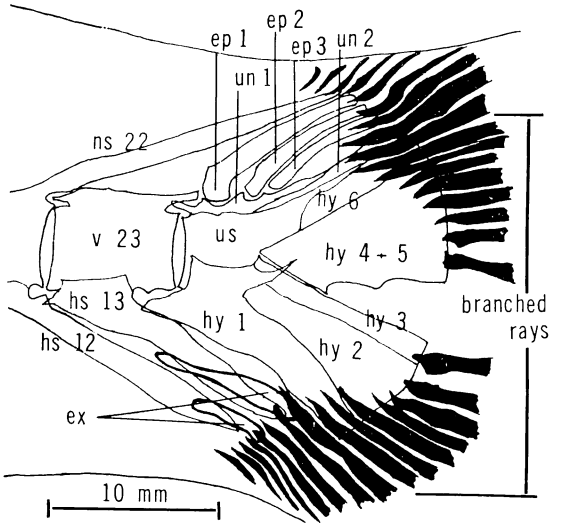

Fig. 7. Caudal-fin supporting elements of *Leptobrama mülleri*. Caudal fin-rays are shaded black. **ep 1~3**, epurals; **ex**, extra ossicles along 12th and 13th haemal spines; **hs 12** and **13**, 12th and 13th haemal spines; **hy 1~6**, hypurals; **ns 22**, 22nd neural spine; **un 1** and **2**, uroneurals; **us**, 24th or urostylar vertebra; **v 23**, 23rd vertebra.

from the typical six to five in *Leptobrama* is brought about by the ankylosis of the fourth and fifth components counted from below (cf. GOSLINE, 1961). No further fusion among the caudal-fin supporting elements is seen in this large (seemingly not juvenile) specimen.

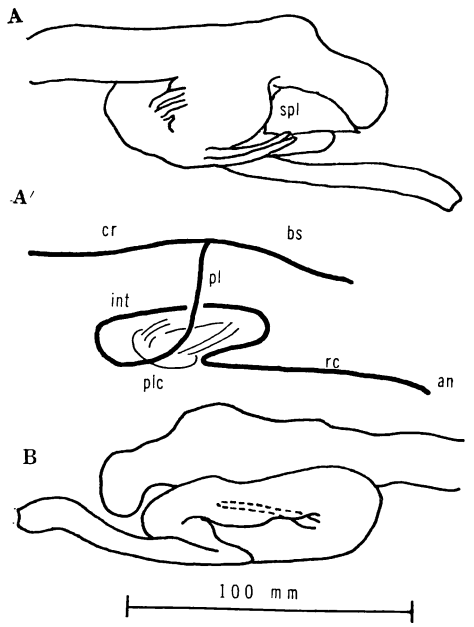

Fig. 8. **A** and **A′**, left lateral views of alimentary canal of *Leptobrama mülleri*, winding pattern is shown in **A′**; **B**, right lateral view. **an**, anus; **bs**, blind sac of stomach; **cr**, cardiac part of stomach; **int**, intestine; **pl**, pyloric part of stomach; **plc**, pyloric caeca; **rc**, rectum; **spl**, spleen.

In addition to the 15 branched and two unbranched *principal rays*, there are eight upper *vestigial rays* and seven lower ones in the caudal fin. The caudal fin-rays are cleft at the base to some extent to clasp the hypural elements, except the median branched rays which hold the hypurals very shallowly.

Viscera (Fig. 8)

The presence of a long blind sac which extends posteriorly makes the *stomach* T-shaped. The wall of the cardiac part and blind sac is thick and muscular and has about nine longitudinal folds; the wall of the pyloric portion is thinner than that of the cardiac part and blind sac, and devoid of marked folds. The *pyloric caeca* (plc) are six in number, simple and short*. The anterior ascending portion of the *intestine* (int) is thick-walled and has about 15 longitudinal folds. The remaining portion of the intestinal wall is very thin and devoid of marked folds. The *rectum* (rc) has fine papillary processes. The winding of the alimentary canal is shown in Fig. 8A′.

The stomach contained four abdominal vertebrae of a fish, which might have been 100 mm or more in length when living.

The *liver* is bilobed; the left lobe is a little larger than the right one. The *air-bladder* is absent.

LEPTOBRAMIDAE, new family

Neopempherinae COCKERELL, 1913, p. 55; introduced as a subfamily of the Pempheridae (diagnosis based on scale characters only). Type of the subfamily: *Neopempheris* MACLEAY, 1881 (=*Leptobrama* STEINDACHNER, 1878).

Leptobraminae OGILBY, 1913, p. 62; introduced as a subfamily of the Pempheridae (diagnosis in the key to the Pempheridae). Type of the subfamily: *Leptobrama* STEINDACHNER, 1878.

* OGILBY (1913, p. 62) reported that the pyloric caeca were absent in his specimen.

Represented by the monotypic genus *Leptobrama*. Type: *Leptobrama mülleri* STEINDACHNER, 1878.

Distribution: Australia and adjacent waters; in sea and estuaries.

Diagnosis

Body slender, compressed. Cranium with five well developed longitudinal ridges; preorbital portion very short. Myodome opens at posterior end of parasphenoid. Supraoccipital extending forward to be in contact with ethmoid; supraoccipital crest restricted on supraoccipital for its full length so that frontals not taking part in forming its anterior portion (8)*. Opisthotic interposed halfway between pterotic and exoccipital in dorsal view (14). Orbitosphenoid absent. Ascending process of premaxillary short and blunt; upper jaw hardly protractile (13); supramaxillary absent. Premaxillary, dentary, vomer, palatine, mesopterygoid, pterygoid, tongue, inferior pharyngeal and posterior three of superior pharyngeals toothed (7). Eye with eye-lid and surrounded by well developed cartilaginous or adipose tissue (2). Orbital bones forming complete chain; suborbital shelf developed; suborbital sensory canal continuous with that of sphenotic (9). A small, slit-like foramen near the center of ceratohyal (12). Branchiostegals six; three of these on epihyal (10). Gills four, a slit behind fourth; pseudobranchiae present. Opercular bones without bony armatures. Scales ctenoid, moderate in size (3). Lateral line arched anteriorly; posterior part straight. No scutes. Vertebrae 24 (10+14, including urostylar vertebra) (5). Ribs eight on each side. All fins scaled. Pelvic fins thoracic. Dorsal and anal fins falciform (4); no isolated posterior fin-lets. Dorsal single, with four spines; its origin posterior to that of anal and its base shorter than that of anal (1); nine rayless predorsal pterygiopheres (6). Anal with three spines; first pterygiophore of anal not adjoined to first haemal spine (11). Caudal-fin supporting elements well separated except for fused fourth and fifth hypurals counted from below; two extra ossicles along distal portion of last two haemal spines. Stomach with a long blind sac, T-shaped as a whole; pyloric caeca six in number. Air-bladder absent.

The Relationship of the Leptobramidae

A. Comparison of the Leptobramidae with the Pempheridae

OGILBY (1913, p. 62) attempted to distinguish the subfamilies Pempherinae and Leptobraminae in his key to the family Pempheridae:

Pempherinae:—Lateral line tubes short and wide; eye large, without adipose lid; preorbital entire; maxillary greatly dilated distally; pterygoids and tongue smooth; dorsal premedian; anal low, originating below or behind dorsal; branchiostegals seven; gill-rakers numerous and long; air-bladder large, constricted anteriorly**; pyloric caeca well devel-

* The numerals in parentheses correspond to the numbers of characters in Table 2, which indicates with what forms the Leptobramidae conforms or conflicts in each relevant character.

** The constricted air-bladder is only seen in group C of the genus *Pempheris* (TOMINAGA, 1963).

oped; vertebrae increasing in length posteriorly.

Leptobraminae:—Lateral line tubes long and narrow; eye small, with well developed adipose lid; preorbital serrulate*; maxillary spatulate, feebly dilating from the front; pterygoids and tongue toothed; dorsal postmedian; anal falciform, originating well in advance of the dorsal; branchiostegals six; gill-rakers few and short; no air-bladder nor pyloric caeca**; vertebrae of similar length throughout.

OGILBY's diagnosis of the Pempheridae, including the two subfamilies, is mainly based on characters which are no more than the common features of the Acanthopterygii. A few characters other than the common features are not common to *Pempheris* and *Leptobrama*, but confined to one or the other of the two forms. The diagnoses of FOWLER (1931, p. 45) and WEBER and BEAUFORT (1936, p. 210) are

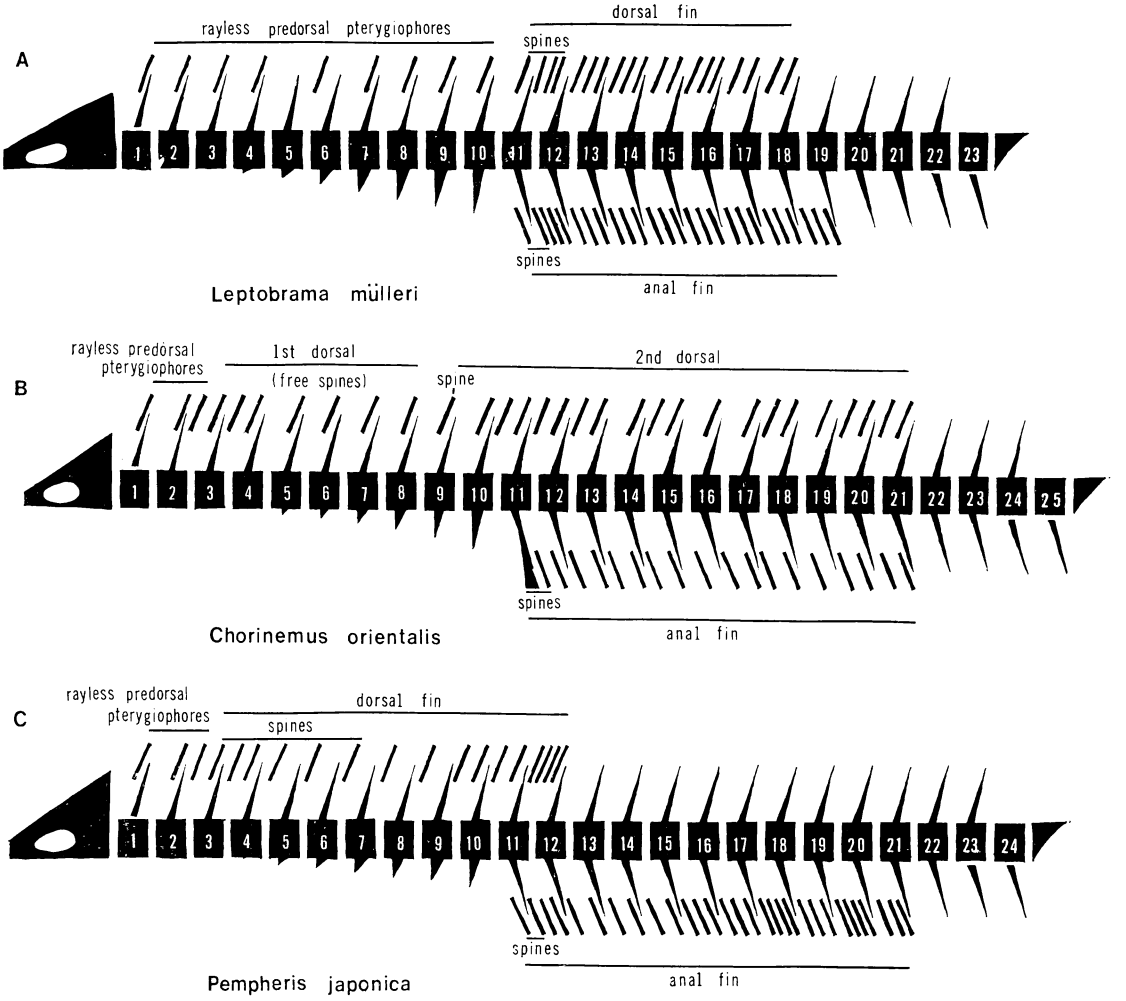

Fig. 9. Relationships between axial skeleton and vertical fin rays.

* The preorbital was not serrulate in my specimen of *Leptobrama*.

** The pyloric caeca are present, six in number in my specimen.

Table 1. Comparison of the dorsal fin-ray supporting elements in the Leptobramidae and Pempheridae.

	Leptobramidae	Pempheridae
Number of rayless predorsal pterygiophores	9	3
Insertion of 1st pterygiophore of dorsal fin	between neural spines of 10th and 11th vertebrae	between neural spines of 2nd and 3rd vertebrae
Insertion of last pterygiophore of dorsal fin	between neural spines of 17th and 18th vertebrae	between neural spines of 11th and 12th vertebrae
Number of vertebrae	10+14	10+15

essentially similar to that of OGILBY.

The one and only character in the literature to support the inclusion of *Leptobrama* within the Pempheridae is that it has a single short dorsal fin. The dorsal fin of the emended Pempheridae (TOMINAGA, 1963; exclusive of *Leptobrama*) is, however, anterior in position, while that of the Leptobramidae is posterior. Moreover, the dorsal fin-ray supporting elements of both forms are fundamentally different from each other (Fig. 9 and Table 1). The dorsal fin of the Pempheridae is located at the position of the first dorsal fin of the usual Acanthopterygii with two dorsals, while that of the Leptobramidae is at the position of the second. The increased number of predorsal pterygiophores in *Leptobrama* can be explained by the complete absence of the first dorsal-fin spines. In the Acanthopterygii with two separated dorsal fins, however, the second dorsal fin is usually composed of a single spine and several soft-rays, or soft-rays only, while in *Leptobrama* the posteriorly situated dorsal fin has four spines and 16 soft-rays.

Since the formation of the shortened dorsal fin is quite different in the two forms, no reason remains for including *Leptobrama* among the Pempheridae. The systematic position of the Pempheridae is another interesting problem, which will be dealt with in a later paper.

B. Taxonomical position of the Leptobramidae

As the first step in seeking reasonable allies of the Leptobramidae, the characters of *Leptobrama* are compared with those of various groups of the Acanthopterygii (Table 2).

The following may be the unique characters of the Leptobramidae among the Acanthopterygii: (1) the toothed pterygoid, (2) the presence of two extra ossicles along the last two haemal spines at the base of the caudal fin, and (3) the presence of six branchiosteagals, three of these are on the epihyal.

The following are the characters of the Leptobramidae which are unusual in the other Acanthopterygii: (1) the single dorsal fin which is posterior in position, and the increased number of rayless predorsal pterygiophores, (2) the toothed mesopterygoid,

Table 2. Comparison of the characters of the *Leptobrama*

Characters of *Leptobrama*	Groups which conform with *Leptobrama* in the relevent character
1. Simple dorsal fin, base of which shorter than anal base	Pempheridae, Toxotidae, Berycidae and forms in the column below
Origin of dorsal posterior to that of anal	Bathyclupeidae, adult *Luvarus*, *Kurtus indicus*
2. Cartilaginous or adipose tissue surrounding eye well developed	Scombridae, Carangidae, Mugilidae, Luvaridae (REGAN, '03), etc.
3. Scales ctenoid, not vestigial	Most percoid families, Bramidae, etc.
4. Falciform dorsal and anal fin	Some forms of Carangidae, Scombridae, Bramidae, Pampidae, etc.
5. Vertebrae 10+14, including urostylar vertebra	Most Carangidae*, many forms of percoid families, *Mupus* and *Psenes* (Stromateidae), Kurtidae, etc.
6. 9 rayless predorsal pterygiophores	*Bathyclupea* (original), adult *Luvarus* (9 or more; WAITE, '02)
7. Toothed Mesopterygoid in addition to toothed vomer and platine	*Chorinemus* (LÜTKEN, 1880, pp. 512 and 600; SUZUKI, '62, p. 149), *Thunnus* (KISHINOUYE, '23), *Toxotes*, (GÜNTHER, 1860, p. 67), *Labracoglossa*
Toothed pterygoid in addition to toothed mesopterygoid	Not known
8. Anterior extension of supraoccipital crest to ethmoid	All Carangidae (STARKS, '11b; SUZUKI, '62, etc.); Scombridae, except *Scomber* and *Rastrelliger* (STARKS, '10, etc.); Stromateidae, *Brama* and *Coryphaena* (STARKS, '26, etc.); *Psettus*, *Velifer*, *Lampris* (GREGORY, '33) and forms in the column below
Frontals not taking part in forming anterior portion of extended crest	*Gasterochisma* (original); *Luvarus* (GREGORY and CONRAD, '37); *Paracaesio*, *Parapristipoma* (KATAYAMA, '34; HOTTA, '61)
9. Complete suborbitals and suborbital sensory canal	Carangidae, Bramidae, *Scomber*, *Rastrelliger*, most percoid families
10. 6 branchiostegals	Sparidae (AKAZAKI, '62); *Callanthias* (KATAYAMA, '59); some Scorpaenidae (MATSUBARA, '43); *Lampris*, some Stromateidae (GÜNTHER, 1860), etc.
3 of 6 attached to epihyal	Not known
11. 1st haemal spine not adjoined with 1st pterygiophore of anal	Scombroid and percoid families, Naucratinae (Carangidae)
12. Presence of foramen on ceratohyal	All Carangidae (STARKS, '11b; SUZUKI, '62); *Stereolepis*, *Synagrops*, *Siniperca* (KATAYAMA, '59); *Antigonia* (STARKS, '02); *Branchiostegus*, *Döderleinia*, *Zenopsis*, *Pempheris*, *Beryx*, *Platax*, *Psenes*, *Gasterochisma*, *Monodactylus*, *Microcanthus* (original), etc.
13. Hardly protractile upper jaw; short and blunt ascending process of premaxillary	Scombridae, *Chorinemus* etc.
14. Opisthotic, interposed half way between pterotic and exoccipital*	Gempylidae, except *Promethyichthys* and *Rexea* (STARKS, '11a; MATSUBARA and IWAI, '58); *Lepidopus* (STARKS, '11a)

with other groups of the Acanthopterygii.

Groups which conflict with *Leptobrama* in the relevant character	Remarks
Most Acanthopterygii, which have either 2 separated or continuous long dorsal fin	
Pempheridae, Berycidae	In Toxotidae, origin of dorsal is just or nearly above that of anal
Percoid families, Bramidae, Gempylidae, Trichiuridae, etc.	
Scombridae*, Carangidae, etc.	* In *Gasterochisma*, scales are large and cycloid
All forms of percoid families	
Scombroid families, Coryphaenidae, Bramidae, Pampidae, etc. (high in number). Pempheridae (10+15)	* 10+16 in *Chorinemus* and 10+15 in several forms (SUZUKI, '62)
Most Acanthopterygii, which have 3 or less. None in scombroid fishes (KISHINOUYE, '23)	High numbers of rayless predorsal pterygiophores are: 7 in *Kurtus indicus* (BEAUFORT, '14); 6 or 7 in *Pomoxis* (Centrarchidae), 5 or 6 in *Vomer* and *Oligoplites* (Carangidae) (SMITH and BAILEY, '61)
Most Acanthopterygii	
? All Acanthopterygii	
Most Acanthopterygii	
Most Acanthopterygii, including forms of above left column	
Scombridae except *Scomber* and *Rastrelliger* (STARKS, '10); Gobiidae	
Most Acanthopterygii, including all Carangidae	
? All Acanthopterygii	
Carangidae, except Naucratinae; Heterosomata, Chatodontidae, etc.	
Most Serranidae (KATAYAMA, '59), *Scomber*, *Apogon* (original), etc.	
Most Acanthopterygii, including all Carangidae, except *Chorinemus*	
Most percoid families and Caranginae (not or scarcely interposed); Scombridae except *Scomber* (completely interposed)	* Intermediate condition between Carangidae and Scombridae

and (3) the anterior extension of the supraoccipital with the supraoccipital crest in contact with the ethmoid, and the frontals which do not take part in forming the anterior portion of anteriorly extended crest. The fishes which share these unusual characters with the Leptobramidae are:

(1) *Bathyclupea*, adult *Luvarus*, *Kurtus indicus*.
(2) *Toxotes*, *Labracoglossa*, *Chorinemus*, *Thunnus* (*Parathunnus*, *Neothunnus*).
(3) *Gasterochisma*, adult *Luvarus*, *Paracaesio*, *Parapristipoma*.

Because the orbitosphenoid is absent, the pelvic fin-ray formula is I, 5, and the caudal branched rays are 8+7, the Leptobramidae belong to the Perciformes and are different from the berycoid fishes and the Allotriognathi.

Table 3 is designed to show the characters in which the Leptobramidae conform or conflict with the carango-scombroid or percoid forms. The Leptobramidae are like the Scombridae and Carangidae but unlike the other percoid families in the characters listed in Section A. The countercharacters are listed in Section B. From the contrast shown in the table, it is apparent that there are good reasons (Section A) to assume that the Leptobramidae are more closely related to the Scombridae or

Table 3. Comparison of the Leptobramidae, Scombridae and Carangidae, and percoid families.

	Families	Leptobramidae	Scombridae and Carangidae	Percoid families
A	Dorsal and anal fin	falciform	mostly falciform	not falciform
	Cartilaginous or adipose tissue around eye	well-developed	well-developed	poorly-developed
	Five longitudinal ridges on dorsal surface of cranium	well-developed and extending anteriorly	mostly well-developed and extending anteriorly	mostly poorly-developed and confined to posterior
	Stomach	T-shaped; with a posterior blind sac	T-shaped; with a posterior blind sac*	rarely T-shaped*
	Auditory bulla	poorly-developed	poorly-developed	mostly well-developed
	Opercular bones in adult	without bony armature	without bony armature	mostly with spines or processes
B	Scales	ctenoid and not minute	mostly cycloid and minute	mostly ctenoid and not minute
	Caudal-fin supporting elements	well-separated	completely or considerably fused	mostly well-separated

Characters of the Leptobramidae approximately conform with those of the Scombridae and Carangidae and conflict with those of the percoid families in Section **A.**

Characters of the Leptobramidae approximately conform with those of the percoid families and conflict with those of the Scombridae and Carangidae in Section **B.**

* cf. SUYEHIRO, 1942 and APSANGIKAR, 1953.

Table 4. Comparison of the Leptobramidae with the Carangidae and Scombridae.

Families		Leptobramidae	Carangidae	Scombridae
C	Upper jaw	hardly protractile	protractile (except *Chorinemus* and *Oligoplites*)	hardly protractile
	Ascending process of premaxillary	short	long (except *Chorinemus* and *Oligoplites*)	short
	1st pterygiophore of anal fine and 1st haemal spine	not adjoined	adjoined (except *Naucrates*, *Seriola*, etc.)	not adjoined
	Air-bladder	absent	consistently present	often absent
D	Number of vertebrae	10+14	10+14~16	more than 30 in total
	Suborbital bones and suborbital sensory canal	complete	complete	incomplete (except *Scomber* and *Rastrelliger*)
	Descending arm of coracoid	long	long	short
	Appearance of parapophyses	3rd vertebra	mostly 3rd vertebra	vertebra far posterior to 3rd
	Isolated fin-lets behind dorsal and anal fin	absent	often absent	consistently present
	Epiotics under supraoccipital	separated from each other	often separated from each other	in contact with each other
E	Caudal-fin supporting elements	well separated	intermediate	fused to form hypural plate
	Caudal fin-ray	cover hypurals rather shallowly	intermediate	cover hypurals completely
	Rayless predorsal pterygiophores	9	3~6 (mostly 3)	absent
F	Opisthotic between exoccipital and pterotic	half-way interposed	not interposed	completely interposed

Characters of the Leptobramidae conform with those of the Scombridae and conflict with those of the Carangidae in Section **C.**

Characters of the Leptobramidae conform with those of the Carangidae and conflict with those of the Scombridae in Section **D.**

Characters of the Carangidae are intermediate between those of the Leptobramidae and Scombridae in Section **E.**

Character of the Leptobramidae which is intermediate between those of the Scombridae and Carangidae in Section **F.**

Sources of the data: Carangidae; see Table 5.
Scombridae; REGAN (1909), STARKS (1910), KISHINOUYE (1923), GODSIL and BYERS (1944).

Table 5. Comparison of the characters of

Family	Leptobramidae		
Genus	*Leptobrama*	*Chorinemus*, *Oligoplites*	*Lichia*
Number of vertebrae	10+**14**	10+16	10+**14**
Scutes	**absent**	**absent**	**absent**
Preorbital region of cranium	**short**	**short**	?
First dorsal fin	**absent**	made up of free spines	made up of free spines
Number of predorsal rayless pterygiophores	**9**	3 (*Chorinemus*); **5** (*Oligoplites*)	**4**
Insertion of 3rd predorsal pterygiophores: in front of neural spine of	**3rd** vertebra	**3rd** vertebra	?
Branchiostegals	**3+3**	5+**3** (*Chorinemus*)	8 or 9 in total
Teeth on mesopterygoid	**present**	**present** (*Chorinemus*)	absent
First pterygiophore of anal and 1st haemal spine	**not adjoined**	adjoined	adjoined
Upper jaw	**not protractile**	**not protractile**	protractile
Ascending process of premaxillary	**short** and **blunt**	**short** and **blunt**	long
Supramaxillary	**absent**	present but small (*Chorinemus*); **absent** (*Oligoplites*)	?
Space between dentary and articular	**absent**	**absent**	present (narrow slit)
Suborbital shelf	**continuous** with suborbitals	**continuous** with suborbitals	?
Basihyal	**elliptical**	**elliptical** (*Chorinemus*)	?
Dorsal surface of basihyal	**entirely toothed**	**entirely toothed** (*Chorinemus*)	?
Second pectoral ray	**dilated**	**dilated** (*Chorinemus*)	?

Sources of the data: GÜNTHER, 1860; STARKS, 1911b; APSANGIKAR, 1953;

Leptobrama with those of the Carangidae

Carangidae			
Naucrates, Seriola, etc.	*Trachinotus*	*Caranx, Trachurus,* etc.	*Apolectus*
10+14~15	10+**14**	10+14~15	10+**14**
absent	**absent**	present	present (vestigial)
short	**short**	generally long	**short**
made up of free spines (*Naucrates*); with fin-membrane (*Seriola*)	made up of free spines	with fin-membrane	continuous with 2nd dorsal
3	3	usually 3; **6** (*Vomer*)	3
3rd vertebra	**3rd** vertebra	2nd vertebra	2nd vertebra
4 1/2+2 1/2 (*Seriola*)	5+2	5+2 or 5 1/2+1 1/2	5 1/2+1 1/2
absent	absent	absent	absent
not adjoined	adjoined	adjoined	adjoined
protractile	protractile	protractile	protractile
long	long	long	long
present	**absent**	present	present
present	present	present	present
continuous with suborbitals	**continuous** with snborbitols	separated from suborbitals	separated from suborbitals
fan-shaped	fan-shaped	fan-shaped or rod-shaped	rod-shaped
partly toothed or edentate	edentate	partly toothed or edentate; **entirely toothed** (*Alectis*)	edentate
usual	**dilated**	usual	usual

SMITH and BAILEY, 1961; SUZUKI, 1962; LE DANOIS, 1963; and original observations.

Carangidae than to the percoid families, although the differences in the scales and caudal fin are marked (Section B).

Carangidae

Table 4 shows in what characters the Leptobramidae conform or conflict with the Carangidae and Scombridae. When the characters in Section D and E are contrasted with those in Section C, it is reasonable to consider that the Carangidae have many more characters in common with the Leptobramidae than does the Scombridae. However, *Leptobrama* lacks the following characteristic features which are limited solely to the forms of the Carangidae*: (1) the presence of two isolated spines in front of the anal fin, (2) the presence of scutes in the lateral line, and (3) the suborbital shelf independent of the suborbital bones (suborbital lamella; SUZUKI, 1962).

The various forms of the Carangidae are compared with the Leptobramidae in Table 5. The table shows that *Chorinemus* and *Oligoplites* have many more characters in common with the Leptobramidae, that *Seriola*, *Naucrates*, *Lichia*, *Trachinotus* are intermediate, and that *Caranx*, *Trachurus*, *Apolectus*, etc. have fewer common characters.

The relationship between *Chorinemus* and *Leptobrama* was once denied because of the differences in (1) the dorsal fin and (2) the scales (STEINDACHNER, 1878, p. 389). However, the cause of the difference in the dorsal fin can only be ascribed to the presence or absence of spines on the anteriorly situated pterygiophores, which are similar in number and position in the two forms. A difference of this sort, for example, cannot be regarded as taxonomically very significant in the Luvaridae and Kurtidae (see below). It is likely that the first dorsal fin of *Chorinemus*, which lacks a fin-membrane and is composed of free spines, represents the intermediate status between the typical first dorsal fin with a fin-membrane and the complete absence of the first dorsal fin in *Leptobrama*, because the principal function of the fin-rays, to support and move the fin-membrane, is already lost in *Chorinemus* (Fig. 9B).

The scales of *Leptobrama* (Fig. 10 and COCKERELL, 1913, p. 54) are quite different from those of *Chorinemus*. The scale characters are, however, often highly variable even in the closely related forms; e. g., in *Gasterochisma* and the tunas, and in the species of the Pempheridae (TOMINAGA, 1963).

In *Naucrates*, *Seriola*, etc. (although not true of most other carangoids as in *Leptobrama*), the first pterygiophore of the anal fin is not adjoined to the first haemal spine. *Oligoplites* and *Trachinotus* agree with *Leptobrama* in the absence of the supramaxillary. The supraoccipital crest of *Trachinotus*, which is mainly formed by the anteriorly extended supraoccipital crest with little participation of the frontals (STARKS, 1911b, p. 37; SUZUKI, 1962, p. 57) approaches that of *Leptobrama*.

* Almost all forms which possess these characters should be included in the Carangidae, but those which lack some of them may not be excluded from the family.

Scombridae

As is discussed just above, the Scombridae seem to be less closely allied to the Leptobramidae than are the Carangidae.

Among the various forms of the Scombridae, *Scomber* and *Rastrelliger* are similar to *Leptobrama* in having complete suborbital bones and suborbital sensory canal, but they differ from *Leptobrama* and the other scombroids in having posteriorly confined longitudinal ridges on the dorsal surface of the cranium and peculiar exoccipital condyles (ALLIS, 1903; STARKS, 1910).

Gasterochisma is a peculiar genus in the Scombridae in that its supraoccipital bone is similar to that of *Leptobrama* (p. 48), but it differs from *Leptobrama* and the other scombroids in the complete absence of a temporal crest on the cranium and in having large cycloid scales. The scales of *Leptobrama* are ctenoid and moderate in size; those of scombroids (except for *Gasterochisma*) are minute and mostly cycloid.

Thunnus agrees with *Leptobrama* in the presence of the teeth on the mesopterygoid (KISHINOUYE, 1923, pp. 303, 321 and 432).

Gempylidae

Like *Leptobrama*, most of the forms of the Gempylidae (except *Promethichthys* and *Rexea*) are intermediate between the Carangidae and Scombridae in the disposition of the opisthotic (cf. Section E, Table 4) (STARKS, 1911a; MATSUBARA and IWAI, 1958).

Bramidae

STEINDACHNER suggested that *Leptobrama* should be placed near the genus *Brama* because he thought that these two forms agree in the characters of the dorsal fin and scales.

The dorsal fin of the Bramidae is long and begins far anterior; as a consequence the number of rayless predorsal pterygiophores is not numerous*. The scales of the Bramidae are like those of the Leptobramidae in being ctenoid and not minute, but unlike in having bony keels which are peculiar to some forms of the Bramidae, and in having not such prominent basal radii as those of *Leptobrama* (Fig. 10).

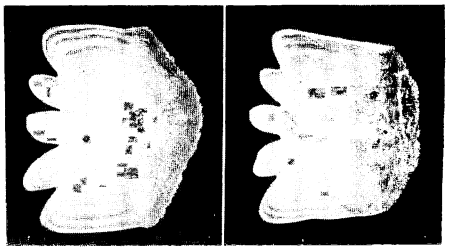

Fig. 10. Body scale (left) and pored scale in lateral line (right) of *Leptobrama mülleri*.

The Bramidae have well developed longitudinal ridges on the dorsal surface of

* ABE (1961, p. 107) reported that the number of the rayless predorsal pterygiophores was seven in *Taractichthys longipinnis* (328 mm in standard length), however, he kindly informed me recently that some of the anterior pterygiophores which he had believed spineless are actually equipped with very minute spines.

the cranium; the supraoccipital crest is formed anteriorly by the frontals. The vertebrae of *Brama* and its allied genera are much more numerous than 10+14 (ABE, 1961).

Luvaridae

The adult *Luvarus* agrees with *Leptobrama* in the characters of the dorsal fin and the supraoccipital crest (pp. 45 and 48).

In a young *Luvarus*, 415 mm in total length, the origin of the dorsal fin is far anterior to that of the anal, and the fin-rays are 22 in number. In specimens more than 1000 mm in length, the origin of the dorsal fin is opposite that of the anal and the number of fin-rays is reduced to 13 (ROULE, 1924). The anterior dorsal fin-rays seem to be lost successively from the front with growth.

Since *Luvarus* has so many peculiarities of its own, the coincidence of adult *Luvarus* with *Leptobrama* in such unusual characters does not provide enough evidence to conclude that they are closely related.

Kurtidae

Kurtus indicus is similar to, but *K. gulliveri* differs from, *Leptobrama* in the character of the dorsal fin (p. 45). The number of rayless predorsal pterygiophores is six or seven in *Kurtus indicus*, but three in *K. gulliveri* (BEAUFORT, 1914)*. The difference between the two congeneric species can be ascribed to the presence or absence of spines on several of the anteriorly situated pterygiophores.

Other forms

While *Bathyclupea* agrees with *Leptobrama* in the character of the dorsal fin (p. 45), this form is said to be physostomous even in the adult (GOODE and BEAN, 1895), p. 190).

Toxotes (vertebrae, 10+14) has the toothed mesopterygoid and the number of the rayless predorsal pterygiophores is five.

Labracoglossa (vertebrae, 10+15) has the toothed mesopterygoid.

Paracaesio (vertebrae, 10+14) and *Parapristipoma* (vertebrae, 11+16) are similar to *Leptobrama* in the character of the supraoccipital crest (p. 48) (KATAYAMA, 1934).

Summary

(1) The internal structure of *Leptobrama mülleri* is described and illustrated.

(2) Mainly on the basis of differences in the structure of the dorsal fin and its pterygiophores (Table 1 and Fig. 9), *Leptobrama* should not be included in the Pempheridae, nor is it related to the family except in a most general way.

* BEAUFORT thought that the high number of the rayless predorsal pterygiophores in *K. indicus* was due to the loss of several spines after the specimens was caught. I have ascertained on the specimens of *K. indicus* from Sarawak (81 mm in standard length) that the number of these bones is six.

(3) The genus *Leptobrama* is placed in the new family, Leptobramidae, with the diagnosis and comparison with other forms (Table 2).

(4) Systematically the Leptobramidae may be close to the Carangidae, especially to *Chorinemus*. The ontogenetical study of *Leptobrama* and the survery of fossil forms are needed to decide its more exact position.

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