

Internal Morphology, Mutual Relationships and Systematic Position of the Fishes Belonging to the Family Pempheridae

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Abstract The Pempheridae belong to the Perciformes and are diagnosed by the presence of a short premedian dorsal fin and a long anal fin, laterally upturned and centrally broadly united exoccipital condyles, and two foramina between the cleithrum and coracoid. Two genera, *Parapriacanthus* and *Pempheris*, belong to the family Pempheridae. The genus *Parapriacanthus* is phylogenetically closely related to *Pempheris*, and several species of *Pempheris* possess transitional characters between *Parapriacanthus* and other species of *Pempheris*. The genus *Pempheris* is subdivided into the *analis*-, *japonica*-, *multiradiata*-, *poyei*-, *mexicana*-, *sasakii*-, and *moluca*-groups. A high variability in the characters of the air bladder, subocular shelf, shoulder girdle, scales, hypurals, abdominal vertebrae, caudal-fin supporting elements, etc., exists in the single family. The predorsal rayless pterygiophores of *Pempheris poyei* are segmented. The Kurtidae have characteristics intermediate between those of the Beryciformes and those of the Perciformes. The possibility is suggested that the evolution of the Perciformes from the Beryciformes occurred in the forms with the single short dorsal fin. In the Perciformes, the serranid genera, *Aeropoma*, *Doederleinia*, *Synagrops*, *Neoscombrops*, and *Malakichthys*, and the families Sciaenidae and Apogonidae share more characteristics with the Pempheridae than do the Priacanthidae, Scorpididae, Kyphosidae, Labracoglossidae, and Kuhliidae. The Bathyclupeidae, Leptobramidae, and the genus *Schuettea* possess no particular affinity with the Pempheridae.

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Introduction

There has been lively controversy in the literature as regards the systematic position and the limits of the family Pempheridae. Precise and detailed knowledge of the morphology of the Pempheridae seems to be indispensable to elucidate perciform phylogeny, because they are thought to be among the most generalized percoids. Little serious attention was paid to the mutual relationships of the genera and species belonging to the Pempheridae until the preliminary discussion of Tominaga (1963), which dealt mainly with Japanese forms.

The present paper aims (1) to give the limits and definition of the family Pempheridae, (2) to elucidate the mutual relationships of the species belonging to the family,

(3) to search for groups which have affinities with the family, and (4) to discuss the validity and consistency of several characters which have been utilized in classifying fishes. To fulfill these purposes, the anatomical information pertaining to the diverse pempherid forms is presented in detail. The names of the bones and anatomical elements are based mainly on Harrington (1955), Weitzmann (1962), Branson and Moore (1962, lateral line system), Adams (1940, otoliths), Matsubara (1943, pelvic girdle), and Nybelin (1963, caudal skeleton), but the selection of the terms are conventional. To avoid misinterpretation of the terms, most of them are indicated in the figures.

History

Sparus? compressus Shaw (1790:267, Fig. 2) was the first binomial name for a pempherid species. Although Shaw's description is brief and unsatisfactory, the accompanying figure is sufficient to indicate that his species was a pempherid. Bloch and Schneider (1801: 164) assigned Shaw's species to the genus *Kurtus**. Günther (1860 : 508) placed *Kurtus* and *Pempheris* in the Kurtina, one of the two subgroups of the family Carangidae. The following year, Günther founded the Kurtiformes, a division with a rank presumably equivalent to a suborder or superfamily of the order Acanthopterygii, for *Kurtus* and *Pempheris*, and removed them from the Carangidae which was assigned to the Cottoscombriformes. The Kurtiformes was characterized by the presence of "one dorsal fin only, much shorter than the anal." Kner (1865 : 170-172) followed Günther (1860) in placing *Pempheris* in the Carangidae. Day (1875 : 175), Macleay (1881 : 150), Klunzinger (1884 : 80), and Jordan and Evermann (1896: 977) assigned *Pempheris* to the Kurtidae.

* The heading of Shaw's description is as follows (sic):

"DOUBTFUL, OR COMPRESSED SPARUS.
SPARUS? COMPRESSUS.

Sparus? Argenteus, compressus"

Although the second line can only be regarded as binomial, Bloch and Schneider adopted "*argenteus*" as the species name, and formed the scientific name *Kurtus argenteus*.

Boulenger (1902 : 200) stressed an affinity of *Beryx* with *Pempheris*; "the two genera agreeing so completely in structure, both external and internal, with the sole exception of the rays in the ventral fins, that I am much inclined to doubt whether the difference between them should be regarded as greater than that between the former (*Beryx*) and *Trachichthys*."

Another chain of opinions started from the proposal of the generic name *Pempheris* by Cuvier (1829a : 195). He placed *Pempheris* in the "squampennes" between the bramids and toxotids. Later, on the basis of anatomical differences, he denied that *Pempheris* was closely related with either *Kurtus* or *Myripristis* (Cuvier, 1831 : 296). He regarded *Kurtus* as a scombroid and *Myripristis* as a genus forming a distinct group (Beryciformes or Berycomorphi of current ichthyologists) together with *Holocentrum*, *Beryx*, and *Trachichthys*. Bleeker (1876, 1877) followed Cuvier and placed "Familia Pempheridoidei" near the toxotids and chaetodontids. Cuvier's opinion was supported by Starks (1904) and by Beaufort (1914) who studied the osteology of the berycoids and the kurtids respectively, and denied their affinities with *Pempheris*. Regan (1913) stressed the similarity of *Pempheris* with the Monodactylidae and postulated *Bramichthys* (= *Schuettea*), which he placed in the Monodactylidae, to be the nearest genus to *Pempheris*. McCulloch (1929 : 193), who placed *Schuettea* in the Pempheridae, represents an extreme trend in this chain of opinions. The majority of current authors have followed Regan's arrangement (e.g. Barnard, 1925; Weber and Beaufort, 1936; Berg, 1940; Bertin and Arambourg, 1957; Lagler et al., 1962; Greenwood et al., 1966).

The genus *Parapriacanthus* was not allocated to a particular family, nor was its systematic position discussed by the original author (Steindachner, 1870). However, as the generic name implies, he might have assumed that it had an affinity with *Priacanthus*. *Pempherichthys* was introduced and placed in the "Pempheridoidei, Anfangsfamilie der Scombroidei," by Klunzinger (1871 : 470). Later, he found *Pempherichthys* to be a

synonym of *Parapriacanthus* (Klunzinger, 1884:81). Since then *Parapriacanthus* has been placed in the Pempheridae.

The genus *Bathyclupea* was affiliated with the Clupeidae by its original author (Alcock, 1891). *Bathyclupea* was placed in the Pempheridae by Boulenger (1902:202; 1904:656) and Weber (1913:193), whereas Goode and Bean (1896:190, citing Gill's manuscript), Regan (1913), Jordan (1923:186), and all current ichthyologists have placed it in the separate, acanthopterygian family Bathyclupeidae.

The genus *Leptobrama* has long been affiliated with the Pempheridae (for the historical note see Tominaga, 1965). Tominaga (1965) studied the internal characters of *Leptobrama*, and concluded that it does not have any actual similarities with the Pempheridae and should be excluded from the family.

So far as I am aware, the remaining groups of fishes which were postulated in the literature to have more or less similarities with the Pempheridae are: characinids (Kner, 1862:135; 1865), sciaenids (Klunzinger, 1884:80), *Priacanthus* (Jordan and Evermann, 1896:977), and *Brama* (Starks, 1904). Some authors (e.g., Jordan; et al., 1913; Tanaka, 1947; Tomiyama and Abe, 1958) have placed the Pempheridae near the Apogonidae, but they did not state the basis for this disposition of the family.

Available information concerning the internal or detailed structures of pempherid forms are scarce and scattered: i.e. Cuvier, 1831:299 (anatomy of *Pempheris oualensis*); Günther, 1860:509 (brief osteological account on *Pempheris otaitensis*; with incorrect number of vertebrae, see on p. 73); Kner, 1862:131 (structure of fin rays), 133 (scales), 135 (teeth); Boulenger, 1902:202 (number of vertebrae and parapophyses in *Pempheris otaitensis* and *P. molucca*); Starks, 1904 (occipital condyle and the first vertebra); Cockerell, 1913 (scales of *Pempheris multi-radiata*); Starks, 1926:240 (ethmoid region of *Pempheris oualensis*); Kobayashi, 1958:fig. 29 (scales of *Pempheris japonicus*); Haneda and Johnson, 1958, 1962a, 1962b (luminescent organ system of *Parapriacanthus ransonneti*);

Smith and Bailey, 1961 (dorsal-fin supports of *Pempheris schomburgki*), 1962 (subocular shelf of *Pempheris oualensis* and *P. schomburgki*); Tominaga 1963 (radiographs of *Parapriacanthus ransonneti* and *Pempheris xanthoptera*, fragmentary descriptions of skeletons, scales, and viscera of Japanese forms); Freihofer, 1963 (nervus lateralis accessorius of *Parapriacanthus dispar*); Tominaga, 1965 (relationship between axial skeleton and vertical fin-ray supporting elements); Haneda et al., 1966 (luminescent organ system of *Pempheris klunzingeri*); Tominaga, S. 1967 (face region, trunk muscles, and alimentary canal of *Pempheris umbrus*).

Several current authors (Fowler, 1931:51 and 58; Weber and Beaufort, 1936:213 and 218; Bauchot, 1963) agree that *Pempheris malabarica* is a synonym of *P. molucca* and that *P. nesogallica* is a synonym of *P. vanicolensis*. I think there is room to doubt that these are identical, and in this paper they are tentatively treated as distinct species. Although Fowler (1931:54) synonymized *Pempheris muelleri* and *P. poeyi* with *P. mexicana*, *P. poeyi* (Fig. 1) is a distinct species, and *P. muelleri* may also be distinct from *P. mexicana*.

Material

The specimens of the Pempheridae radiographed are arranged below, and the specimens dissected, radiographed in successive stages of dissection, and stained with alizarin red are represented by the catalogue numbers in bold-faced type. Museum and institutional names are abbreviated as follows:

AM—Australian Museum, Sydney.

BOC—Bingham Oceanographic Collection, Yale University.

CSIRO—Commonwealth Scientific and Industrial Organization, Marine Laboratory, Sydney.

MNH—Muséum National d'Histoire Naturelle, Paris.

RMNH—Rijksmuseum van Natuurlijke Historie, Leiden.

SM—Sarawak Museum, Kuching, Sarawak.

USNM—United States National Museum, Washington, D. C.

YCM—Yokosuka City Museum, Yokosuka, Kanagawa Prefecture.

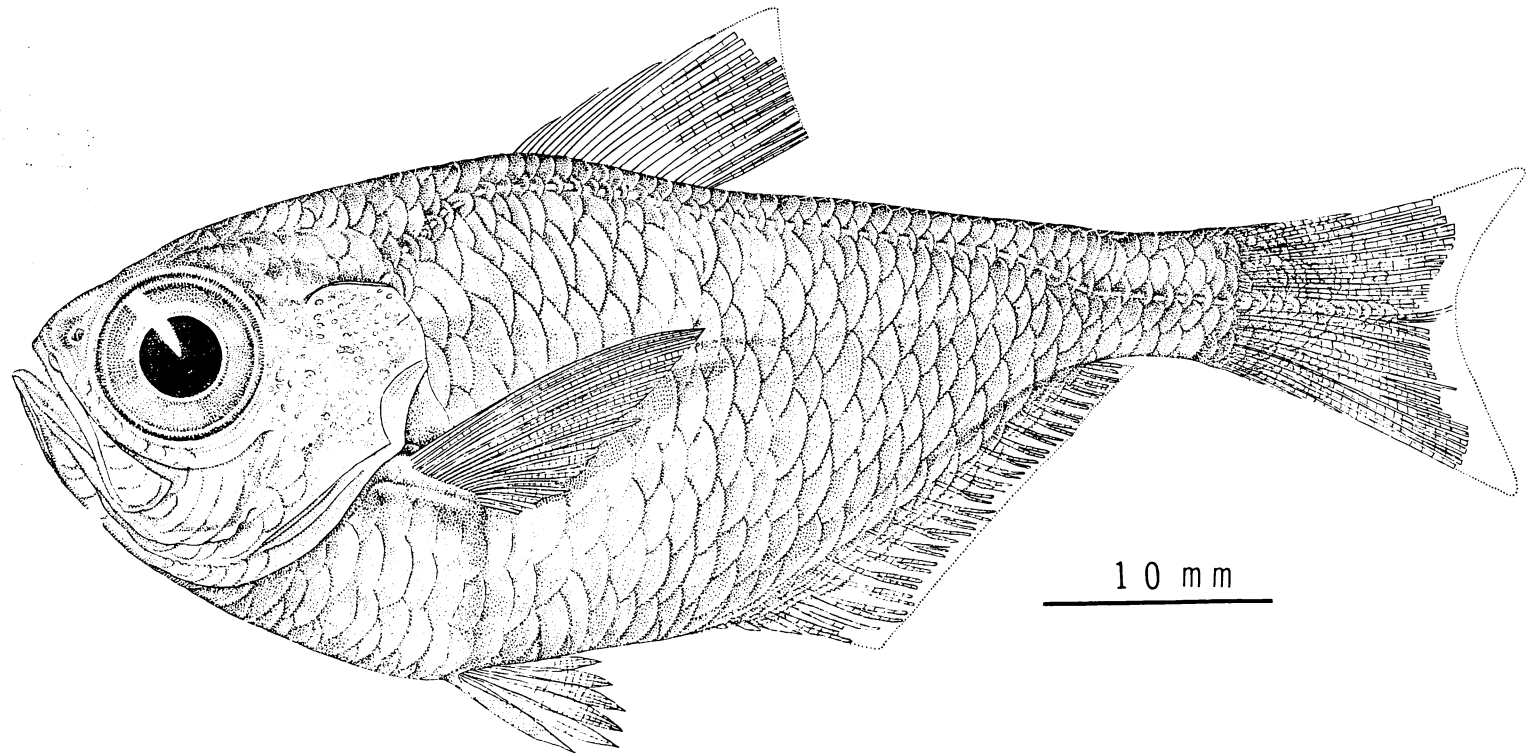


Fig. 1. *Pempheris poeyi*; the largest specimen (53 mm in standard length) of BOC 383.

ZUMT—Section: Zoology, University Museum, University of Tokyo.
Standard length and locality are in parentheses.

Parapriacanthus

P. ransonneti Steindachner: **ZUMT 52342** (56 mm, near Misaki, Japan). In addition, more than 100 specimens registered in ZUMT, ranging 10 to 76 mm in standard length and from various localities of Japan, were radiographed, and non-registered specimens were dissected to supplement the observations.

P. dispar (Herre): USNM 117316 and 117317 paratypes of *Pempheris dispar* (52 and 46 mm, Solomon Is.).

Pempheris

P. analis Waite: CSIRO C-2640 (105 mm, Dampier Archipel., Western Australia). CSIRO C-2786 (100 mm, Exmouth Gulf (?), Western Australia).

P. klunzingeri McCulloch: CSIRO C-2280 (132 mm, West of Garden I., Western Australia). CSIRO C-2659 (137 mm, Rottneet I., Western Australia).

P. compressa (Shaw): USNM 29003 (139 mm, New South Wales). USNM 59908 (142 mm, Port Jackson, New South Wales). USNM 82988 (95 mm, Sydney, New South Wales).

P. japonica Döderlein: **ZUMT 52327** (131 mm, Totoro, Miyazaki Pref., Japan). USNM 68229 holotype of *Catalufa umbra* Snyder (132 mm, Misaki, Japan). In addition, 10 specimens registered in ZUMT, ranging 105 to 154 mm, in standard lengths and from various localities of Japan, were radiographed, and non-registered specimens were dissected to supplement the observations.

P. multiradiata Klunzinger: CSIRO C-712 (132 mm, Eden, New South Wales).

P. poeyi Bean: USNM 37184 holotype (45 mm, Cuba). One specimen of **BOC 383** (26 mm, Corrientes Bay, Cuba). Other 4 specimens of **BOC 383** (23, 23, 25 and 53 mm, Corrientes Bay, Cuba).

P. mexicana Cuvier: MNHN A-241 holotype (111 mm, Acapulco, Mexico).

P. muelleri Poey: USNM 24957 holotype (89 mm, Cuba).

P. nyctereutes Jordan and Evermann: ZUMT 42902 holotype (162 mm, Pescadores I., Formosa). ZUMT 19048 (126 mm, Taihoku (?), Formosa).

P. sasakii (Jordan and Hubbs): **ZUMT 52326** (102 mm, Totoro, Miyazaki Pref., Japan). ZUMT 51966 topotype (89 mm, Toba, Japan). ZUMT 22662 (137 mm, Fukushima V., Miyazaki Pref., Japan). ZUMT 22667 (135 mm, Fukushima V., Japan). ZUMT 33016 (67 mm, Izu Pen., Japan). ZUMT 48293 (123 mm, near Misaki, Japan). ZUMT 52159, 52160 and 52192 (106, 109 and 99 mm, Totoro, Japan). In addition, 2 non-registered specimens were dissected to supplement the observations.

P. oualensis Cuvier: MNHN A-221 holotype (172 mm, Oualan I.).

P. otaitensis Cuvier: MNHN A-927 holotype (134 mm, Tahiti).

P. moluca Cuvier: MNHN A-220 holotype (115 mm, Moluccas Is.). MNHN A-217 paratype (102 mm, Batavia). **ZUMT 52328** (=SM P-3061) (104 mm, Sarawak). ZUMT 52329 (=SM P-3062) (105 mm, Sarawak). ZUMT 52330 (=SM P-3060) (107 mm Sarawak).

P. malabarica Cuvier: MNHN A-219, A-417 and B-2511 syntypes (128, 136 and 122 mm, Malabar).

P. vanicolensis Cuvier: MNHN A-224, A-418, B-2512 and B-2513 syntypes (136, 117, 69, and 137 mm, Vanikoro I.).

P. nesogallica Cuvier: MNHN A-222 and B-2514 syntypes (141 and 133mm, Mauritius).

P. iioui Fowler: USNM 89994 holotype (110 mm, Tanakeke I., Flores Sea). USNM 122597 paratypes (105 and 103 mm, Tanakeke I., Flores Sea).

P. schwenkii Bleeker: RMNH 6160 syntype (95 mm, Batu I.).

P. xanthoptera Tominaga: ZUMT 51967 holotype (119mm, Manazuru, Japan). **ZUMT 52325** (107 mm, Goto Is., Japan). In addition, 43 specimens registered in ZUMT, ranging 32 to 134 mm in standard lengths and from various localities of Japan, were radiographed, and non-registered specimens including young ones, 7 mm in standard length, were dissected or stained with alizarin red to supplement the observations.

In addition to pempherid fishes, the following non-pempherids were examined:

Leptobramidae

Leptobrama muelleri Steindachner: ZUMT 52319 (=AM J-12904) (265 mm, Port Hedland, Western Australia).

Bathyclupeidae

Bathyclupea argentea Goode and Bean: ZUMT 52322 (donated by Dr. M. M. Dick of Museum of Comparative Zoology, Harvard University) (205 mm, 16°58'N, 87°53'W.).

(?) Scorpididae

Schuettea scalaripinnis Steindachner: ZUMT 52323 (=AM T-11306) (137 mm, Australia).

Kurtidae

Kurtus indicus Bloch: ZUMT 52320 (=SM P-4314) (88 mm, Mouth of Oya River, Sarawak).

Anomalopidae

Photoblepharon palpebratus (Boddaert): YCM (64 mm, Banda I.).

Anomalops katoptron (Bleeker): YCM (114 mm, Hachijo I., and 50 mm Banda I.).

Non-registered specimens of *Beryx splendens* Lowe (Berycidae), *Priacanthus macracanthus* Cuvier (Priacanthidae), *Kuhlia taeniura* (Cuvier) (Kuhliidae), *Doederleinia berycoides* (Hilgendorf), *Malakichthys griseus* Döderlein, *Acropoma japonicum* Günther (Percichthyidae, sensu Gosline, 1966a), *Scorpiis* sp. (Scorpididae), *Monodactylus argenteus* (Lacépède) (Monodactylidae), *Labracoglossa argenteiventris* Peters (Labracoglossidae), *Toxotes jaculator* (Pallas) (Toxotidae), *Apogon semilineatus* Temminck and Schlegel (Apogonidae), Sciaenidae spp., etc. were also examined.

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Description of the Pempherid Forms

The following accounts are mainly based on specimens belonging to one species of *Parapriacanthus* and five species of *Pempheris* which were actually dissected (catalogue numbers of these specimens are represented in the list by bold-faced type). Because one dissected specimen of *Pempheris poeyi* is of small size and its several characters are thought to be of juvenile nature, or were difficult to investigate, they are excluded from the following description.

The structure and disposition of the vertebrae, ribs and fins were ascertained by the examination of radiographs; the descriptions and comparison of these characters are given for all the pempherid species listed above. CRANIUM (Figs. 2, 3, and 4)

The components of the cranium are transparent, without ornaments and not heavily ossified except otoliths. The orbital cavity is very large and the anterior and posterior portions of the cranium to the cavity are abbreviated. The cranium is slenderer and the elements constituting the cranium are, on the whole, narrower and lower in *Parapriacanthus* than in *Pempheris*. Proportional

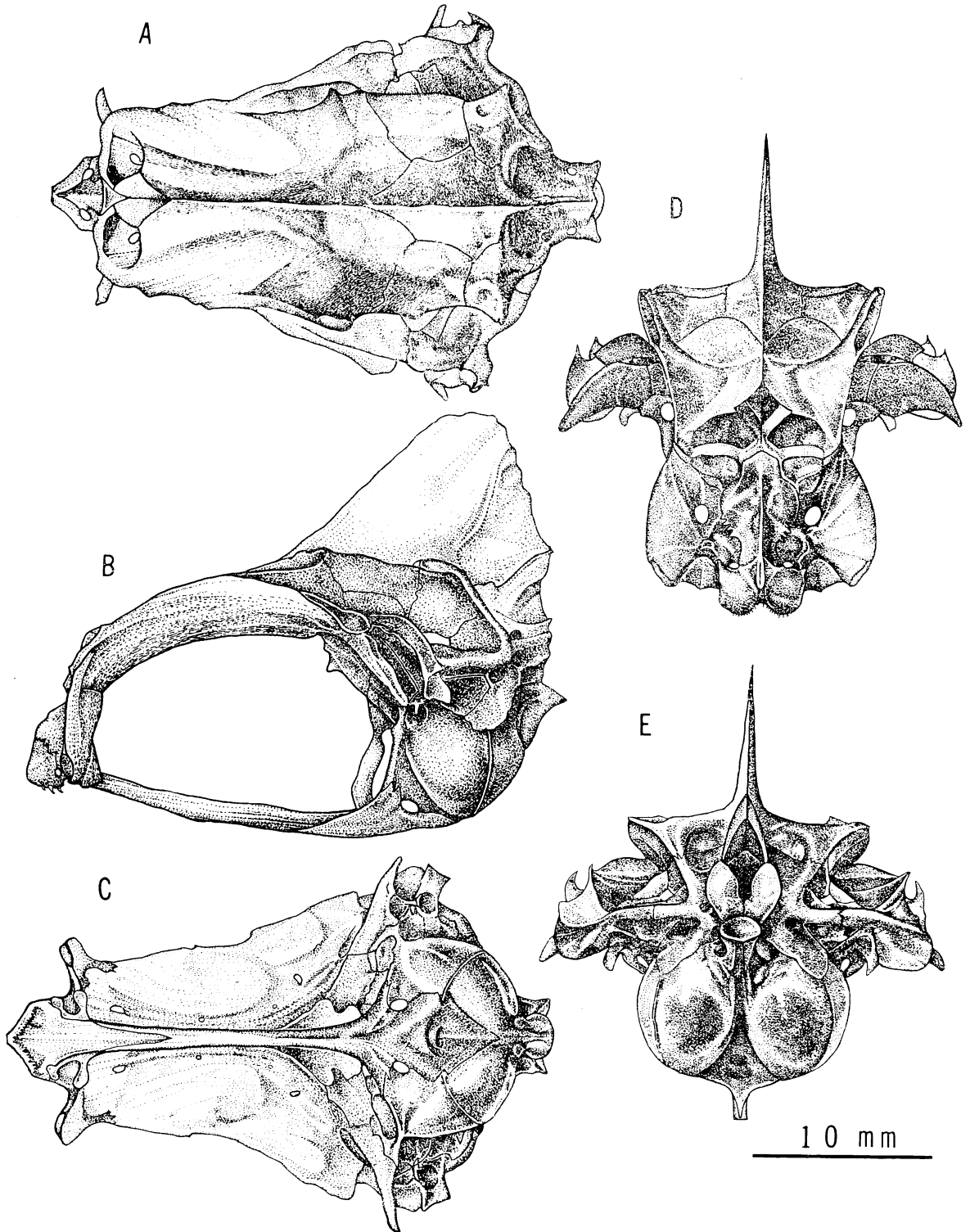


Fig. 2. The cranium of *Pempheris japonica*. A. dorsal view; B. lateral view; C. ventral view; D. anterior view; E. posterior view.

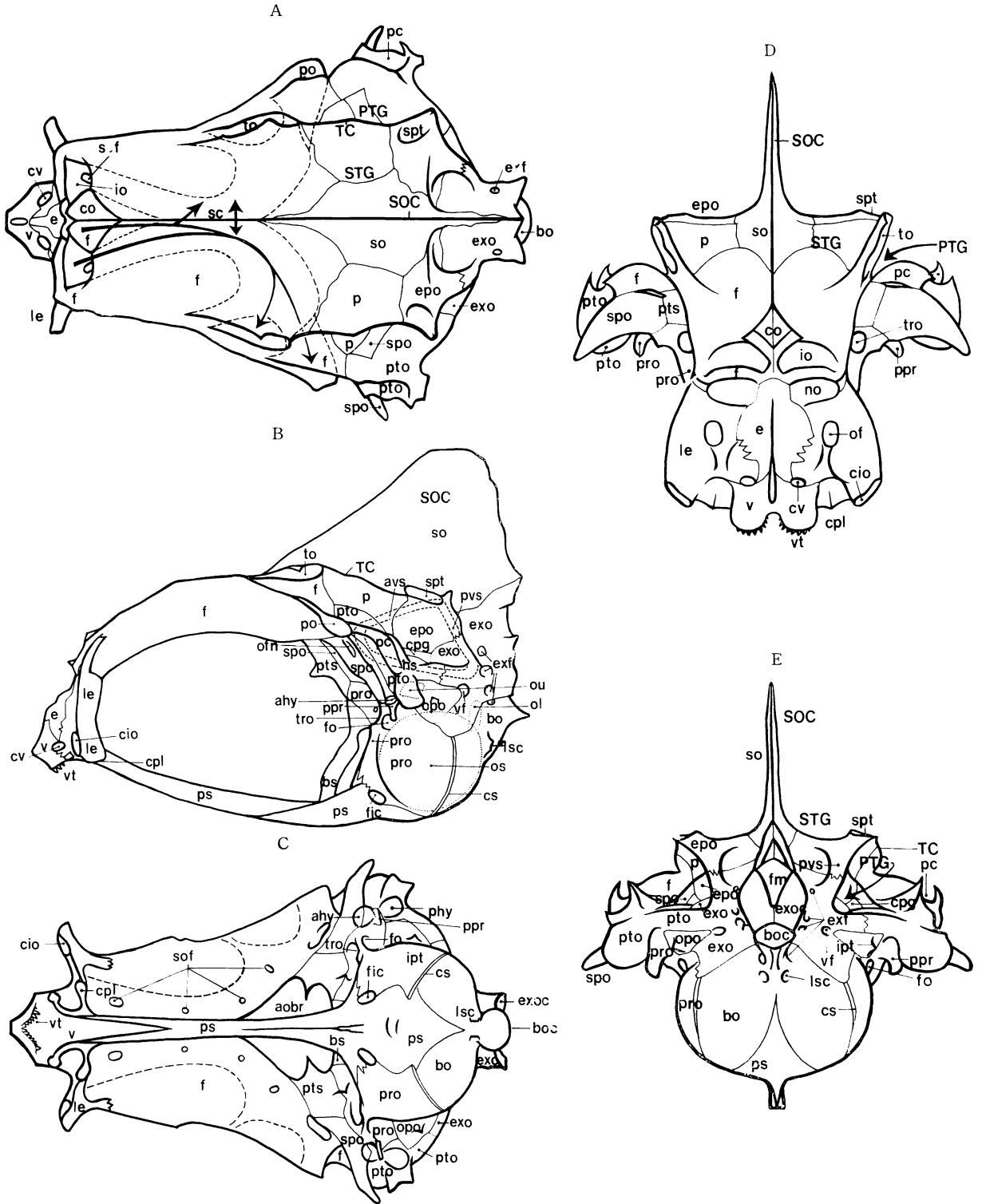


Fig. 3.

Table 1. Proportional measurements of the crania of the Pempheridae.

	<i>Parapriacanthus ransonneti</i>	<i>Pempheris japonica</i>	<i>Pempheris sasakii</i>	<i>Pempheris xanthoptera</i>
Length of cranium in mm	14.5	31.0	23.0	25.0
In hundredths of standard length	25.4	24.4	22.7	21.6
In hundredths of length of cranium				
Width of cranium	57.6	68.3	62.2	67.6
Height of cranium	63.0	77.8	74.0	82.4
Preorbital length	17.6	15.3	17.1	14.0
Horizontal diameter of orbital cavity	49.2	54.2	52.0	56.3
Postorbital length	33.2	30.1	30.1	29.3
Horizontal diameter of sacculith	17.2	19.3	19.5	17.7

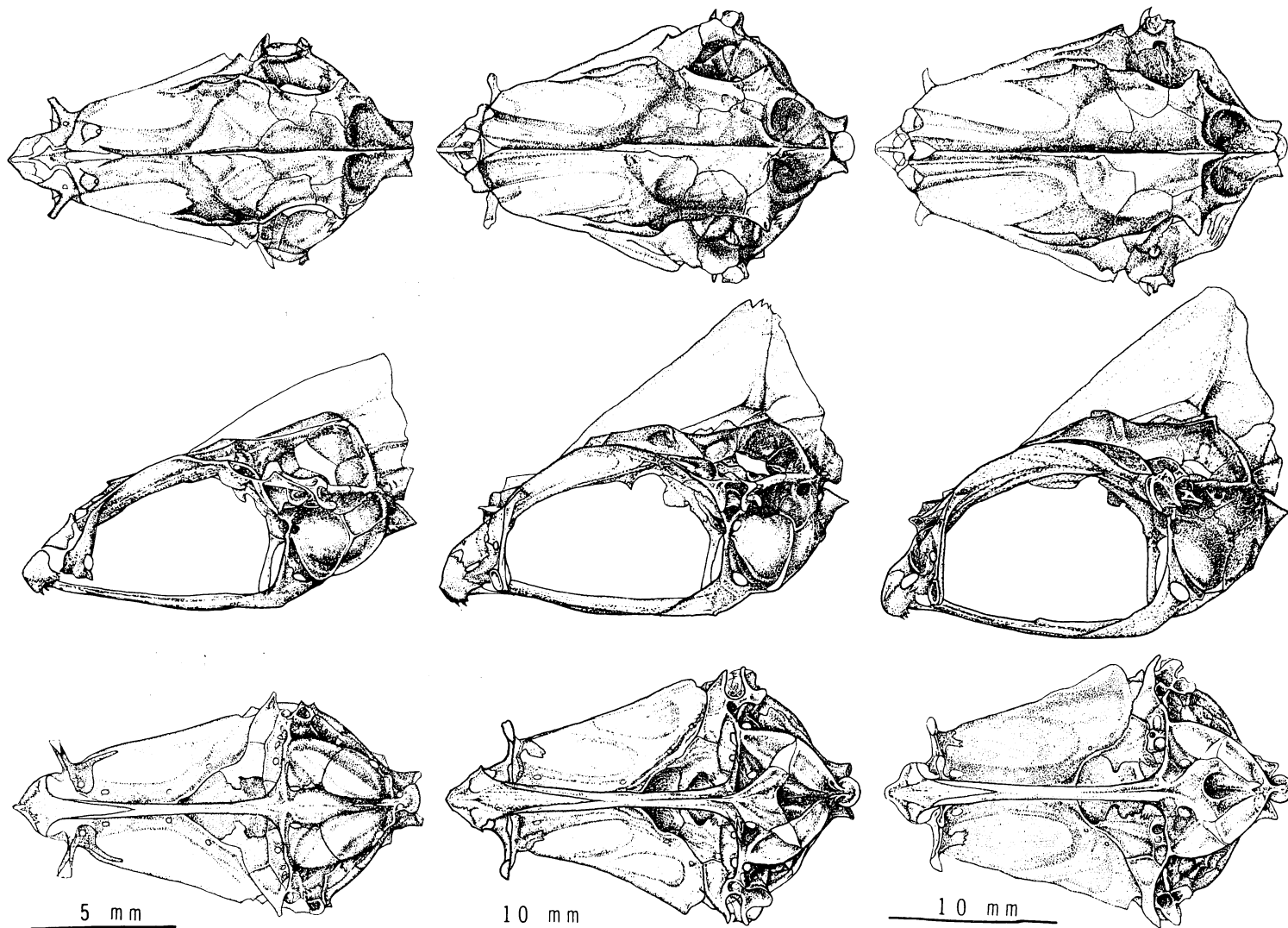
measurements are given in Table 1.

The head of the **prevomer** (v) (vomere of ichthyologists) is made up of a ventral and two lateral thin bony plates investing a central cartilaginous core. A deep notch is present along its dorsal median line. The teeth on the prevomer (vt) are arranged along the anteroventral \wedge -shaped edge. In *Pempheris sasakii* and *P. moluca* they are confined to the posterior half of the \wedge . The teeth are arranged in a single row in all the species examined except *Pempheris japonica*, in which they are in two irregular rows. The number of the prevomerine teeth are about 10 in *Pempheris poeyi*, 12 to 14 in *P. sasakii* and *P. moluca*, 16 to 18 in *Parapriacanthus ransonneti* and *Pempheris xantho-*

ptera, and about 40 in *P. japonica*.

The **mesethmoid** (e) (ethmoid) is flimsy superficial ossification on cartilage and peltate in shape. It is in contact with the prevomer, lateral ethmoids, and frontals in *Pempheris*, whereas in *Parapriacanthus* it is separated by cartilage from the prevomer. The mesethmoid is almost perpendicular to the dorsal surface of the frontals and the preorbital region is shorter in *Pempheris*, whereas in *Parapriacanthus* the mesethmoid is tilted forward so as to make a longer preorbital region. On either side of the bone is the surface of attachment for the mesethmoid-maxillary ligament. A pair of thin bony projections protrude from the bone to cartilage between the frontals.

Fig. 3. The key figure of the cranium of *Pempheris japonica*. A. dorsal view; B. lateral view; C. ventral view; D. anterior view; E. posterior view. ahy, anterior facet for hyomandibular; aobr, anterior opening of brain cavity; avs, anterior vertical semicircular canal; bo, basioccipital; boc, basioccipital condyle; bs, basisphenoid; cio, condyle for first infraorbital; co, coronal opening of supraorbital canal; cpg, cartilaginous area in posttemporal groove; cpl, condyle for palatine; cs, cartilaginous area on sacculus chamber; cv, cartilage between prevomer and lateral ethmoid; e, mesethmoid; epo, epiotic; exf, exoccipital foramina; exo, exoccipital; exoc, exoccipital condyle; f, frontal; fic, foramen for internal carotid artery; fm, foramen magnum; fo, facial opening of trigemino-facialis chamber; hs, horizontal semicircular canal; io, interorbital opening of supraorbital canal; ipt, attaching surface of lower arm of posttemporal; le, lateral ethmoid; lsc, attaching surface of ligament from supracleithrum; no, nasal opening of supraorbital canal; of, olfactory foramen; ofn, foramen for otic branch of facial nerve; ol, lagenalith; opo, intercalary; os, sacculith; ou, utriculith; p, parietal; pc, postorbital commissure; phy, posterior facet for hyomandibular; po, postorbital opening of supraorbital canal; ppr, process of prootic below facets for hyomandibular; pro, prootic; ps, parasphenoid; PTG, posttemporal groove; pto, pterotic; pts, pterosphenoic; pvs, posterior vertical semicircular canal; sc, supraorbital commissure of supraorbital canal; so, supraoccipital; SOC, supraoccipital crest; sof, foramina for superficial ophthalmic branch of facial nerve; spo, sphenotic; spt, attaching surface of upper arm of posttemporal; STG, supratemporal groove; TC, temporal crest; to, temporal opening of supraorbital canal; tro, trigeminal opening of trigemino-facialis chamber; v, prevomer; vf, vagus foramen; vt, prevomerine teeth.



Parapriacanthus ransonneti *Pempheris sasakii* *Pempheris xanthoptera*
Fig. 4. The crania of *Parapriacanthus ransonneti*, *Pempheris sasakii*, and *Pempheris xanthoptera* Top, dorsal view; middle, lateral view; bottom, ventral view.

The **lateral ethmoid** (le) (prefrontal, prefrontal-lateral ethmoid complex) is in contact with the prevomer, mesethmoid, and parasphenoid, and its ascending wing is joined to the ventral surface of the frontal by cartilage. It is separated from its counterpart of the opposite side by the mesethmoid anteriorly and by cartilage posteriorly. Its two condyles, the abaxial one of which (cio) is for the first infraorbital and the adaxial one (cpl) for the palatine, are filled and capped with cartilage. The olfactory nerve passes through the bone obliquely and issues from the foramen (of). The bone on the whole and its condyles are slenderer in *Parapriacanthus* than in *Pempheris*. In *Parapriacanthus ransonneti*, *Pempheris japonica*, and *P. poeyi* the ascending wing is narrower than it is in *Pempheris sasakii*, *P. moluca*, and *P. xanthoptera*. In front view, the lateral margin of the lateral ethmoid is convex in *Pempheris japonica*, whereas it is concave in the remaining species. There is a cartilaginous surface (cv) surrounded by the prevomer, mesethmoid, and lateral ethmoid on either side. In reverse proportion to the degree of ossification of the surrounding bones, the space is the narrowest in *Pempheris japonica*, and the widest in *Parapriacanthus ransonneti*.

The **frontals** (f) form more than half of the skull roof. They are covered almost entirely by the anteriorly extended epaxial trunk muscles.

The supraorbital canal of the lateral line system is in a bony tube and well developed. Four openings are present in each frontal and there is an opening at the junction of the frontals. The nasal opening (no), an anteriormost opening of the supraorbital canal from which the canal passes forward to the nasal, is separated by a transverse bony strap from the interorbital opening (io), situated immediately behind the former. The bony strap is absent and the two openings are continuous in *Pempheris poeyi*. It is narrow in *Pempheris japonica*, although its width is subject to considerable individual variation. In the remaining species it extends forward as a pent roof of the nasal opening. The supraorbital canals of both sides converge posteriorly to anastomose with each other

along the median line (supraorbital commissure) (sc). The coronal opening (co) leading to the supraorbital commissure is situated near the anterior end of the junction of the frontals, and only slightly behind the interorbital openings. The canal connecting the coronal opening with the supraorbital commissure is roofed by the median edge of the paired frontals, which form a low median ridge continuous posteriorly with the supraoccipital crest. The ventral floor of the canal, also composed of the inner narrow flanges of the adjoined frontals, extends forward beyond the dorsal roof to the level of the bony straps which separate the nasal and infraorbital openings in *Pempheris japonica*, whereas in the other species the ventral floor does not extend beyond the dorsal roof. Consequently, the frontals are in contact with each other to near its anterior end in *Pempheris japonica*, whereas in the other species the anterior parts of the frontals are separated by cartilage. Behind the supraorbital commissure, the supraorbital canal forks into upper and lower branches. The upper branch opens by the temporal opening (to), a large and elongate pore with a raised margin. The opening lies along the dorsolateral margin of the frontal immediately in front of the parietal and leads to the canal of the anterior element of the supratemporals. The lower branch runs obliquely downward and opens by the postorbital opening (po), a pore similar in shape and size to the preceding one. The opening is situated at the ventroposterior margin of the frontal and leads to the canal of the pterotic and that of the sixth infraorbital. Four (or more) foramina (sof) for the superficial ophthalmic branch of the facial nerve are present in the ventral surface of the frontal along the floor of the supraorbital canal. The anteriormost foramen is just below the interorbital opening in *Parapriacanthus ransonneti* and *Pempheris japonica*, whereas it is considerably posterior to the opening in *Pempheris sasakii*, *P. moluca*, and *P. xanthoptera*.

A deep notch in the frontal between the postorbital and temporal opening of the sensory canal represents the anterior portion of the posttemporal groove.

On the ventral surface just anterior to the pterosphenoid, each of the frontals possesses a wing extended toward the orbital cavity which serves as a side wall of the anterior portion of the brain cavity. The wing is conspicuous in *Pempheris sasakii*, *P. xanthoptera*, and *P. moluca*, whereas it is inconspicuous in *Parapriacanthus ransonneti* and *Pempheris japonica*.

The **supraoccipital crest** (SOC) ascends steeply from the anterior end of the supraoccipital; anterior to it the ridged roof of the supraorbital commissure extends forward on the frontal to the coronal opening. The anterior end of the **supraoccipital** (so) extends forward, covering the median junction of the frontals. The anterior end of the bone is posterior to the anterior end of the temporal opening in *Parapriacanthus ransonneti* and *Pempheris japonica*, whereas in *Pempheris sasakii*, *P. moluca*, and *P. xanthoptera* it reaches more anteriorly. The hinder margin of the supraoccipital crest is vertical and ends above the foramen magnum. The dorsoposterior margin of the crest is slightly serrated in *Pempheris sasakii*, *P. moluca*, and *P. poeyi*. The crest is lower in *Parapriacanthus* than in *Pempheris*.

The anterior epaxial trunk muscles extend forward in the supratemporal groove (STG) to immediately behind the interorbital opening of the sensory canal.

The **temporal crest** (TC) originates from the wall of the temporal opening of the frontal, traverses the parietal, and ends in the epiotic at the lateral ridge of the articulating surface for the posttemporal. The crest is lower in *Parapriacanthus* than in *Pempheris*.

The **posttemporal groove** (PTG) opens laterally, and is bounded by the temporal crest above, and the thin bony walls of the postorbital opening and postorbital commissure below. It is deep in *Pempheris* but shallow in *Parapriacanthus*. An interspace of cartilage (cpg) in the floor of the posttemporal groove is bounded in *Pempheris* by the epiotic, pterotic, and sphenotic, whereas in *Parapriacanthus* it is bounded by the parietal in addition to these three bones. This cartilaginous space is larger in *Parapriacanthus* than in *Pempheris*. In *Pempheris*

moluca the space is elongate and very narrow, and the margins of the epiotic and the pterotic are close together.

The **parietal** (p) partly overlies the supraoccipital and epiotic in the supratemporal groove, and the sphenotic and epiotic in the posttemporal groove. The raised bony flange of the parietal forms the main part of the temporal crest and overhangs the deep posttemporal groove in *Pempheris*, whereas it is low anteriorly and absent posteriorly so as to make the posttemporal groove shallow in *Parapriacanthus*. There is no foramen for the parieto-dorsal branch of the nervus lateralis accessorius in the parietal in *Parapriacanthus dispar* (Freihofer, 1963).

The dorsal face of the **epiotic** (epo) is partly overlain by the parietal and supraoccipital. The shallowly hollowed portion (spt) is the articulating surface for the upper limb of the posttemporal. The articulating surface is triangular and markedly projects laterally in *Pempheris moluca*. From the posterior end of the articulating surface, a rounded bony ridge running posteroventrally contains the dorsal half of the posterior vertical semicircular canal (pvs). This ridge is joined by a suture to the exoccipital. The anterior vertical semicircular canal (avs) is lodged in the laterodorsal ridge of the epiotic.

The **pterotic** (pto) is in contact with the frontal above the sphenotic. The postorbital commissure (pc), the sensory canal of this bone, is represented by a groove, and connects the postorbital opening of the supraorbital canal with the canal in the posterior element of the supratemporals. The postorbital commissure is as long as half the length of the bone and runs obliquely downward in *Parapriacanthus ransonneti* and *Pempheris japonica*, whereas it is short and horizontal in *Pempheris sasakii*, *P. moluca*, and *P. xanthoptera*. There is a narrow bony strut of the pterotic over the postorbital commissure in *Pempheris moluca*.

A waved bony wing posteroventral to the postorbital commissure serves as a surface for the attachment of the muscles and as a roof of the posterior hyomandibular facet. In posterior view, the wing is convex in *Pempheris japonica*, whereas in all other

species it is deeply notched. Internally the endosteal component of the pterotic (autopterotic) is occupied by a hollow tube containing the anterior half of the horizontal semicircular canal (hs). The bony tube opens anteriorly into the oval space of the same bone, which lodges the utriculus (ou).

The dilatator groove is bounded by the laterally projected process of the sphenoid and the waved wing of the pterotic. This groove is wide and shallow in *Parapriacanthus*. In *Pempheris japonica*, it is narrower and deeper than in *Parapriacanthus ransonneti*, but wider and shallower than in *Pempheris sasakii* and *P. xanthoptera*. In *Pempheris moluca* the tips of the sphenotic process and pterotic wing are close together, so that the groove is extremely narrow and deep. There is an interspace connecting the posttemporal and dilatator grooves between the sphenotic and the overlying bony bridge of the frontal and pterotic in *Pempheris poeyi*, *P. sasakii*, *P. moluca*, and *P. xanthoptera*. In *Parapriacanthus ransonneti* and *Pempheris japonica* the interspace is absent and the two grooves do not communicate. The facet for the head of the hyomandibular is divided into two: the anterior one (ahy) is placed at the junction of the prootic and sphenotic, the posterior one (phy) is situated in the pterotic.

The **sphenotic** (spo) projects laterally under the junction of the frontal and pterotic as a stout triangular process. The cranium is broadest between the tips of the sphenotics. Within the orbit the sphenotic meets the pterosphenoid adaxially, and the prootic ventrally. It meets the pterotic in the dilatator groove, and the prootic in the anterior hyomandibular facet. The process of the sphenotic is overlain by the sixth infraorbital. The otic branch of the facial nerve enters through a foramen in the orbital face of the bone, and emerges through a foramen (ofn) at the dorsolateral edge of the process. The exposed surface of the same bone in the posttemporal groove is bounded by the frontal, pterotic, and parietal. In *Parapriacanthus ransonneti* the sphenotic is widely separated from the epiotic by a cartilaginous space, whereas in *Pempheris sasakii*, *P. moluca*, and *P. xanthoptera* the bone is

narrowly separated from the epiotic, and in *Pempheris japonica* the two bones are in contact with each other.

The **prootic** (pro) is deeper in *Pempheris japonica* than in the other species. The dorsal portion (trigemino-facialis region) is larger in *Parapriacanthus* than in *Pempheris*. The bony protuberance (ppr), situated below the border of the anterior and posterior facets for the condyles of the hyomandibular and above the posterior opening of the trigemino-facialis chamber, projects laterally as a wing in *Pempheris japonica*, whereas in the other species it is low and inconspicuous. The pars jugularis of the trigemino-facialis chamber is bridged by a thin vertical bony strut of the prootic. The number, size and shape of the foramina for the passages of the nerves and blood vessels around the trigemino-facialis region are highly variable. Two neighboring foramina, which are widely separated from each other on one side, may be narrowly separated or fused together to form a single opening even on the other side of the same individual. The separate foramen for the hyomandibular trunk of the facial nerve is absent in the pars jugularis of the trigemino-facialis chamber (cf. Patterson, 1964 : 434). The prootic sends off a bony shelf extending inward to meet its fellow in the median line, which separates the myodome from the brain cavity.

Each **pterosphenoid** (pts) (*alisphenoid* of ichthyologists, *pleurosphenoid*) has an adaxially directed wing; these cause the anterior opening of the brain cavity to be constricted from both sides. In *Pempheris sasakii* and *P. moluca* the wings of the pterosphenoids are longer and the anterior opening of the brain cavity is more constricted than in the remaining species. The orbitosphenoid is absent.

The **parasphenoid** (ps) is gently curved. The anterior portion of the ventral surface is excavated to accommodate the shaft of the prevomer. A median longitudinal ridge is present on the dorsal surface of the bone below the orbit. Posterior to the ridge, a groove is present in which the pedicel of the basisphenoid is inserted. A longitudinal ridge is also present on the ventral surface

below the basisphenoid. The ascending process of the parasphenoid meets the prootic in a close suture. The tip of the first upper pharyngeal attaches to this suture. Between the prootic and the hinder edge of the ascending process of the parasphenoid lies the internal carotid foramen (fic). No groove or foramen for the efferent pseudobranchial artery is present. The posterior part of the ventral surface of the parasphenoid is gouged along the median line in *Pempheris*, whereas this part is convex in *Parapriacanthus*. Posteriorly, the parasphenoid underlies the ventral surface of the basioccipital and ends far anterior to its posterior end. The posterior end of the parasphenoid is a single sharp process in *Pempheris japonica*, whereas it is bifurcate in *Parapriacanthus ransonneti*, *Pempheris sasakii*, *P. moluca*, and *P. xanthoptera*.

The **basisphenoid** (bs) is Y-shaped and its ventral process is inserted into the groove in the parasphenoid. Each of the upper arms of the basisphenoid meets the pterosphe- noid and prootic in *Pempheris sasakii*, *P. moluca*, and *P. xanthoptera*, whereas in *Parapriacanthus ransonneti* it meets the prootic only and the pterosphe- noid is excluded from the junction. On the left side of one specimen of *Pempheris japonica*, the upper arm of the basisphenoid was attached to the pterosphe- noid, whereas on the other side of the same individual and in the other specimens it was not.

The myodome ends in the anterior half of the basioccipital and does not open to the exterior posteriorly.

The large sacculus chamber is invested by the thin-walled and greatly inflated posterior part of the prootic, the anteroventral part of the exoccipital, and the anterodorsal part of the basioccipital. The chamber is deeper in *Pempheris japonica* than in the other species. A cartilaginous area (cs) is between the hind margin of the prootic and the front margin of the basioccipital.

The **intercalar** (opo) (opisthotic) rests on the exoccipital, pterotic and prootic. The bone faces downward, and its dorsoposterior margin does not reach even the lateroposterior contour of the cranium. Consequently the bony protuberance of the intercalar (ipt) for

the articulation of the lower limb of the posttemporal is located on the ventral side of the cranium just above the sacculus chamber.

Forward and dorsoanteriorly directed bony ridges originate from the center of the **exoccipital** (exo). In sutures, the former is continuous with the ridge of the pterotic and the latter with that of the epiotic. Internally these ridges contain tubular spaces where the posterior half of the horizontal (external), and ventral half of the vertical semicircular canals are respectively lodged. Adaxial to the horizontal canal, the posterior perpendicular wall of the exoccipital bears an oval depression which extends dorsally on to the epiotic. The exoccipital sends off a bony shelf extending inward to meet its fellow in a broad junction along the median line which separates the sacculus and lagena chambers from the brain case. A large vagus foramen (vf) is just posterior to the intercalar. The foramina (exf) for the passages of the occipital nerve are three or more, and variable in number and shape even in the right and left sides of the same individual.

The **exoccipital condyles** (exoc) for the first vertebra are broadly in contact with each other and are peculiar in that they expand laterodorsally. They are inclined at about 60° to the vertebra-like condyle of the basioccipital. The dorsal wing of the exoccipital is united with its counterpart to form the upper wall of the foramen. The supraoccipital lies above a dorsal thickening of this dorsal wing. The foramen magnum (fm) is high and rhomboidal in shape.

Anteriorly, the **basioccipital** (bo) flares markedly to form the posteroventral part of the wall of the inflated sacculus chamber. In the median line, the basioccipital bears a vertical crest which separates the sacculus chambers of the two sides. The crest is high and a foramen is present near its center in *Pempheris japonica*, whereas in *Parapriacanthus ransonneti*, *Pempheris sasakii*, and *P. xanthoptera* the crest is deeply notched and no foramen is present. A pair of small rounded areas (lsc) which mark the attachment surfaces of the ligaments from the supracleithra are on the ventral surface of

the basioccipital, and lateral to the end of the parasphenoid. The face of the vertebra-like condyle (boc) is deeply concave and faces dorsoposteriorly.

OTOLITHS (Fig. 5).

Of three otoliths, the **utriculith** (ou) (lapillus, utriculolith) and **lagenolith** (ol) (asteriscus, lagenolith) are small, the former being oval and the latter elliptical. The **sacculith** (os) (sagitta, sacculolith) is very large, its horizontal diameter being about one-fifth the length of the cranium. Its outer side is concave and the inner, convex. The dorsal rim is serrated but the ventral rim is smooth or barely serrated. The ostium (ost) opens on the anterior rim and is as long as the cauda (cd) in *Parapriacanthus ransonneti*, *Pempheris japonica*, and *P. xanthoptera*. In *Pempheris sasakii* the cauda reaches the posteroventral rim and is longer than the ostium. There is a lower, but no upper angle, between the ostium and cauda. In *Pempheris japonica* the area below the ostium and cauda is large and the shape of the bone is almost circular, whereas in *Parapriacanthus ransonneti* the ventral area is narrow and the shape of the bone is elliptical. The shape of the sacculith in *Pempheris sasakii*, and *P. xanthoptera* is intermediate. The excisura (exc) is conspicuous in *Parapriacanthus ransonneti*, whereas in *Pempheris japonica* and *P. sasakii* this notch is very small.

NASAL, INFRAORBITALS, AND SUPRATEMPORALS (Fig. 6)

The **nasal** (ns) is loosely bound to the cranium by connective tissue. The whole bone is formed by the floor and side-walls of the anteriormost portion of the infraorbital canal. From the posterodorsal end of the nasal, the sensory canal enters the nasal opening of the supraorbital canal in the frontal, so that the supra- and infraorbital canals are continuous through the sensory canal on the nasal. One or two foramina are present on the floor of the bone transmitting the branches of the buccal branch of the facial nerve to the sensory canal. A bony flange along the posterior rim of the bone overhangs the sensory canal; another narrow flange arises from the anteroventral angle. These two

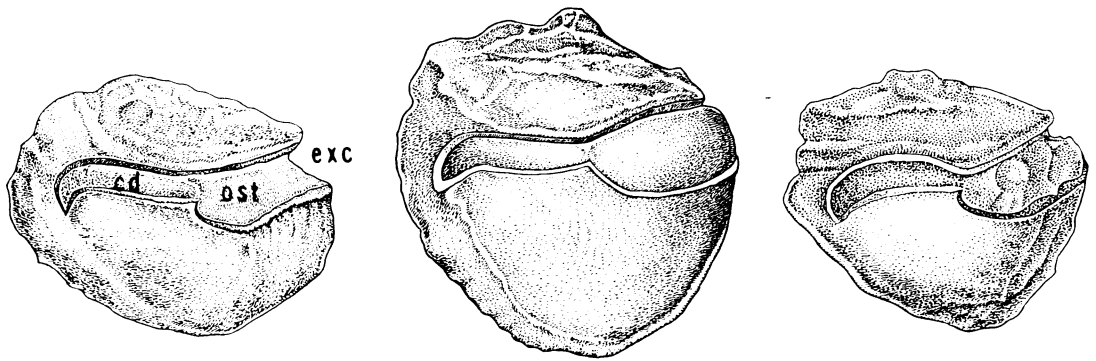
flanges are continuous and form a bridge over the sensory canal in *Pempheris xanthoptera*. A dorsoposterior expansion of the nasal covers the dorsoanterior half of the olfactory apparatus.

The **infraorbitals** (suborbitals of ichthyologists, see Weitzman, 1962 : 28) are six in number including the preorbital and dermosphenotic. The infraorbital sensory canal is in an open groove, and each of the infraorbitals bears a flange overhanging the groove. In *Pempheris moluca* and *P. xanthoptera* the distal ends of the flanges are deeply and complexly indented, especially in the third to sixth infraorbitals, whereas they are shallowly and sparsely indented in *Parapriacanthus ransonneti*, *Pempheris japonica*, *P. poeyi*, and *P. sasakii*. The foramina for the passages of the branches of the buccal branch of the facial nerve are present on each of the infraorbitals; more than four foramina on the first infraorbital, two on the third, and one or two on each of the others.

The first infraorbital (i1) (preorbital, lachrymal) is the longest of the infraorbitals but not wider than the second. The anterodorsal corner of the first infraorbital bears a thickened facet (ale) on its adaxial surface for the lateral ethmoid. The groove for the sensory canal is bridged anteriorly by two bony bars, but the posterior bar is often broken and represented by disjunct bony projections from the flange and from the floor of the bone. In *Pempheris japonica* the anterior bridge is present but there is no trace of the posterior one.

The second infraorbital (i2) is shorter than the first and third. It is not or scarcely overlain by the third, except in *Pempheris xanthoptera*.

The third infraorbital (i3) is the second longest of the series. The subocular shelf (ss) is present along the posterior half of its dorsal margin, and is well developed in *Pempheris japonica* and *P. moluca*, whereas it is small in *Parapriacanthus ransonneti* and *Pempheris xanthoptera*. The subocular shelf is absent in *Pempheris poeyi*. It is reported to be present in *Pempheris oualensis* and absent in *Pempheris schomburgki* (Smith and Bailey, 1962 : 8).

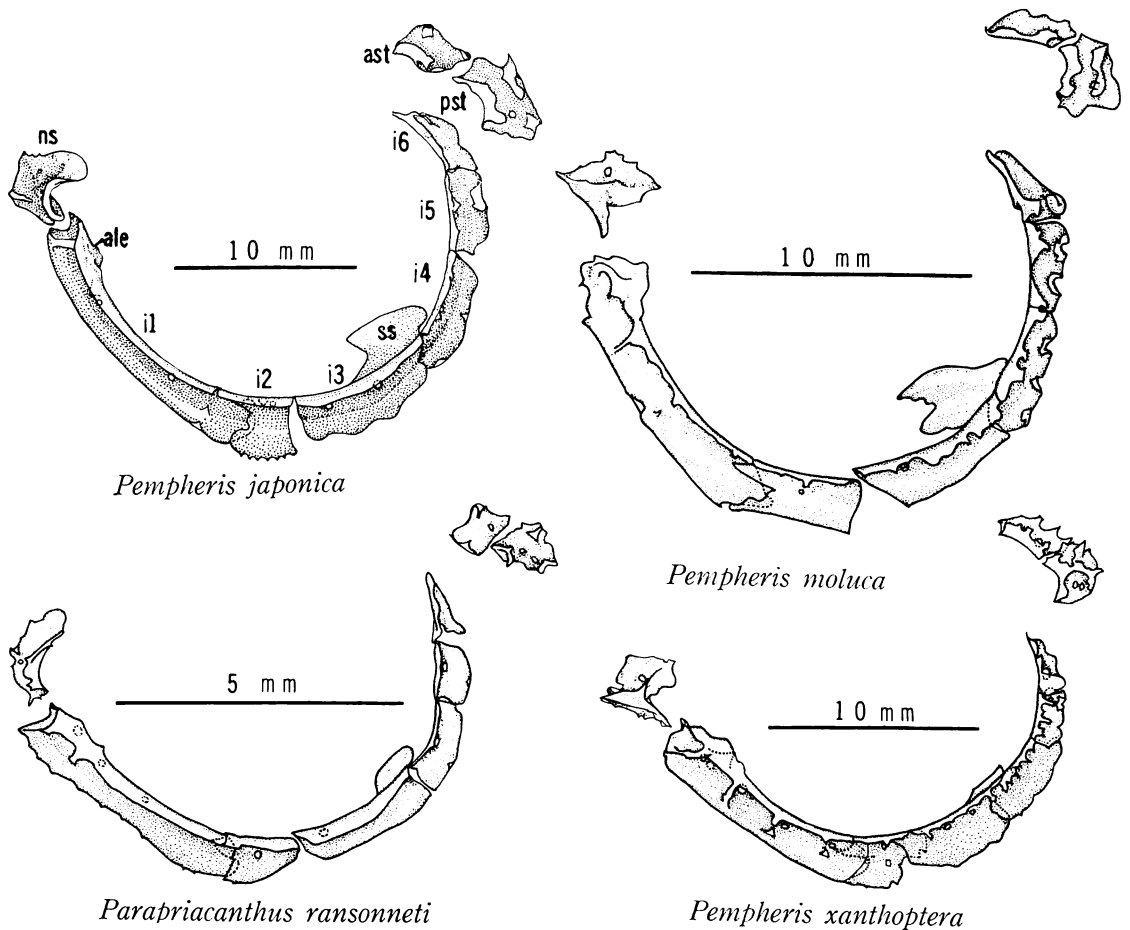


Parapriacanthus ransonneti

Pempheris japonica

Pempheris xanthoptera

Fig. 5. The sacculith of the Pempheridae. cd, cauda; exc, excisura; ost; ostium.



Pempheris japonica

Pempheris moluca

Parapriacanthus ransonneti

Pempheris xanthoptera

Fig. 6. The nasal, infraorbitals and supratemporals of the Pempheridae. ale, articulating surface for lateral ethmoid; ast, anterior element of supratemporals; i1~i6, infraorbitals; ns, nasal; pst, posterior element of supratemporals; ss, subocular shelf.

The fourth infraorbital (i4) is slightly shorter than the third. Its anterior end slightly overlaps the posterior margin of the third. One to three protuberances are present at the posterior rim of the bone in *Parapriacanthus ransonneti*, *Pempheris japonica*, *P. sasakii*, and *P. moluca*, whereas there are none in *Pempheris poeyi* and *P. xanthoptera*.

The fifth (i5) is shorter than the fourth. One or two bony eminences arise at the posterior edge of the bone.

The sixth (i6) (dermosphenotic) rests on the laterally projected process of the sphenotic and transmits the infraorbital sensory canal to the postorbital opening of the supraorbital canal. The floor of the bone tapers dorsally. A bony eminence is present at the posterior edge in *Pempheris poeyi*, *P. sasakii*, and *P. moluca*, whereas it is absent in *Parapriacanthus ransonneti*, *Pempheris japonica*, and *P. xanthoptera*.

There are anterior and posterior supratemporals. The **anterior supratemporal** (ast) bears a flange along its anteroventral edge overhanging the grooved sensory canal. In *Parapriacanthus ransonneti* and *Pempheris japonica* another small flange is present at the dorsal angle of the bone. The sensory canal from the temporal opening of the supraorbital canal passes through the bone and enters the posterior supratemporal. The bone has a foramen for the passage of the branch of the facial nerve.

The **posterior supratemporal** (pst) has three flanges. In *Pempheris xanthoptera* these flanges meet to form a bridge over the sensory canal. Two foramina for the branches of the facial nerve are present on the floor of the bone. On the posterior supratemporal, three sensory canals coming from different directions join: the anterodorsal canal from the anterior supratemporal, the posterior one from the posttemporal, and the ventral one from the postorbital commissure of the pterotic. There is no supratemporal commissure.

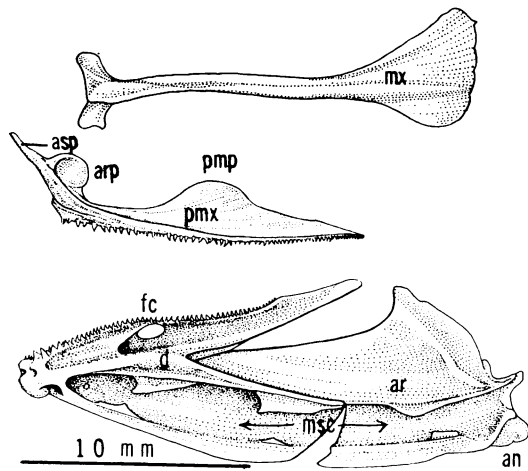
BONES OF THE UPPER AND LOWER JAWS (Fig. 7)

The upper jaw is protrusile, and composed of the premaxillary and maxillary. The

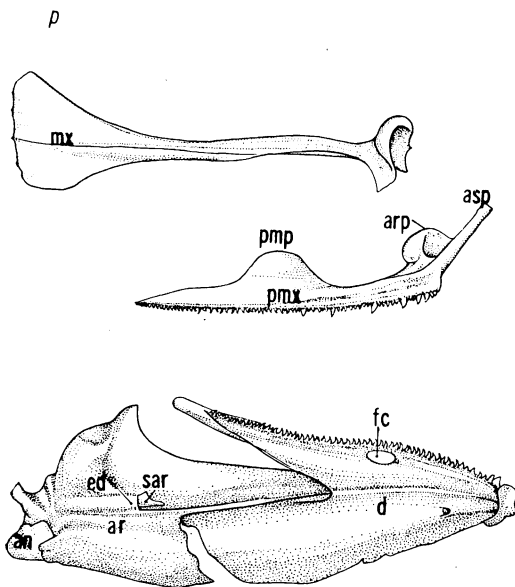
supramaxillary (supplemental maxillary) is absent.

The angle between the **premaxillary** (pmx) and its ascending process is about 60°. Three ligaments (the maxillary-premaxillary, palatine-premaxillary, and interpremaxillaries) meet in front of the ascending process of the premaxillary, but they are not so firmly bound to the process as to allow it to move up and down freely. The ascending process (asp) is well separated from the articular process (arp) by a notch. On the dorsal surface near the middle of the bone there is the postmaxillary process (pmp). The posterior end of the premaxillary is slightly anterior to that of the maxillary. Along its oral border the premaxillary is thickened and bears a **band** of teeth. The teeth of the hinder part are definitely smaller than the anterior ones. The teeth are arranged in a single row throughout and number about 90 in *Pempheris sasakii*; in double rows anteriorly and in a single row posteriorly and about 60 in *Pempheris poeyi*; in irregular double rows throughout and about 90 in *Parapriacanthus ransonneti*; in double or triple rows and far more than a hundred in *Pempheris japonica*, *P. moluca*, and *P. xanthoptera*. In *Parapriacanthus ransonneti* the teeth of the outer row are slightly larger than those of the inner row. Several anterior and external teeth are markedly large and stout in the specimens of *Pempheris japonica* and *P. moluca* more than 100 mm in standard length. However, in the smaller specimens, such modified teeth are absent.

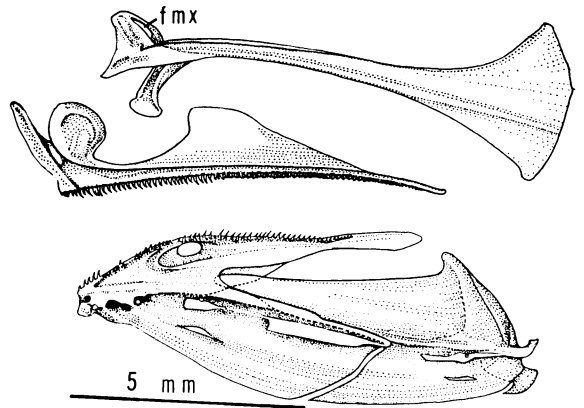
The **maxillary** (mx) has a facet on the anterior thickened head, on which the articular process of the premaxillary fits. The ethmoid-maxillary and maxillary-premaxillary ligaments originate from the external surface of the maxillary near the ventral edge of the facet for the premaxillary. Just behind the area where the ligaments attach, the first infraorbital and maxillary process of the palatine are attached to the maxillary. The head of the maxillary is hollow and being filled with cartilage, and a pit (fmx) leads to this space in *Parapriacanthus ransonneti*. The anterior half of the maxillary is covered entirely by the first infraorbital. The pos-



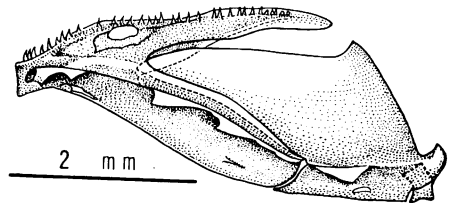
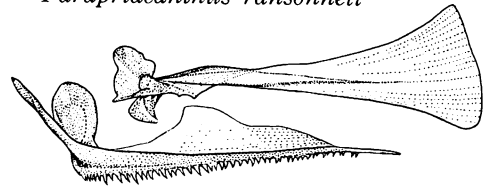
Pempheris japonica: abaxial view



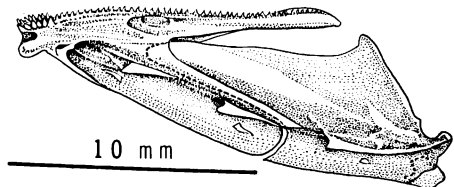
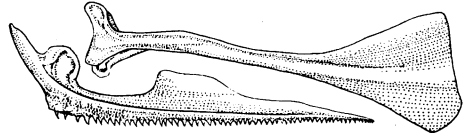
Pempheris japonica: adaxial view



Parapriacanthus ransonneti



Pempheris poeyi



Pempheris moluca

Fig. 7. The upper and lower jaws of the Pempheridae. an, angular; ar, articular; arp, articular process of premaxillary; asp, ascending process of premaxillary; d, dentary; ed, endosteal process; fc, foramen on coronoid process of dentary; fmx, foramen at the head of maxillary in *Parapriacanthus*; msc, mandibular sensory canal; mx, maxillary; pmp, postmaxillary process; pmx, premaxillary; sar, coronomeckelian.