



Fig. 17. The alimentary canal of the Pempheridae. Upper figures, left view; lower figures, right view. A figure showing winding pattern of *Pempheris japonica* is also presented. dl, luminous duct; es, esophagus; int, intestine; p4~p10, 4th to 10th pyloric caeca counted from left; st, stomach; spl, spleen.

deepening of the body below the level of the vertebral column; (2) shortening of the cephalic and abdominal regions; and (3) anterior displacement of the origin of the anal fin.

The various proportions of the body are different in the two species as the result of one, or of coordinate effects, of the above transformations. The following features are found in *Pempheris moluca*, and also in the majority of the compressed and deep-bodied teleosts: an expanded coracoid, long ribs and postcleithra, and long and stout first haemal spine and first pterygiophore of the anal fin. These modifications are obviously necessary to cope with the increased torsion in the deep-bodied forms. As the result of the third factor, there follow in *Pempheris moluca* a longer anal-fin base, an increased number of anal soft-rays, a backward-directed first pterygiophore of the anal fin, and a forward-directed first haemal spine.

Second, there are many marked differences between the two species which may be independent of the differences in the body forms, as shown in Table 5 (characters 4 to 21).

These differences between *Parapriacanthus ransonneti* and *Pempheris moluca* would be sufficient to segregate the family or even higher taxa in other groups of fishes. However, the common peculiarities in the dorsal fin and the exoccipital condyles, not or scarcely found elsewhere in fishes, indicate the actual close relationship between the two species. Further evidence to justify the inclusion of both species in a single family is the presence of transitional forms between them.

Pempheris analis is intermediate in all of the three essential transformations of the body form between *Parapriacanthus ransonneti* and *Pempheris moluca*. In *Pempheris analis*, the radiographed image of the shoulder girdle is like that of *Parapriacanthus*. The characters of *Pempheris analis* have not been studied by dissection of actual specimens, but only by external observations and radiographs. *Parapriacanthus unwini*, *P. elongatus*, and *P. argenteus* have a deeper body than is usual for the genus. When the internal morphology of these deep-bodied species of *Parapriacanthus* and *Pempheris analis* is known, it is

possible that the apparent differences between the two genera will become less distinct.

Pempheris klunzingeri, *P. compressa*, and *P. japonica* resemble *Pempheris moluca* in their body form, but their cephalic and abdominal regions are long, as compared with the latter species. They are similar to *Parapriacanthus* and *Pempheris analis* in the peculiarities of their scales. All these forms have strongly ctenoid scales which are divided into proximal and distal halves by an inflection. The pores for the passage of the sensory canal of the lateral line scales are wider than long in all the species in question. The scales on the sensory canal system of the head are irregularly and deeply notched from the proximal margin. In the remaining species of *Pempheris*, the scales are modified otherwise (Table 5, characters 10 and 11).

One of the outstanding features of *Parapriacanthus* is the presence of a luminescent organ system. However, the presence of such an organ system is not the peculiarity of *Parapriacanthus* only, because *Pempheris klunzingeri* is, and *Pempheris analis* may be, a luminescent fish. The characters of *Parapriacanthus* which interrelate with the presence of the luminescent organ system are the modifications of the shoulder girdle, pyloric caeca, and, probably, urohyal. The luminescent species of *Pempheris* are expected to share some or all of these characters with *Parapriacanthus*.

Among the forms studied by dissection of actual specimens, *Parapriacanthus ransonneti* and *Pempheris japonica* share the following characters, in which they differ from *Pempheris poeyi*, *P. sasakii*, *P. moluca*, and *P. xanthoptera*: (1) The wing of the frontal which marks the anterior end of the brain cavity is low. (2) The anterior end of the supraoccipital is posterior to the anterior end of the temporal opening. (3) The postorbital commissure is long and runs obliquely downward. (4) No slit connects the posttemporal groove with the dilatator groove. (5) The subpelvic keel is longer and extends more anteriorly than the accessory subpelvic keel. (6) The pyloric caeca are ten in number.

Parapriacanthus ransonneti shares rather

many characters with *Pempheris japonica* than *Pempheris japonica* does with *Pempheris moluca*.

MUTUAL RELATIONSHIPS OF THE SPECIES OF THE PEMPHERIDAE

The genus *Pempheris* is tentatively subdivided herewith into the following seven groups of species. The genus *Pempheris* as defined in this paper may comprise too diverse forms, and some of the genera, which have been considered to be synonymous with *Pempheris*, may deserve full generic rank. I feel it premature, however, to revive some of these generic synonyms or to apply new formal taxonomic names to these groups of species, until a thorough revisional study on a world-wide basis is completed.

Key to the genera and groups of species of the family Pempheridae, based on the external characters

- 1. Anal fin scaleless; lateral line not extending to hinder margin of caudal fin..... *Parapriacanthus*
- 1'. Anal fin scaled; lateral line extending to hinder margin of caudal fin..... *Pempheris* 2
- 2. Each of scales divided into distal and basal halves by transverse inflection. 3
- 3. Origin of anal fin posterior to end of dorsal fin. *analis*-group
- 3'. Origin of anal fin below or anterior to end of dorsal fin..... *japonica*-group
- 2'. Each of scales not divided into distal and basal halves by transverse inflection. 4
- 4. Ventral median line behind anteroventral end of cleithrum not keeled. *multiradiata*-group
- 4'. Ventral median line behind anteroventral end of cleithrum keeled. 5
- 5. Less than 30 anal soft-rays... *poeyi*-group
- 5'. More than 30 anal soft-rays... 6
- 6. Scales in lateral line to caudal base more than 67; concealed scales absent or

less than 2 under each surface scale.

..... *sasakii*-group

- 6'. Scales in lateral line to caudal base less than 65; concealed scales more than 5 under each surface scale 7

7. Dorsal spines 5. *mexicana*-group

7'. Dorsal spines usually 6, very rarely 5..... *moluca*-group

Species of *Pempheris* which have not been accessible to me and have therefore been only tentatively affiliated with a certain group of species are not included in Table 4, they are dealt with below in the discussion of each of the groups of species. Characters which are useful for comparison and segregation of genera and groups of species are presented in Table 5.

The differences between *Parapriacanthus* and *Pempheris* are found in the anal fin and the lateral line (Table 5, characters 3 and 4). Two radiographed species of *Parapriacanthus ransonneti* and *P. dispar* differ in the number of dorsal pterygiophores between the ninth and 11th neural spines from all the radiographed species of *Pempheris*.

Among the species which were studied by dissection of actual specimens, *Parapriacanthus ransonneti* differs from the five species of *Pempheris* in the following characters, in addition to the characters 7 and 8 (Table 5): (1) A foramen is present on the articular head of the maxillary. (2) The posteroventral margin of the fourth radial of the pectoral fin is in contact with, and supported by, the posterior process of the coracoid. (3) The fifth and sixth pyloric caeca counted from the left are connected with the luminescent organ system.

As discussed above, the *analis*-group is intermediate between *Parapriacanthus* and the *japonica*-group. Like *Pempheris klunzingeri*, which belongs to the *japonica*-group, *P. analis* has a pigmented area between the pelvic fins and anus. The study of the internal morphology of *P. analis*, especially the structure of the luminescent organ system, is desirable.

Table 4. Subdivisions of the family Pempheridae.

| Genera and groups of species | Species examined* | Comparison of groups of species proposed by Tominaga (1963) |
|------------------------------|--|---|
| <i>Parapriacanthus</i> | <i>ransonneti</i> , <i>dispar</i> | |
| <i>Pempheris</i> | | |
| <i> analis</i> -group | <i> analis</i> | constituent of group A |
| <i> japonica</i> -group | <i> klunzingeri</i> , <i> compressa</i> , <i> japonica</i> ** | constituent of group A |
| <i> multiradiata</i> -group | <i> multiradiata</i> *** | affiliated with group C, but lacking several diagnostic characters of the group |
| <i> poeyi</i> -group | <i> poeyi</i> | |
| <i> mexicana</i> -group | <i> mexicana</i> , <i> muelleri</i> **** | |
| <i> sasakii</i> -group | <i> nyctereutes</i> , <i> sasakii</i> | equivalent to group B |
| <i> moluca</i> -group | <i> oualensis</i> , <i> otaitensis</i> , <i> moluca</i> , <i> mala-barica</i> , <i> vanicolensis</i> , <i> nesogallica</i> , <i> itoi</i> , <i> schwenkii</i> , <i> xanthoptera</i> | equivalent to group C |

* The species examined by dissection of actual specimens are indicated by bold-faced type.

** *Catalufa umbra* Snyder, type species of *Catalufa* Snyder, 1911, is synonymous with *Pempheris japonica*.

*** Type species of *Liopempheris* Ogilby, 1913.

**** Type species of *Priacanthopsis* Fowler, 1906.

The *japonica*-group provides, on the other hand, a link between the *analis*-group and the remaining groups of species of *Pempheris*. The species of the *japonica*-group have a higher number of dorsal pterygiophores (=spines+soft-rays, Table 3). In this group, *P. klunzingeri* is the closest to *Parapriacanthus* and the *analis*-group in having fewer dorsal fin spines and a paucity of the brownish and blackish pigment cells on the body, as well as in having a luminescent organ system.

The following are the characters of *Pempheris japonica* which are unique among the dissected forms of the Pempheridae: (1) The prevomerine teeth are arranged in double rows. (2) The lateral margins of the lateral ethmoid and of the wings of the pterotic are convex. (3) The sacculus chamber and sacculith are the deepest. (4) A foramen is present on the median septum of the basi-occipital. (5) The parasphenoid ends posteriorly in a single sharp process.

The *multiradiata*-group resembles the *japonica*-group in the characters of the shoulder girdle (Table 5, characters 15 to 17). In having a large number of dorsal soft-rays and a small number of anal soft-rays, *P. multiradiata* resembles *P. japonica* and *P.*

compressa of the *japonica*-group. On the other hand, *P. multiradiata* lacks the characters of the scales peculiar to *Parapriacanthus* and the *analis*- and *japonica*-groups. In having numerous concealed scales, *P. multiradiata* resembles the groups of species below it in Table 4. The radiographed image of the shoulder girdle and the presence of a pigmented area between the pelvic fins and anus suggest the possibility that this species is a luminescent fish (Tominaga, 1963 : 276). The presence or absence of the luminescent organ system in this species must be determined by dissection. *P. multiradiata* is unique among the Pempheridae in having the first pterygiophore of the anal fin inserted posterior to the first haemal spine.

The following four groups of species are distinguished from the preceding ones by the characters of the shoulder girdle (Table 5, characters 15 to 17).

The *poeyi*-group is characterized by a short anal fin, which has fewer than 30 soft-rays (Table 3). In addition to the characters of the anal fin, *Pempheris poeyi* and *Parapriacanthus* resemble each other in their small number of dorsal spines, their longer cephalic and abdominal regions, in having fewer teeth

in both jaws and on the palatine, and in the low and blunt bony processes overhanging the sensory canal system of the head. The pyloric caeca of *Pempheris poeyi* are nine in number like those of the *sasakii*- and *moluca*-groups. The subocular shelf is absent in this species.

Pempheris poeyi has the following peculiarities which are not found in any other of the species examined by dissection of actual specimens: segmented predorsal rayless pterygiophores, the absence of an air bladder, the absence of modified abdominal vertebrae, and a blunt and short hypuropophysis. The presence in this species of a segment near the proximal end of each of the predorsal rayless pterygiophores is an outstanding feature, which may not have been reported in the other Acanthopterygii, and may provide an important key to elucidate the origin and nature of these bones. Although the dissected specimen of *P. poeyi* is only 26 mm in standard length, this unexpected feature cannot be regarded as a juvenile character, because the specimen of *P. xanthoptera* of similar size lack this feature.

In the following three groups of species the cephalic and abdominal regions are more shortended in proportion to the caudal region than in the preceding four groups (Table 5, character 18).

The *mexicana*-group have the characters of the lateral line and dorsal pterygiophores in common only with the *poeyi*-group (Table 5, characters 24 and 26). This group has only five dorsal spines. Although Cuvier (1831: 308) reported that the holotype of *Pempheris mexicana* had six dorsal spines, the radiograph of Cuvier's holotype clearly shows that there are only five spines. Because the *mexicana*-group seems to be closely allied to the *poeyi*-group, examination of the character of the predorsal rayless pterygiophores of this group is highly desirable.

The *sasakii*-group resembles the *moluca*-group but is distinguishable from the latter in having more numerous pored scales in the lateral line, relatively few concealed scales, few and large teeth in both jaws, and on the prevomer, palatine, and pharyngeals. Moreover, *P. sasakii* differs from the *moluca*-group in the absence of the three peculiarities of

the latter group enumerated below. *P. sasakii* is closely allied to, or conspecific with, *P. nyctereutes*.

The *moluca*-group shares the fewest characters with *Parapriacanthus*. The bony processes overhanging the sensory canal system of the head have a complicated shape in this group. *P. moluca* and *P. xanthoptera*, both of which belong to this group and were examined by dissection of actual specimens, possess characteristics of the dentary, gill rakers, and air bladder (Table 5, characters 19 to 21), which are common to each other but different from the remaining species of *Pempheris* studied by dissection of actual specimens. The *moluca*-group is the largest of the seven groups of species of *Pempheris*. *P. affinis* Ogilby and *P. rhomboidea* Kossman and Räuber seem to belong to this group.

Family Pempheridae

Type genus: *Pempheris* Cuvier, 1829.

Genera:

Pempheris Cuvier, 1829 (generic synonyms: *Priacanthopsis* Fowler, 1906; *Catalufa* Snyder, 1911; *Liopempheris* Ogilby, 1913)

Parapriacanthus Steindachner, 1870 (generic synonyms: *Pempherichthys* Klunzinger, 1871; *Parapempheris* Bonde, 1922).

Rejected genera:

Leptobrama Steindachner 1878 (generic synonym: *Neopempheris* Macleay, 1880).

Bathyclupea Alcock 1891.

Schuettea Steindachner, 1866 (generic synonym: *Bramichthys* Waite, 1905).

EXTERNAL CHARACTERS

D. IV~VII, 7~12; A. (II)~III, 17~45; P₁ ii, 14~17; P₂. I, 5 (i, 5 in some specimens of *Parapriacanthus ransonneti*); branched caudal fin-rays 8+7; pored scales in lateral line to caudal base 35~80.

Perciformes less than 300 mm in standard length; body compressed; eye large; nostrils two; mouth oblique; upper jaw protrusile; gill membrane free from isthmus; opercular bones thin along their posterior and ventral margins, and without spines and stout bony projection; dorsal premedian, single and much

Table 5. Comparison of the diagnostic characters

| Character | <i>Parapriacanthus</i> | | |
|--|------------------------|-----------------------------|---|
| | | <i>analis</i> -group | <i>japonica</i> -group |
| 1. Dorsal fin | IV-VI, 7-12 | VI, 9 | V-VII, 10-12 |
| 2. Anal fin | (II)-III, 17-27 | III, 31-34 | III, 30-39 |
| 3. Lateral line scales to caudal base | 59-80 | 67-70 | 59-82 |
| 4. Scales on anal fin | absent | present | present |
| 5. Lateral line scales extending to | middle of caudal fin | hinder margin of caudal fin | hinder margin of caudal fin |
| 6. Pterygiophores between 1st and 2nd haemal spine | 2-3 | 4 | 7 |
| 7. Fenestra on ceratohyal | absent | ? | present |
| 8. Lateroposterior bony processes of urohyal | present | ? | absent |
| 9. 1st pterygiophore of anal fin directing to | origin of dorsal | origin of dorsal | end of dorsal |
| 10. Surface scales | with inflection | with inflection | with inflection |
| 11. Concealed scales | absent | ? few | few |
| 12. Luminescent organ | present | ? present | present (<i>klunzingeri</i>) or absent |
| 13. Pigmented area between pelvic fins and anus | single bar | Y-shaped | Y-shaped (<i>klunzingeri</i>) or absent |
| 14. Pyloric caeca | 10 | ? | 10 |
| 15. Posterior expansion of coracoid | none | none | slight |
| 16. Ventral fenestra between coracoid and cleithrum | large | large | large |
| 17. Ventral fenestra between coracoid and cleithrum opens across | horizontal plane | ? horizontal plane | vertical plane |
| 18. Average length of anterior 12 caudal vertebrae in that of posterior 6 abdominal ones | 1.02 | 1.23-1.28 | 1.11-1.33 |
| 19. Air bladder | simple | simple | simple |
| 20. Intervenient small gill rakers | absent | ? | absent |
| 21. Fenestra below tooth-band of dentary | present | ? | present |
| 22. Subocular shelf | present | ? | present |
| 23. Modified abdominal vertebrae | present | present | present |
| 24. Pterygiophores between 3rd and 4th neural spines | 2 | 2 | 2 |
| 25. 1st pterygiophore of anal fin | straight | straight | bent backward |
| 26. Distance between lateral line and dorsal contour | large | large | large |
| 27. 1st and 2nd hypurals, and 3rd and 4th ones counted from below | fused together | separate | separate |

TOMINAGA: Morphology and Relationships of Pempheridae

of the genera and groups of species of the Pempheridae.

| <i>Pempheris</i> | | | | |
|-----------------------------|-----------------------------|-----------------------------|--|-----------------------------|
| <i>multiradiata</i> -group | <i>pozysi</i> -group | <i>sasakii</i> -group | <i>mexicana</i> -group | <i>moluca</i> -group |
| V, 12 | IV, 8 | VI, 9-10 | V, 9 | V-VI, 8-10 |
| III, 35-37 | III, 23-24 | III, 41-45 | III, 33-35 | III, 34-45 |
| 49 | 56 | 67-80 | 56-60 | 44-67 |
| present | present | present | present | present |
| hinder margin of caudal fin | hinder margin of caudal fin | hinder margin of caudal fin | hinder margin of caudal fin | hinder margin of caudal fin |
| 4* | 4 | 7 | 6 | 5-8 |
| ? | present | present | ? | present |
| ? | absent | absent | ? | absent |
| middle of dorsal | middle of dorsal | end of dorsal | end of dorsal | end of dorsal |
| without inflection | without inflection | without inflection | without inflection | without inflection |
| numerous | numerous | few | ? numerous | numerous |
| ? | absent | absent | absent | absent |
| single bar | absent | absent | ? absent | absent |
| ? | 9 | 9 | ? | 9 |
| slight | enormous | enormous | enormous | enormous |
| large | very small | small | small | small |
| ? horizontal plane | vertical plane | vertical plane | vertical plane | vertical plane |
| 1.27 | 1.10-1.11 | 1.48 | 1.41-1.54 | 1.31-1.53 |
| simple | absent | simple | ? | constricted |
| ? | absent | absent | ? | present |
| ? | present | present | ? | absent |
| ? | absent | present | absent at least in <i>schomburgkii</i> | present |
| present | absent | present | present | present |
| 2 | 1 | 2 | 1 | 2 |
| straight | bent forward | straight | straight | straight or bent backward |
| large | small | large | small | large |
| separate | separate | separate | fused together | separate |

* See first foot-note on p. 75.

shorter than anal; dorsal spines graduated; end of dorsal near origin of anal; pelvic thoracic; axillary process of pelvic present, often indistinct; anus and genital pore just in front of anal; anal scaled or naked; scales ctenoid or cycloid, modified variously.

INTERNAL CHARACTERS

Prevomere toothed. Supraoccipital crest well developed; epaxial trunk muscle extending in supratemporal groove near anterior end of frontal. Sphenotic projecting laterally as a stout triangular process. Exposed surface of sphenotic in posttemporal groove. Anterior opening of brain cavity constricted, but not divided into two by wings of pterosphenoids. Orbitosphenoid absent. Myodome closed posteriorly. Posterior end of parasphenoid far anterior to posterior end of basioccipital. Separate foramen for hyomandibular trunk of facial nerve absent in pars jugularis of trigemino-facialis chamber. Sacculus chamber and sacculith very large. Intercalar situated ventrally; lower limb of posttemporal inserted on ventral side of cranium. Exoccipital condyles broadly in contact with each other and peculiar in that they expand laterodorsally. Foramen magnum high and rhomboidal. Baudelot's ligament originating from basioccipital. Lateral line system of head well developed; supraorbital canal in bony tube; other canals in open grooves. Supraorbital commissure present; supratemporal commissure absent. Infraorbital sensory canal continuous with supraorbital canal through nasal. Infraorbitals 6; 1st infraorbital longest of series but not deeper than the succeeding ones. Subocular shelf present or absent in 3rd infraorbital. Supramaxillary absent. Teeth on premaxillary, dentary, and palatine. Ecto- and endopterygoid toothless. Spines on flange of preopercle overhanging sensory canal. Opercular bones without stout spines or processes along their hinder or ventral margins. Ceratohyal with or without a foramen. Branchiostegals 7; 5 from ceratohyal and 2 from epihyal. Narrow and short gill slit behind 4th branchial arch. Pseudobranchiae present. Basihyal toothless. Third epibranchial with a small tooth-plate. Pharyngeals separate. Lower pharyngeal and 2nd to 4th upper pharyngeals toothed.

Scapular foramen present. Two fenestrae present between cleithrum and coracoid. Coracoid highly variable. Pectoral radials 4; postcleithra 2. Pelvic girdle depressed, joined to cleithrum by cartilage; with suprapelvic, subpelvic, and accessory subpelvic keels, and postpelvic and subpelvic processes.

Vertebrae 10+15 including urostylar vertebra. Parapophyses appear from 3rd vertebra. Floors of haemapophyses of some abdominal vertebrae expand to form a continuous bony tube investing haemal canal, except in *Pempheris poeyi*. Neural pre- and postzygapophyses more or less developed; haemal pre- and postzygapophyses absent or vestigial in caudal vertebrae. First neural spine not ankylosed with centrum. Last three haemal spines not ankylosed with centra. Ribs 8 on either side, attaching to 3rd to 10th vertebrae. Predorsal rayless pterygiophores 3. Pterygiophores of dorsal fin 13 to 17. Pterygiophores of anal fin 19 to 46. Epurals 3, uroneurals 1 or 2. Hypurals 5; sometimes 1st counted from below fused with 2nd, and 3rd with 4th.

Air bladder simple or constricted at middle; absent in *Pempheris poeyi*. Pyloric caeca 9 or 10. Luminescent organ system present in *Parapriacanthus ransonneti*, *P. unwini*, *P. elongatus*, *Pempheris klunzingeri*, and possibly in *P. analis*.

Comparison of the Pempheridae with Other Forms

BERYCIFORMES, WITH SPECIAL REFERENCE TO *BERYX*

Characters which distinguish the Beryciformes from the Perciformes are the retention of the orbitosphenoid, and the presence of more than 15 branched rays in the caudal fin (Starks, 1904; Regan, 1911). However, Gosline (1960) pointed out that in the perciform *Pseudogramma*, *Plesiops*, and *Grammistes*, the caudal fin has more than 15 branched rays. In the Beryciformes the pelvic fin generally has more than five soft-rays except for the Monocentridae (I, 3), and the Caristiidae and Anomalopidae (I, 5) (Regan, 1912; Weber and Beaufort, 1929). Since the family Pempheridae has a spine and five soft-rays in the pelvic fin and 15 branched rays in the caudal, and

has not retained the orbitosphenoid, it cannot be assigned to the Beryciformes.

The genus *Beryx* and the Pempheridae can be distinguished from each other not only by these essential differences, but in many other ways. A pair of prominent anterior projections of the mesethmoid over the prevomer are present in *Beryx**, whereas there is no trace of such projections in the Pempheridae. Two supramaxillaries are present (Regan, 1911) (Starks, 1904 : 609, reported only a single supramaxillary), and a separate foramen for the passage of the hyomandibular trunk of the facial nerve is present in the trigemino-facials chamber in *Beryx* (cf. Günther, 1887: pl. 6), whereas these are absent in the Pempheridae. The pelvic girdle is much higher than broad in *Beryx* (Starks, 1904; also in *Myripristis* and *Holocentrus*, Günther, 1859 : 24 and 38; Gregory, 1933 : 235 and 236), whereas it is broader than high in the Pempheridae. The vertebrae number 10+14 in *Beryx* (Günther, 1887: pl. 6; Boulenger, 1902: 202; Hotta, 1962), and 11+17 in *Myripristis* (Agassiz, 1834: Tab. B, Fig. 1), whereas there are 10+15 in the Pempheridae. The number of branchiostegals is often more than seven in *Beryx* (Agassiz, 1839 : 114; Günther, 1887: 32; Starks, 1904; Abe, 1959), and in *Holocentrus* and *Myripristis* (Agassiz, 1836:106; 1839:110), whereas it is always seven in the Pempheridae. As Starks pointed out, a concave face of the condyle is formed by the exoccipitals in addition to the basioccipital in *Beryx*, whereas in the Pempheridae the face of the exoccipital condyles are not concave and are independent of the face formed by the basioccipital alone. The first vertebra is convex anteriorly to fit the occipital condyle in *Beryx*, whereas it is anteriorly concave in the Pempheridae as in the other Perciformes. However, the exoccipital condyles are broadly joined with each other in the Pempheridae, and in this regard the Pempheridae are nearer to *Beryx* than to the specialized Perciformes, in which the exoccipital condyles are barely joined with each other.

Although *Beryx* differs in many ways from the Pempheridae, the two forms have

* Starks (1904) erroneously considered these two projections as belonging to the frontals.

in common several peculiar characters. In addition to the similarities in the general body shape, the structure of the dorsal fin is almost the same in the two forms. There are three rayless pterygiophores, and there are no pterygiophores behind the 13th neural spine (of the third caudal vertebrae). The only difference in the structure of the dorsal fin is that its first pterygiophore is inserted, together with the third rayless pterygiophore, between the second and third neural spines in the Pempheridae, whereas it is inserted between the third and fourth neural spine in *Beryx*.

The sensory canal system of the head is well developed in both families, but the frontal is cavernous and the epaxial trunk muscles do not extend anteriorly over the frontal in *Beryx*. The sacculus chamber is very much dilated in both families, and the myodome does not open to the exterior posteriorly. The lateral line extends to the hinder margin of the caudal fin in both *Beryx* and *Pempheris*. The scales of *Beryx* and *Diretmus* (Matsubara, 1954), are similar to those of *Parapriacanthus*, as well as the *analisis-* and *japonica-*groups of *Pempheris* in that they are divided into distal and proximal parts by a transverse inflection. The Anomalopidae approach the Perciforms in having a spine and five soft-rays in the pelvic fin. In this family, *Photoblepharon* is similar to the Pempheridae in having a single short dorsal fin with graduated spines. The number of vertebrae is 13+16 in *Photoblepharon*, and 14+15~16 in *Anomalops*. For further discussion on relationships between the Beryciformes and Pempheridae see below on p. 88.

KURTIDAE

Although the presence of the orbitosphenoid in *Kurtus* was pointed out years ago by Beaufort (1914), little attention has been paid to this important fact. Even Beaufort (1951: 82) himself noted: "what I thought was an orbitosphenoid is only the ossified interorbital membrane, and I agree with Tate Regan that the Kurtoidei can be given the rank of a suborder among the Percomorphi." He obviously intended to deny the homology of "the ossified interorbital membrane of *Kurtus*" with the orbitosphenoid. In the cranium of *Kurtus*

indicus which I observed, the bone in question is quite well stained with alizarin red, and I find no reason to deny its homology with the orbitosphenoid of *Beryx*. The bone in *Kurtus* is not only the ossified interorbital membrane but also has laterally expanded wings under the frontals.

Like the Berycidae and unlike the Pempheridae, *Kurtus* has a compressed pelvic girdle and 10+14 vertebrae. The exoccipital condyles of *Kurtus* approach those of the Beryciformes in that their lateral rims are raised to form a continuous hollow space together with the condyle of the basioccipital. *Kurtus* has the pelvic fin with a spine and five soft-rays, as in the typical Perciformes. As to the caudal fin, Beaufort (1914) wrote, "Caudale mit 17 geteilten Strahlen." Gosline (1968: 15) has reported 14 or 15 branched rays in *Kurtus indicus*, and also in a specimen of *K. indicus* at hand, there are 15. If Beaufort's count was exactly made, the genus *Kurtus* has either 14, 15, or 17 branched caudal-rays. Most of the Perciformes possess 15 or fewer branched rays in the caudal fin.

Kurtus is similar to the Pempheridae in having seven branchiostegals, and lacking supramaxillaries. The genus differs from both the Pempheridae and Berycidae by the presence of modified ribs enclosing the air

bladder, small eyes, numerous anal pterygiophores in front of the first haemal spine, a modified caudal fin support, and a modified supraoccipital crest in the males. I can add the following to the characteristics of *Kurtus* reported by Beaufort (1914):

1. The myodome does not open to the exterior posteriorly.
2. Contrary to Beaufort's description, the basisphenoid is present; as Beaufort reported and contrary to Boulenger (1904: 687), the scapula is present.
3. There is no separate foramen for the hyomandibular trunk of the facial nerve in the wall of the pars jugularis of the trigemino-facialis chamber.
4. The neural spine of the penultimate vertebra is developed normally, and the three epurals are inserted posterior to it.

As Cuvier (1831: 296), Starks (1904) and Beaufort (1914) pointed out, *Beryx*, *Kurtus*, and *Pempheris* cannot be regarded as closely related to each other. Of course neither *Beryx* nor *Kurtus* can be the direct ancestor of the Pempheridae, because these two genera possess too many unique characters of their own. In view of the evolutionary pathway from the typical Beryciformes to the typical Perciformes, however, the fact that gradual changes of the characters are found in these forms

Table 6. Comparison of the characters of *Beryx*, *Kurtus*, and *Pempheris*, showing a possible evolutionary pathway.

| | BERYCIFORM CHARACTERS | | |
|---|---------------------------------------|--------------------------|-----------------------------|
| Orbitosphenoid | present | present | absent |
| Exoccipital condyles | with raised lateral rims | with raised lateral rims | without raised lateral rims |
| Pelvic girdle | compressed | compressed | depressed |
| Branched caudal fin-rays | 9+8 | ? 9+8 | 8+7 |
| Articulating condyle of 1st vertebra to cranium | convex | 8+7, or 14 in total | concave |
| Pelvic fin | I, 9~10 | concave | concave |
| | | I, 5 | I, 5 |
| | | PERCIFORM CHARACTERS | |
| ctenothrissiform ancestors | beryciform ancestors | intermediate | perciform ancestors |
| | specializations | of | their own |
| | <i>Beryx</i> | <i>Kurtus</i> | <i>Pempheris</i> |
| | all with a premedian short dorsal fin | | |

with the single short dorsal fin, is very suggestive.

Patterson (1964:472) postulated polyphyletic origins for the Perciformes, and proposed the probable lines from the six beryciform families to the families of the perciform level. Gosline (1966b) objected to Patterson's hypothesis of polyphyletic origins, and criticized the pertinence of several of his lines. One seemingly fairly cogent possibility, besides those of Patterson, is that the evolution of the Perciformes from the Beryciformes occurred in the forms with the single short dorsal fin (Table 6).

SERRANID FORMS

The genera *Acropoma*, *Doederleinia*, *Synagrops*, *Neoscombrops*, and *Malakichthys* were affiliated with the three subfamilies of the Serranidae (Acropominae, Doederleininae, and Malakichthyinae) by Katayama (1959), and with an oceanic group of the Percichthyidae by Gosline (1966a). Katayama (1959: 173 and 178) wrote that these genera are the most undifferentiated representatives of the serranids, and that they bear resemblance to the berycoids in many points. Gosline (1966a) considered that the family Percichthyidae is one of the basal or lower percoid families, and that it is less specialized than the Serranidae restricted by him.

I am much inclined to regard these five genera as comprising a compact, homogeneous group, and to have a close affinity with the Pempheridae. Comparison of Katayama's account with the result of my investigation of the Pempheridae reveals that there are many common characters shared by the Pempheridae and these serranid genera.

1. The exoccipital condyles are broadly united with each other.
2. The myodome does not open to the exterior posteriorly.
3. The subocular shelf, if present, extends only from the third infraorbital.
4. The sensory canal system of the head is fairly well developed.
5. The number of vertebrae is invariably 10+15, including the urostylar vertebra.
6. Only 1/2 or 1 radial of the pectoral fin articulates with the coracoid.
7. The predorsal rayless pterygiophores number three and the third is inserted

together with the first pterygiophore of the dorsal fin between the second and third neural spines.

8. The crania of *Acropoma*, *Malakichthys* and *Doederleinia* illustrated by Katayama (1959: fig. 15) are similar in general appearance to those of the Pempheridae.

In most of the above characters wherein these five genera is similar to the Pempheridae, they differ from other members of the Percichthyidae and the Serranidae (sensu Gosline, 1966a).

On the other hand, these genera conflict with the Pempheridae in having a well-developed supramaxillary and an opercular spine. The dorsal and anal fin-ray formulae are also markedly different.

The presence of a luminescent organ system in both *Acropoma* and *Parapriacanthus* is not the evidence to indicate their affinity, because in *Acropoma* symbiotic bacteria are the source of the luminescence, whereas in *Parapriacanthus* a luciferin-luciferase system, which cross-reacts with that of the crustacean *Cypridina*, is present. The anterior position of the anus in *Acropoma japonicum* does not indicate that this form is very aberrant, because the congeneric species, *A. hanedai*, has the anus situated almost normally. In *Doederleinia* and *Synagrops*, the air bladder has a pair of anterior projections and the cranium has a pair of basioccipital fossae to accommodate them. In *Acropoma* and *Malakichthys*, the air bladder enters the first pterygiophore of the anal fin. Such types of modifications of the air bladder are found in none of the pempherids. In *Synagrops* the pterosphenoid meets with its counterpart and the anal spines are two.

SCIAENIDAE AND APOGONIDAE

In having a greatly inflated sacculus chamber, a well-developed sacculith, and exoccipital condyles which are broadly in contact with each other, the Sciaenidae and Apogonidae are similar to the Pempheridae. The sensory canal system of the head is well developed in the Sciaenidae, Apogonidae, and Pempheridae, but the roof of the supraorbital canal is absent and the epaxial trunk muscles do not extend anteriorly over the frontals in the former two families. In having a short anal fin with two

or less spines, the Sciaenidae and Apogonidae resemble each other but differ from the Pempheridae.

In most species of Sciaenidae the lateral line extends to the hinder margin of the caudal fin; in this regard the family is similar to *Pempheris*. The haemapophyses of the several abdominal vertebrae expand to form a continuous plate below the centra in the sciaenid genera, *Pseudosciaena*, *Nibeia*, and *Argyrosomus* (Hotta, 1961 : 61; Takahashi, 1962 : 23 and 24, figs. 10 and 11). Such modification of the vertebrae is, to my knowledge, found only in the Sciaenidae and Pempheridae. The basic number of the vertebrae seems to be 10+15 in the Sciaenidae; more than 25 are frequently found, but rarely 10+14 (Agassiz, 1837: Tab. K; Günther, 1860 : 256 to 318; Clothier, 1950: 55 to 57; Hotta, 1961 : 61 and 62; Takahashi, 1962 : 23 and 24). The basic number is the same as that of the Pempheridae.

The Pempheridae are similar to the genus *Apogon* in the peculiarity pointed out by Gosline (1966 a); i.e., the intercalar is included in the convex wall of the greatly inflated auditory bulla, hence the lower limb of the posttemporal is attached to the bulla wall. The number of vertebrae is 24 or 25 (10+14, 11+14, 9+16) in the species of *Apogon* (Cuvier, 1828:150; Agassiz, 1836:64; Günther, 1859:231 to 240; Hotta, 1961; Takahashi, 1962), and 10+14 or 10+15 in those of *Siphamia* (Smith, 1955; Tominaga, 1964).

Apogon ellioti is luminescent fish, and it is highly probable that the luciferin of this form is identical with that of *Parapriacanthus ransonneti* and the crustacean *Cypridina* (Haneda et al., 1958, 1959; Johnson et al., 1960, 1961; Sie et al., 1961). Tsuji and Haneda (1966) demonstrated that the luciferase of *Apogon ellioti* is immunologically different from that of *Cypridina*. The two fishes of different families may independently exploit the luciferin of *Cypridina* taken as food as the source of luminescence (Haneda et al., 1966). In the case of *Siphamia versicolor*, another luminescent apogonid fish, symbiotic bacteria are responsible for the luminescence (Haneda, 1965).

PRIACANTHIDAE

Jordan and Evermann (1896) postulated an affinity between the Pempheridae and Pri-

acanthidae. The generic names *Parapriacanthus* Steindachner (1870) and *Priacanthopsis* Fowler (1906) (introduced as a subgenus of *Pempheris*) of the Pempheridae suggest that the authors of these names implicitly admitted the affinity of *Priacanthus* with the Pempheridae. Some of the species belonging to these two families resemble each other in having large eyes, reddish coloration, and a similar aspect of the scales. The scales of *Priacanthus* are provided with a crescentic or sclerous plate (Boulenger, 1895 : 351) and are divided by the plate into distal and proximal halves. In this regard *Priacanthus* resembles *Parapriacanthus*, and the *analisis-* and *japonica-* groups of *Pempheris*. The supramaxillary is absent in the Priacanthidae, as in the Pempheridae. A reduction in the number of bony elements tends to occur in the Priacanthidae, namely, there are 22 to 24 (9~10+13~14) vertebrae (Cuvier, 1829 b : 100; Boulenger, 1895 : 352; Hotta, 1961 : 55-56; Takahashi, 1962 : 20), a single postcleithrum, 14 branched caudal rays (Regan, 1913), and six branchiostegals (Günther, 1859 : 215). In these characters the family differs from the Pempheridae. Contrary to Regan (1913), the basisphenoid is present in *Pristigenys nipponia* and *Priacanthus macracanthus* (Hotta, 1961 : 55 and 56, pl. 28, figs. 83 and 84). Although further information on the anatomy of the Priacanthidae is much needed in order to compare them with the Pempheridae, the relationship between the two families seems rather remote.

SCHUETTEA

The systematic position of the genus *Schuettea* is not yet well established, the genus having been affiliated variously with the Bramidae, Scorpionidae, Monodactylidae and Pempheridae. Following Regan (1913) and Jordan (1923), most current authors place the genus in the Monodactylidae, but it had better be placed, in my opinion, in a distinct family of its own.

The outstanding features which I found in *Schuettea scalaripinnis* are the presence of slender rib-like ossicles originating from the first and second haemal spines, an air bladder which extends back beyond the fifth haemal spine, and three pterygiophores of the anal fin which are inserted in front of the first

haemal spine.

As in the Pempheridae, the number of vertebrae is 10+15, the lateral line reaches the hinder margin of the caudal fin, and the epaxial trunk muscles extend anteriorly over the frontals. In other regards *Schuettea* shows no peculiar characters indicating an affinity with the Pempheridae. The dorsal fin of *Schuettea* is single but long, and the predorsal rayless pterygiophores are four.

Schuettea differs from the Monodactylidae in lacking teeth on the endopterygoid and ectopterygoid, and a separate foramen for the hyomandibular trunk of the facial nerve in the lateral wall of the pars jugularis of the trigemino-facialis chamber. The posterior ribs originate from the haemapophyses in *Schuettea*, but not in the Monodactylidae.

SCORPIDIDAE, KYPHOSIDAE, MONODACTYLIDAE, LABRACOGLOSSIDAE, etc.

According to Patterson (1964: 467 and 470), the Scorpididae, Kyphosidae, and Monodactylidae retain certain primitive characters, such as toothed endopterygoid and a separate foramen for the hyomandibular trunk of the facial nerve in the lateral wall of the pars jugularis of the trigemino-facialis chamber. Because they retain these characters, they are regarded as the most primitive Perciformes (Greenwood et al., 1966: 390). I found that the genus *Labracoglossa* (Labracoglossidae) also possesses these characteristics. In the absence of the above characters, the Pempheridae differ from these families, and according to the above authors it follows that the family Pempheridae is more specialized than these families. However, Gosline (1966b) opposed Patterson's view that these families are the most primitive Perciformes, on the basis of the highly modified jaws found in them. In having 10+15 vertebrae, except for *Psettus sebae* (10+14; Günther, 1860: 487) and *Kyphosus cinerascence* (10+16; Hotta, 1961: 63), these families resemble the Pempheridae.

The Centrarchidae, *Kuhlia* (Kuhliidae) and *Toxotes* (Toxotidae) have a toothed endopterygoid (Günther, 1860: 67; Boulenger, 1895: 35; Regan, 1913) but no information is available concerning the characteristics of the trigemino-facialis chamber. The basihyal is also toothed in *Toxotes*. The Centrarchidae

have 29 to 33 (13~18+15~17) vertebrae (Boulenger, 1895: 5, *Elassoma* and *Kuhlia* are excluded from his Centrarchidae), the Kuhliidae 10+15, 11+14 (Boulenger, 1895: 5; Regan, 1913) or 10+16 (my observation of a specimen of *Kuhlia taeniura*), and the Toxotidae 10+14 (Agassiz, 1832: 262; Günther, 1860: 67).

BATHYCLUPEIDAE

Contrary to Goode and Bean (1896: 190) the Bathyclupeidae are physoclistous. The orbitosphenoid is absent, the pars jugularis of the trigemino-facialis chamber has no separate foramen for the hyomandibular trunk of the facial nerve, and the caudal fin has 15 branched fin-rays (Patterson, 1964: 242). Although the abdominal vertebrae are ten, the caudal vertebrae of the Bathyclupeidae are much more numerous (21) (Boulenger, 1902: 202) than those of the Pempheridae (15). The sensory canal system of the head is well developed in both families, but the frontal is cavernous and the epaxial trunk muscles do not extend anteriorly over it in the Bathyclupeidae.

Like the Pempheridae, the Bathyclupeidae possess a single short dorsal fin and a long anal fin. However, the dorsal fin is postmedian in the Bathyclupeidae. The outstanding features of the Bathyclupeidae are, according to my observation of a specimen of *Bathyclupea argentea*, that there are nine predorsal rayless pterygiophores, that the four pterygiophores of the anal fin are inserted in front of the first haemal spine, and that the vertebrae entirely lack zygapophyses. The Bathyclupeidae cannot be close relatives of the Pempheridae.

LEPTOBRAMIDAE

The differences in the structure of the dorsal fin between the Pempheridae and Leptobramidae were pointed out by Tominaga (1965). The lengthy list of the different characteristics found in the two families may be unnecessary here, since the Leptobramidae possess no characters indicating an affinity with the Pempheridae.

I reexamined the same material as that of Tominaga (1965), and can supplement that account with a few additional characters of

the Leptobramidae:

1. A separate foramen for the hyomandibular trunk of the facial nerve is absent in the wall of the pars jugularis of the trigemino-facialis chamber.
2. The sphenotic has no exposed surface on the floor of the posttemporal groove.
3. Tominaga (1965) reported that the second superior pharyngeal has two separate tooth patches. Actually, the smaller posterodistal tooth-patch is on an independent extra ossification. Another tooth patch, similar in size to this, is present on the third upper pharyngeal.

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ハタンボ科魚類の内部形態、相互類縁関係及び分類学的位置について。富永義昭。ハタンボ科はスズキ目に属し、体の前半に位置する一基の短い背鰭と、長い臀鰭をもつこと、外後頭骨が側上方に延びることなどにより特徴づけられる。同科にはハタンボ属とキンメドキ属が含まれるが、この二属は真の類縁関係を有する。ハタンボ属の幾つかの種には、他のハタンボ属の種とキンメドキ属の中間の形質の組み合わせがみられる。ハタンボ科の種の間では、鰓、肩帯、鱗などの形質に顕著な変異が認められ、世界のハタンボ属の種はこれ等の形質の違いに基づいて、7個の種類群に細分することができる。コモリウオ科はキンメダイ目とスズキ目の中間の形質の組み合わせをもっている。キンメダイ型からスズキ型への進化の過程が、体の前半に位置する短い背鰭をもつ魚類において起った可能性が考えられる。スズキ目の中では、ホタルジャコ属、アカムツ属、スミクイウオ属、バケスミクイウオ属、オオメハタ属、イシモチ科、ネンプツダイ科などが、ハタンボ科と共有する形質が多く、キントキダイ科、Scorpididae、テンジクイサキ科、ヒメツバメウオ科、ユゴイ科などとの共通点は多くない。ソコニシ科、Leptobramidae、*Schuettes* 属がハタンボ科に近いことを示す根拠はない。

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