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Comparative Anatomy and Phylogeny of the Family Mullidae (Teleostei : Perciformes)

Byung-Jik KIM[1)2)]

Contents

[1)] *Laboratory of Marine Biodiversity (Systematic Ichthyology), Graduate School of Fisheries Sciences, Hokkaido University, 3-1-1, Minato-cho, Hakodate, Hokkaido 041-8611, Japan*

[2)] *Present address : Faculty of Biological Sciences, College of Natural Science, Chonbuk National University, Chonju 561-756, Korea*

Abstract

The skeletal and muscular systems of the family Mullidae were described in detail, and monophyly of the family and phylogenetic relationships among mullid genera were analyzed based on the cladistic methodology. The family Mullidae is a monophyletic group supported by 26 synapomorphies. Thirteen synapomorphic characters, including myological and osteological differentiations of the hyoid arch, were unique to the family Mullidae. A comparison of 41 transformation series among 41 mullid species produced seven most parsimonious cladograms. One of them was accepted as a cladistic hypothesis showing the phylogenetic relationships within the family based on the reconstruction of character evolution of preorbital scales. The family Mullidae comprises six clades, each corresponding to a currently recognized genus. *Upeneus* is supported by five apomorphies, *Mullus* by six apomorphies, *Upeneichthys* by two apomorphies, *Mulloidichthys* by five apomorphies, *Pseudupeneus* by one apomorphy, and *Parupeneus* by two apomorphies. Although sister groups of the family Mullidae could not be determined, two characters were considered as most probable indicators suggesting haemuloid or sparoid fish as a sister group.

Key words: Phylogeny, Mullidae, monophyly, anatomy, classification

I. Introduction

The family Mullidae, commonly called goatfishes, red mullets or surmullets, is one of the morphologically specialized groups among the percoid fishes. It is composed of 18 described genera and 177 nominal species (Eschmeyer, 1998). About 55 species are recognized as valid within the following six genera: *Mullus* Linnaeus, 1758; *Upeneus* Cuvier, 1829; *Upeneichthys* Bleeker, 1855; *Mulloidichthys* Whitley, 1929; *Pseudupeneus* Bleeker, 1862; and *Parupeneus* Bleeker, 1863 (Nelson, 1994).

This highly specialized fish group is characterized by having a pair of hyoid barbels; two widely separated dorsal fins, the first with seven or eight spines, and the second with nine soft rays; anal fin with a small spine and seven soft rays; deeply forked caudal fin with seven and six branched rays in upper and lower lobes, respectively; and 24 vertebrae. The hyoid barbel in the mullids is a unique structural peculiarity among the percoids, and is formed by modification of the anteriormost branchiostegal ray (Lo Bianco, 1907; Caldwell, 1962; McCormick, 1993; pers. obs.). The barbel bears numerous sensory organs on its surface and is innervated by the ramus facialis (VII) (Sato, 1937; McCormick, 1993). It plays an important role in detecting food items on or slightly below the surface of the substrate (Gosline, 1984). The mullids occur in tropical and temperate waters of all major oceans, including the Mediterranean and Black Seas. Three genera, *Upeneus, Mulloidichthys* and *Parupeneus*, are distributed predominantly in the Indo-Pacific Ocean (Fowler, 1933; Thomas, 1969). The species of *Pseudupeneus* are distributed in the eastern Pacific and western Atlantic Oceans, and those of *Mullus* are in the Atlantic Ocean, including the Mediterranean Sea and Black Sea. The distribution of *Upeneichthys* is restricted to the coastal waters of southern and eastern Australia and New Zealand (Ben-Tuvia, 1986; Hutchins, 1990).

Although many of taxonomic works on the mullids have been published by various workers since Linnaeus (1758) first brought two Mediterranean species, *Mullus barbatus* and *M. surmuletus*, to our knowledge, most are limited regional reviews, except for that of Lachner (1954) who revised the genus *Upeneus*. Snyder (1907), for example, revised the mullids of Japanese waters, Herre and Montalban (1928) and Fowler (1933) of the Philippines and adjacent seas, Bleeker (1874) and Weber and Beaufort (1931) of the Indo-Australian Archipelago, Lachner (1960) of the Marshall Islands, Thomas (1969) of the Indian Sea, and Ben-Tuvia and Kissil (1988) of the Red Sea and eastern Mediterranean Sea. Thomas (1969) also compared osteological aspects of three Indo-Pacific genera (*Upeneus, Mulloidichthys* and *Parupeneus*), and Gosline (1984) reported on internal features of the mullids. Several works concerning partial skeletons of mullid species have been published, for example, the primary shoulder girdle by Starks (1930), branchiostegals and associated opercular, gular and hyoid bones by McAllister (1968), urohyal by Kusaka (1974) and caudal skeleton by Fujita (1990). A comprehensive osteological work covering the whole skeletal system of all genera of the mullids is, however, wanting. In addition, neither monophyly of the family Mullidae nor interrelationships of the mullid genera have been clarified to date.

The goals of this study are to describe the comparative anatomy of the family Mullidae based on osteological and myological observations, to verify the monophyly of the Mullidae, to resolve the phylogenetic relationships within the Mullidae, and to propose a classification of the family based on the phylogeny.

II. Materials and methods

Materials used for anatomical examinations are listed below. Osteological and myological observations were made on specimens stained with Alizarin Red-S under

the dissecting microscope (Leica MZ 12 and Nikon SMZ-10) with a camera lucida. Terminology follows generally Johnson et al. (1996) for osteology, but that for cartilaginous elements in the caudal skeleton follows Fujita (1990), that for myology follows Winterbottom (1974), that for laterosensory canal system of head follows Weitzman (1962), and that for nerves follows Freihofer (1978). Definitions of higher taxonomic categories in the materials list follow Nelson (1994), and institutional abbreviations follow Leviton et al. (1985), except for CNUC, Chonbuk National University, Chonju, Korea.

Abbreviations in each figure are listed in Appendix 1.

Abbreviations for each genus name are as follows: *M.* for *Mullus, Mu.* for *Mulloidichthys, P.* for *Parupeneus, Ps.* for *Pseudupeneus, U.* for *Upeneus* and *Up.* for *Upeneichthys.*

Upeneus asymmetricus, USNM 267584, 2 specimens, 73.7-76.8 mm SL ; *Upeneus japonicus*, CNUC 23686, CNUC 23694, CNUC 23697, HUMZ 105764, HUMZ 141203, 5 specimens, 78.5-101.5 mm SL ; *Upeneus luzonius*, AMS I.34398-034, 100.8 mm SL ; *Upeneus moluccensis*, BSKU 084674, HUMZ 82104, 2 specimens, 84.1-160.7 mm SL ; *Upeneus parvus*, HUMZ 31349, NSMT-P 54126, USNM 346104, USNM 346105, 4 specimens, 102.9-156.4 mm SL ; *Upeneus pori*, HUJ 13549, 10 specimens, 69.9-117.4 mm SL ; *Upeneus quadrilineatus*, HUMZ 35096, HUMZ 36345, 2 specimens, 80.9-103.5 mm SL ; *Upeneus sulphureus*, NSMT-P 54127, URM-P 25778, 2 specimens, 98.7-131.6 mm SL ; *Upeneus crosnieri*, USNM 306101, 124.8 mm SL ; *Upeneus tragula*, AMS I.34398-034, HUMZ 62175, 2 specimens, 90.2-114.8 mm SL ; *Upeneus taeniopterus*, HUMZ 155966, 221.1 mm SL ; *Upeneus vittatus*, HUMZ 46769, HUMZ 46773, 2 specimens, 114.6-169.8 mm SL ; *Mulloidichthys martinicus*, HUMZ 32262, 136.7 mm SL ; *Mulloidichthys flavolineatus*, NSMT-P 19933, UW 013326, UW 015145, 3 specimens, 135.0-145.1 mm SL ; *Mulloidichthys vanicolensis*, BSKU 10249, URM-P 26052, 2 specimens, 91.4-110.4 mm SL ; *Mulloidichthys* sp. : UW 016232, 79.9 mm SL ; *Mullus argentinae*, NSMT-P 52642, 2 specimens, 148.6-151.3 mm SL ; *Mullus barbatus*, HUMZ 154853, 109.8 mm SL ; *Mullus surmuletus*, HUMZ 154868, HUMZ 154869, 2 specimens, 97.5-110.2 mm SL ; *Parupeneus barberinoides*, HUMZ 39251, BSKU 015278, 2 specimens, 111.7-156.3 mm SL ; *Parupeneus barberinus*, NSMT-P 30698, UW 010541, 2 specimens, 113.9-146.4 mm SL ; *Parupeneus bifasciatus*, HUMZ 155960, 132.7 mm SL ; *Parupeneus chrysonemus*, HUMZ 155963, 107.0 mm SL ; *Parupeneus chrysopleuron*, BSKU 084163, HUMZ 155973, 2 specimens, 75.7-222.2 mm SL ; *Parupeneus ciliatus*, HUMZ 58846, HUMZ 62115, 2 specimens, 154.9-177.5 mm SL ; *Parupeneus cyclostomus*, HUMZ 39268, HUMZ 63100, 2 specimens, 104.1-154.7 mm SL ; *Parupeneus forsskali*, HUJ 9977, 132.1 mm SL ; *Parupeneus heptacanthus*, BSKU 084326, 95.7 mm SL ; *Parupeneus indicus*, HUMZ 39671, 128.3 mm SL ; *Parupeneus macronemus*, HUMZ 89496, 162.0 mm SL ; *Parupeneus margaritatus*, HUMZ 155965, 122.8 mm SL ; *Parupeneus multifasciatus*, HUMZ 48200, HUMZ 62786, 2 specimens, 98.1-177.7 mm SL ; *Parupeneus pleurostigma*, BSKU 025978, HUMZ 48219, UW 013330, 3 specimens, 75.7-152.4 mm SL ; *Parupeneus porphyreus*, UW 026780, 157.7 mm SL ; *Parupeneus procerigena*, HUMZ 74033, 153.1 mm SL ; *Parupeneus signatus*, WAM P. 25728.002, 102.6 mm SL ; *Parupeneus spilurus*, HUMZ 62150, HUMZ 62174, 2 specimens, 149.9-184.2 mm SL ; *Parupeneus* sp., USNM 288478, 190.4 mm SL ; *Pseudupeneus grandisquamis*, UW 022550, 2 specimens, 149.0-178.4 mm SL ; *Pseudupeneus prayensis*, HUMZ 31015, NSMT-P 54121, 2 specimens, 145.4-186.4 mm SL ; *Upeneichthys lineatus*, AMS I. 16879-006, 2 specimens, 113.5-130.8 mm SL ; *Upeneichthys porosus*, AMS I. 17033-021, 2 specimens, 97.4-99.0 mm SL ; *Upeneichthys vlamingii*, AMS I. 20194-028, 2 specimens, 99.8-106.0 mm SL ; *Upeneichthys stotti*, WAM P. 30880.002, 2 specimens, 114.0-125.4 mm SL.

Centropomidae : *Lates microlepis*, HUMZ 138066, 101.9 mm SL. Percichthyidae : *Stereolepis doederleini*, HUMZ 71230, 101.6 mm SL ; *Howella zina*, HUMZ 130513, 75.1 mm SL. Serranidae : *Chelidoperca hirundinacea*, HUMZ 110863, 111.0 mm SL ; *Sacura margaritacea*, HUMZ 87048, 93.1 mm SL ; *Niphon spinosus*, HUMZ 48446, 147.5 mm SL. Banjosidae : *Banjos banjos*, HUMZ 37284, 119.6 mm SL. Centrarchidae : *Lepomis macrochirus*, HUMZ 119326, 97.4 mm SL. Priacanthidae : *Priacanthus macracanthus*, HUMZ 97044, 143.0 mm SL. Apogonidae : *Apogon semilineatus*, HUMZ 107056, 83.5 mm SL. Malacanthidae : *Branchiostegus japonicus*, HUMZ 65566, 104.6 mm SL. Carangidae : *Trachurus japonicus*, HUMZ 124654, 94.1 mm SL. Leiognathidae : *Leiognathus nuchalis*, HUMZ 48518, 95.9 mm SL. Lutjanidae : *Lutjanus ophuysenii*, HUMZ, 107051, 82.4 mm SL ; *Lutjanus russellii*, HUMZ 132022, 99.2 mm SL ; *Lutjanus fulvus*, HUMZ 80510, 102.2 mm SL ; *Etelis radiosus*, HUMZ 47652, 121.8 mm SL ; *Macolor macularis*, HUMZ 63074, 123.7 mm SL ; *Pristipomoides argyrogrammicus*, HUMZ 75043, 148.7 mm SL. Caesionidae : *Pterocaesio digramma*, HUMZ 39826, 110.9 mm SL. Haemulidae : *Hapalogenys mucronatus*, HUMZ 143107, 98.8 mm SL ; *Plectorhinchus cinctus*, HUMZ 13202, 108.3 mm SL ; *Parapristipoma trilineatum*, HUMZ 49224, 103.6 mm SL. Sparidae :

Acanthopagrus schlegeli, HUMZ 103537, 77.9 mm SL; *Dentex caeruleopunctatus*, HUMZ 73314, 133.4 mm SL. Lethrinidae: *Lethrinus semicinctus*, HUMZ 113328, 132.4 mm SL; *Lethrinus xanthochilus*, HUMZ 41408, 112.5 mm SL. Nemipteridae: *Scolopsis bilineata*, HUMZ 62770, 116.8 mm SL; *Nemipterus virgatus*: HUMZ 107573, 80.7 mm SL. Polynemidae: *Polydactylus plebeius*, HUMZ 48733, 180.4 mm SL. Sciaenidae: *Larimichthys polyactis*, HUMZ 108742, 129.2 mm SL. Pempheridae: *Pempheris schwenkii*, HUMZ 101191, 91.0 mm SL. Pentacerotidae: *Pentaceros japonicus*, HUMZ 90278, 117.2 mm SL. Kyphosidae: *Microcanthus strigatus*, HUMZ 131762, 77.7 mm SL; *Girella punctata*, HUMZ 131887, 82.8 mm SL. Terapontidae: *Rhyncopelates oxyrhynchus*, HUMZ 39480, 141.1 mm SL. Kuhliidae: *Kuhlia taeniura*, HUMZ 48520, 74.1 mm SL. Oplegnathidae: *Oplegnathus fasciatus*, HUMZ 136882, 91.7 mm SL. Cheilodactylidae: *Goniistius zebra*, HUMZ 36355, 113.6 mm SL. Cichlidae: *Oreochromis niloticus*, HUMZ 117915, 70.7 mm SL. Embiotocidae: *Neoditrema ransonneti*, HUMZ 133232, 117.1 mm SL. Labridae: *Semicrossyphus reticulatus*, HUMZ 78486, 113.0 mm SL. Trichodontidae: *Arctoscopus japonicus*, HUMZ 80864, 126.4 mm SL. Pinguipedidae: *Parapercis multifasciata*, HUMZ 65563, 117.8 mm SL. Sphyraenidae: *Sphyraena obtusata*, HUMZ 39257, 116.4 mm SL.

Mugiliformes. Mugilidae: *Mugil cephalus cephalus*, HUMZ 107570, 101.5 mm SL.

Atheriniformes. Atherinidae: *Atherinomorus lacunosus*, HUMZ 124892, 81.5 mm SL.

Beryciformes. Holocentridae: *Sargocentrodon diadema*; *HUMZ 40259, 128.2 mm SL. Trachichthyidae: *Hoplostethus* sp., *HUMZ 74186, 114.6 mm SL; *Centroberyx druzhinini*, *HUMZ 40251, 81.6 mm SL.

Scorpaeniformes. Scorpaenidae: *Scorpaena ornaria*, HUMZ 80674, 75.9 mm SL; *Sebastes schlegeli*, HUMZ 103000, 97.3 mm SL; *Sebastes taczanowskii*, HUMZ 149882, 98.8 mm SL; *Minous pictus*, HUMZ 80678, 77.1 mm SL. Hexagrammidae: *Hexagrammos octogrammus*, HUMZ 43908, 92.8 mm SL. Cottidae: *Myoxocephalus stelleri*, HUMZ 107235, 75.9 mm SL.

*, previously dissected materials.

III. Systematic methodology

To explore the relationships among the mullid genera, cladistic methods (Hennig, 1966; Wiley, 1981) were adopted, that is, if the members of a subgroup share a derived character state within the group, the monophyly of the subgroup is corroborated. A fundamental process in the method is to determine the evolutionary polarity, whether an observed character state is primitive (plesiomorphic) or derived (apomorphic). There are many methods to determine the polarity of characters, for example, fossil-taxa criterion, common-equals-primitive criterion, character correlation and primitive-taxa criterion, ontogenetic criterion and outgroup criterion (Mayden and Wiley, 1992). Among them, one of the most widely accepted method is the outgroup criterion (Watrous and Wheeler, 1981; Maddison et al. 1984), and this method is employed to determine the polarity of characters in the present study.

Mullid fishes belong to the suborder Percoidei, but the members of the suborder have not satisfactorily been examined phylogenetically, and the sister group of the Mullidae is quite poorly suggested. Only Gosline (1984) implied that the sparoids (*sensu* Johnson, 1980), comprising the families Sparidae, Centracanthidae, Lethrinidae and Nemipteridae, might be closely related to the family Mullidae. Even the percoids have been recognized as a non-monophyletic group by some workers (for example, Johnson, 1993; Mooi, 1993; Nelson, 1994). Under these circumstances, I have accepted the representatives of the general percoids as outgroups to determine the polarity of characters, that is, the most common character states found in these general percoids are treated as being primitive for the mullids. When the character states are variable among these percoid genera, the condition possessed by the lower percoids is considered as primitive. Although the limit of "lower percoid" has not been well defined, I have regarded *Acropoma, Doederleinia, Malakichthys* and *Synagrops* as the representatives of the lower percoids following Sasaki (1989). The data were analyzed using PAUP* 4.0b4a (Swofford, 2000), including a heuristic search option. Character evolution was assumed as "ordered" (Wagner parsimony; Farris [1970]), or "unordered" (Fitch parsimony; Fitch [1971]) when characters in a transformation series (TS) were difficult to order owing to their many modifications.

The character labels "0", "1" to "2" and "r" indicate plesiomorphy, apomorphies and reversal, respectively, throughout the paper. The characters showing intraspecific variation, mentioned under "Other variations", were not included in the phylogenetic analysis.

IV. Comparative morphology

1. Osteology

1-1. Neurocranium (Figs. 1-16)

Description

The neurocranium (Figs. 1-3) comprises eleven paired and six unpaired bones. The former includes the nasal,

lateral ethmoid, frontal, parietal, epioccipital, sphenotic, pterotic, intercalar, prootic, exoccipital and pterosphenoid bones. The latter includes the vomer, mesethmoid, supraoccipital, parasphenoid, basisphenoid and basioccipital bones.

The nasal is a flat expanded bone, firmly attached to the mesethmoid medially, the frontal and lateral ethmoid posteriorly, and bears a nasal canal continuing from the supraorbital sensory canal on the frontal. The nasal canal is branched in *Mulloidichthys, Parupeneus* and *Pseudupeneus* (Figs. 1B, 1E-F, 4B-C), while it is simple in the remaining genera of the mullids (Figs. 1A, 1C-D). It is connected with the maxilla by a strong nasal-maxillary ligament (Fig. 5).

The mesethmoid forms the antero-dorsal border of the neurocranium, and joins the nasal laterally, the frontal posteriorly and the vomer ventrally. There is a projected ethmoid cartilage which is articulated with the palatine (Fig. 6).

The lateral ethmoid, situated on each side of the mesethmoid, joins the nasal and frontal dorsally, the mesethmoid medially, the vomer antero-ventrally and the parasphenoid postero-ventrally. The dorsal portion of the bone is expanded and strengthened to provide an attachment site for the nasal (Fig. 6). It has a developed lateral wing which forms the anterior border of the orbit and bears an olfactory-tract foramen. There are two articular heads ventro-laterally, the upper one receiving the lacrimal and the lower the palatine. In *Mulloidichthys*, there is a weak articular facet to receive the palatine at the antero-ventral region of the lateral ethmoid (Fig. 7B), whereas in the other genera the facet is on the vomer (Fig. 7A). The lower articular head is prominently projected in *Upeneus, Mullus, Upeneichthys* and *Mulloidichthys* (Fig. 8A), but it is weak and nearly fused with the body of the lateral ethmoid in *Parupeneus* and *Pseudupeneus* (Fig. 8B).

The frontal is the largest bone forming the anterior half of the skull roof. It joins the mesethmoid, nasal and lateral ethmoid anteriorly, the supraoccipital, parietal and pterotic posteriorly, and the fifth infraorbital (dermosphenotic), sphenotic and pterosphenotic

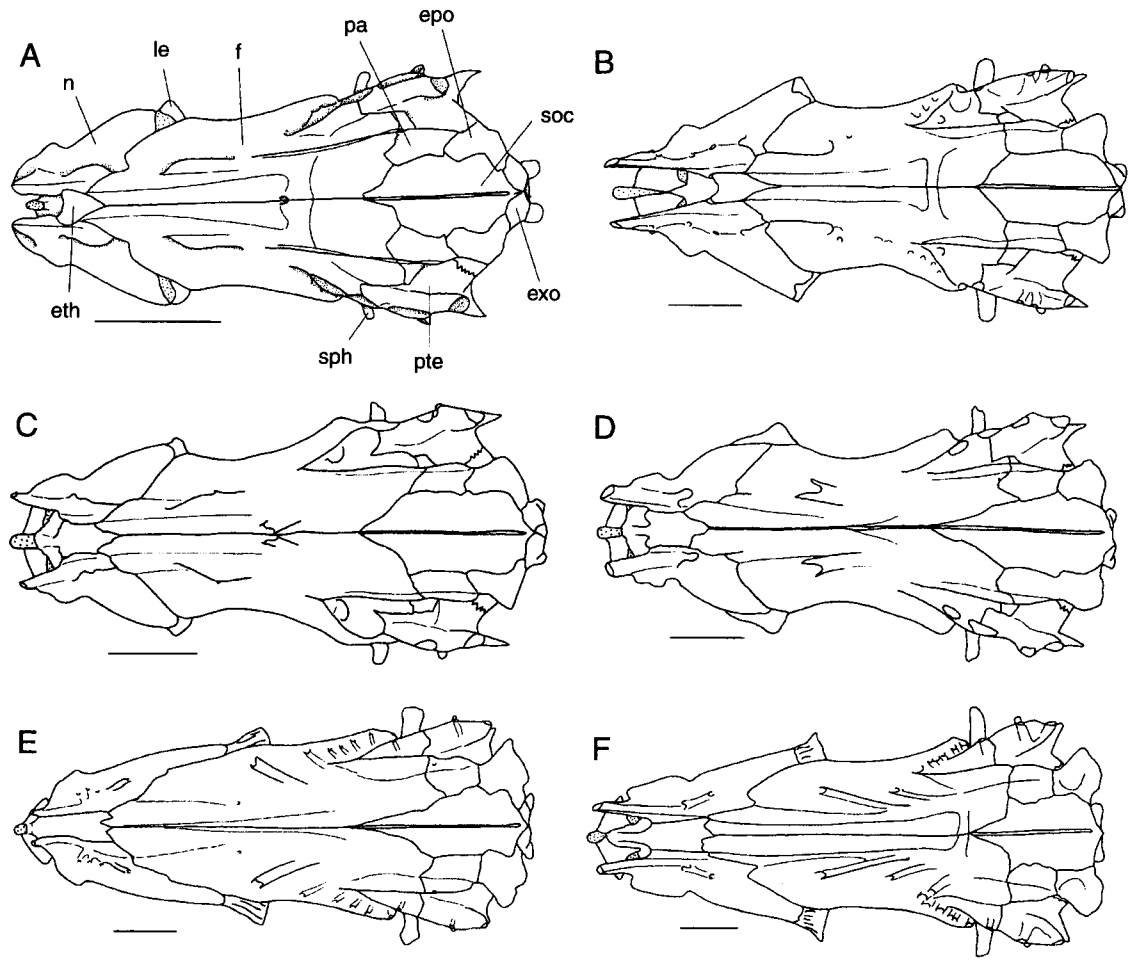

Fig. 1. Dorsal view of neurocranium. A, *Upeneus japonicus*, CNUC 23686; B, *Mulloidichthys flavolineatus*, UW 015145; C, *Mullus surmuletus*, HUMZ 154869; D, *Upeneichthys stotti*, WAM P. 30880.02; E, *Parupeneus barberinoides*, BSKU 015278; F, *Pseudupeneus prayensis*, NSMT-P 54121. Scales indicate 5 mm.

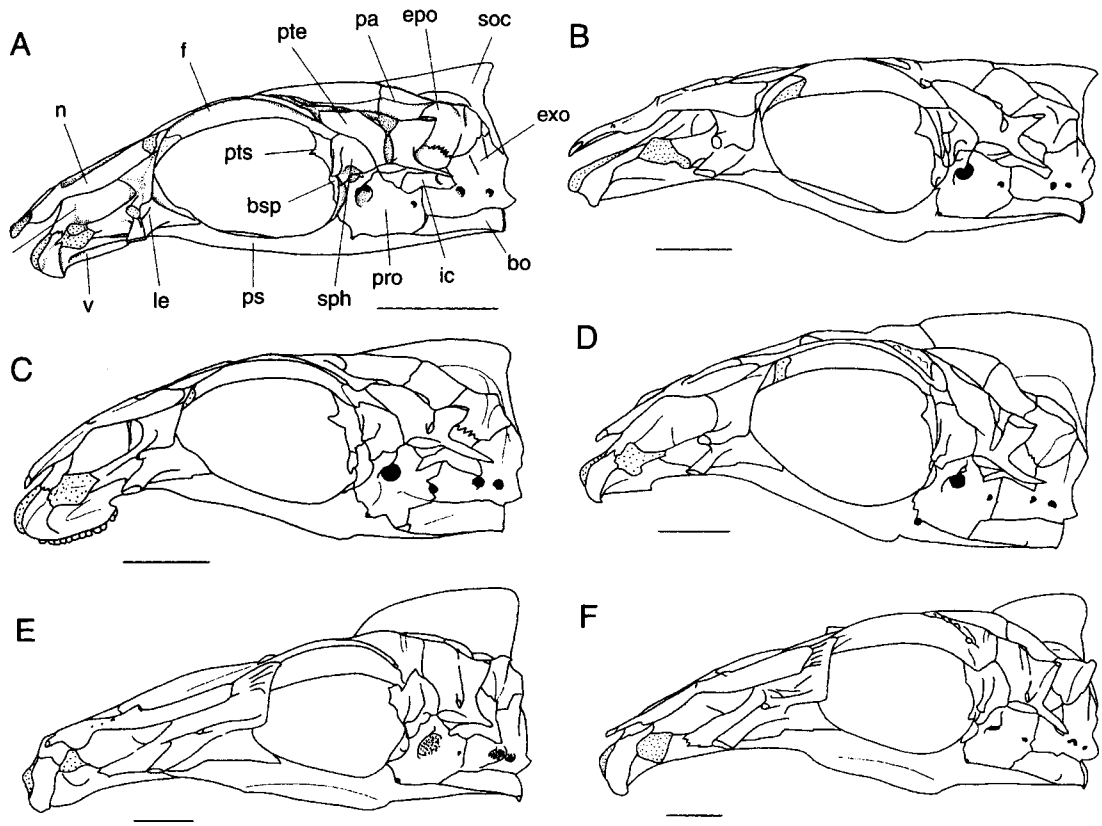

Fig. 2. Lateral view of neurocranium. A, *Upeneus japonicus*, CNUC 23686; B, *Mulloidichthys flavolineatus*, UW 015145; C, *Mullus surmuletus*, HUMZ 154869; D, *Upeneichthys stotti*, WAM P. 30880.02; E, *Parupeneus barberinoides*, BSKU 015278; F, *Pseudupeneus prayensis*, NSMT-P 54121. Scales indicate 5 mm.

postero-ventrally. The laterosensory canal leaving the pterotic enters the postero-lateral region of the frontal and branches medially to form an epiphyseal branch. The branches from each frontal extend medially to open near the dorsal midline in *Mullus* (Fig. 9B), whereas in the remaining genera the branches on each side connect with each other medially. In addition, the sensory canal on the postero-lateral region of the frontal is branched into several sub-branches in *Mulloidichthys, Parupeneus* and *Pseudupeneus* (Figs. 9C, 9E-F). The anterior portion of the supraorbital canal is continuous with the nasal canal. The dorsal surface of the frontal is relatively flat in *Upeneus, Mulloidichthys, Mullus* and *Pseudupeneus* (Figs. 2A-C, 2F), while it is elevated at the anterior portion of the frontal in *Upeneichthys* and *Parupeneus* (Figs. 2D-E). In *Upeneichthys* and *Parupeneus procerigena*, the frontal crest is prominently elevated and connected to the supraoccipital crest posteriorly (Fig. 2D).

The parietal, occupying the postero-dorsal region of the skull, joins the frontal anteriorly, the epioccipital posteriorly, the pterotic laterally and the supraoccipital medially. It forms a thin crest, namely, the fronto-parietal crest, continuing from the frontal. The crest is relatively well developed in *Parupeneus* and *Pseudupeneus*. The parietal is expanded posteriorly to overlap the epioccipital and pterotic in *Upeneus moluccensis, U. quadrilineatus, U. sulphureus, U. vittatus, Parupeneus* and *Mullus argentinae* (Fig. 10C), while it is not expanded to have cartilaginous portion among these bones in *U. asymmetricus, U. japonicus, U. luzonius, U. parvus, U. pori, U. taeniopterus, U. tragula, Mulloidichthys, Mullus surmuletus* (Fig. 10A), *Pseudupeneus* and *Upeneichthys*. In *M. barbatus*, the parietal bone is slightly expanded posteriorly, but complete overlapping of the epioccipital and pterotic was not recognized (Fig. 10B).

The supraoccipital forms the posterior roof of the neurocranium. It makes contact with the frontal anteriorly, the parietal and epioccipital laterally, and the exoccipital ventrally. The thin supraoccipital crest is present in the midline with various developments. Usually this crest is well developed in *Upeneichthys, Parupeneus* and *Pseudupeneus* compared to those of *Upeneus, Mulloidichthys* and *Mullus*.

The epioccipital, located posterior to the parietal, joins the pterotic laterally, the supraoccipital medially and the exoccipital postero-ventrally. It provides an

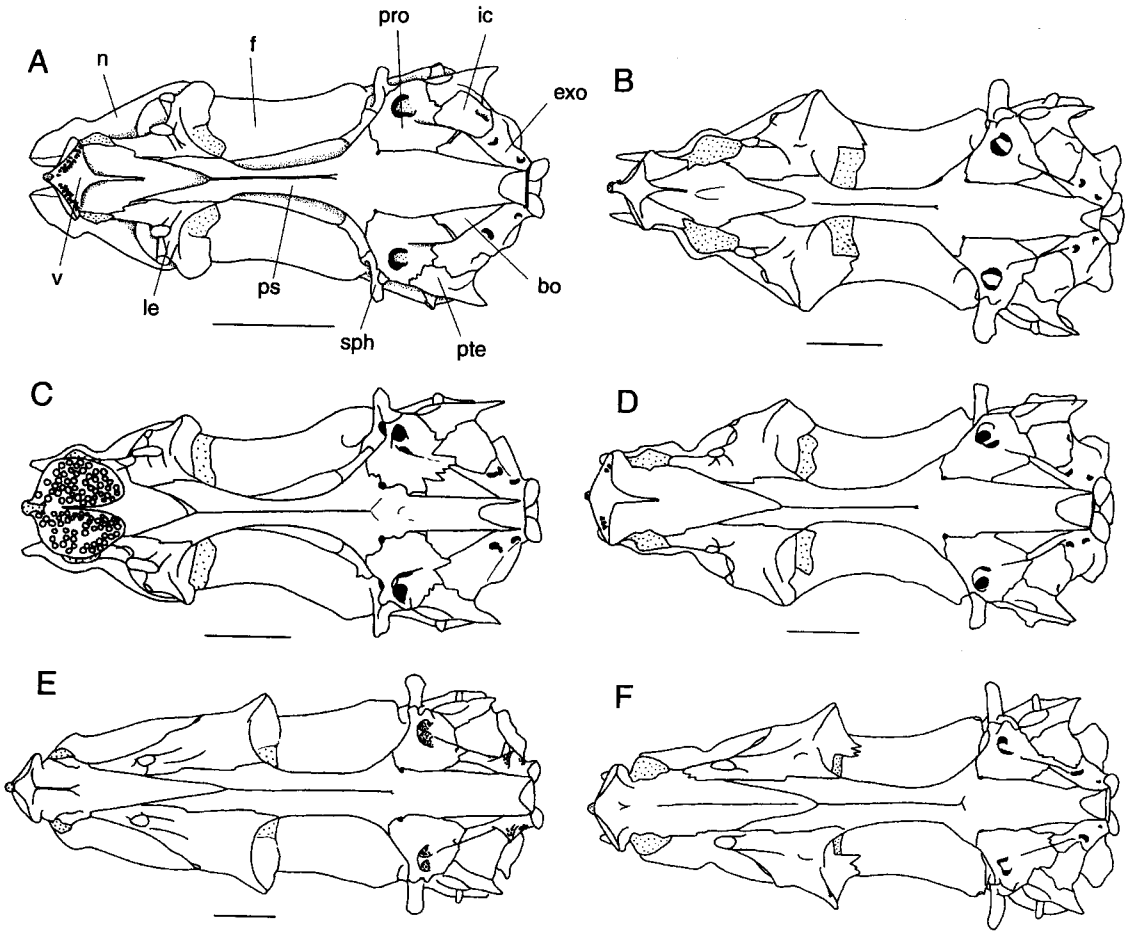

Fig. 3. Ventral view of neurocranium. A, *Upeneus japonicus*, CNUC 23686 ; B, *Mulloidichthys flavolineatus*, UW 015145 ; C, *Mullus surmuletus*, HUMZ 154869 ; D, *Upeneichthys stotti*, WAM P. 30880.02 ; E, *Parupeneus barberinoides*, BSKU 015278 ; F, *Pseudupeneus prayensis*, NSMT-P 54121. Scales indicate 5 mm.

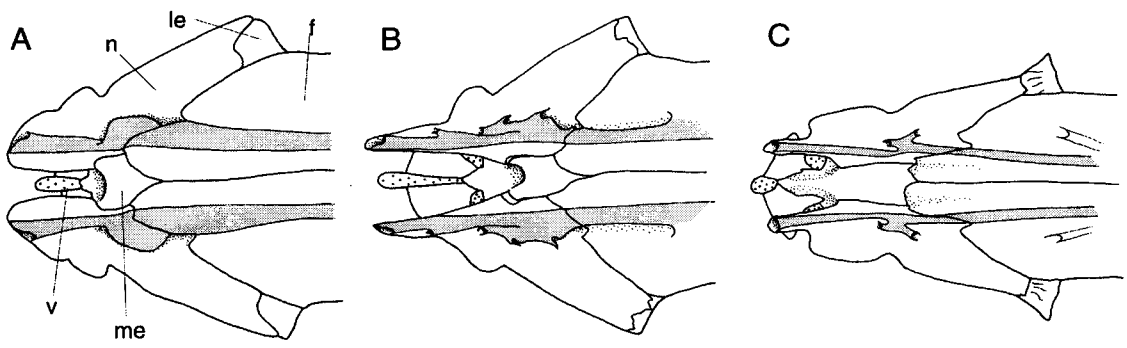

Fig. 4. Dorsal view of anterior portion of neurocranium. A, *Upeneus luzonius*, AMS I. 34389-034 ; B, *Mulloidichthys flavolineatus*, NSMT-P 19933 ; C, *Pseudupeneus prayensis*, NSMT-P 54121. Dotted areas show supraorbital sensory canal. Scales indicate 2 mm.

attachment site for the dorsal limb of the posttemporal on its posterior region.

The sphenotic, located on the postero-dorsal corner of the orbit, joins the frontal and pterotic dorsally, the prootic ventrally and the pterosphenoid antero-medially. It is projected laterally to form the dilatator groove, which provides the site of origin for the dilatator operculi along its dorsal region. The bone also forms ventrally a socket for the antero-dorsal condyle of the hyomandibula with the prootic.

The pterotic, occupying the postero-lateral region of the neurocranium, contacts the frontal and sphenotic

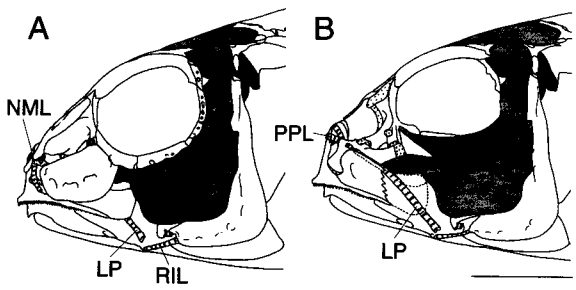

Fig. 5. Lateral view of head portion in *Upeneus japonicus* (A), HUMZ uncatalog. B, after removal of circumorbital bones. Scales indicate 5 mm.

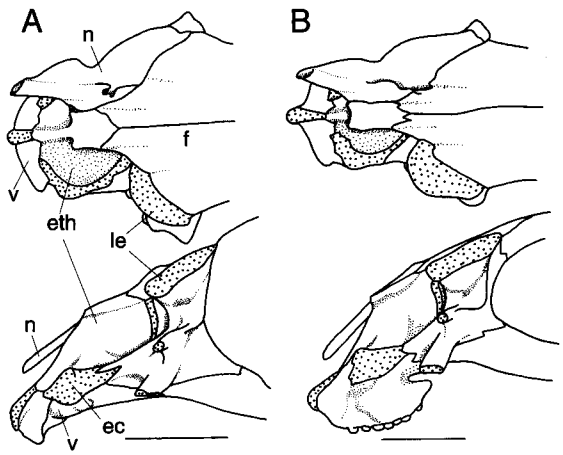

Fig. 6. Dorsal (above) and lateral (below) views of anterior portion of neurocranium. A, *Upeneichthys lineatus*, AMS I. 16879-006; B, *Mullus barbatus*, HUMZ 154853. Scales indicate 5 mm.

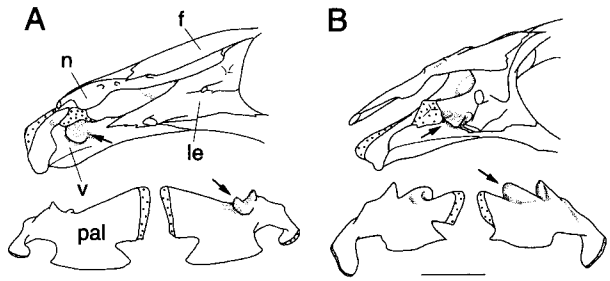

Fig. 7. Lateral view of anterior portion of neurocranium (above), and lateral and medial views of palatine (below). A, *Parupeneus cyclostomus*, HUMZ 63100; B, *Mulloidichthys flavolineatus*, NSMT-P 19933. Arrows indicate palatal articulation socket and its articular facet of skull. Scales indicate 5 mm.

anteriorly, the parietal and epioccipital medially, and the prootic and intercalar ventrally. It bears the pterotic canal, which is connected with the extrascapular canal posteriorly, the preoperculo-mandibular canal laterally and enters the frontal anteriorly. There is an elongated socket for the postero-dorsal condyle of the hyomandibula on the ventral region of the bone. In *Par-*

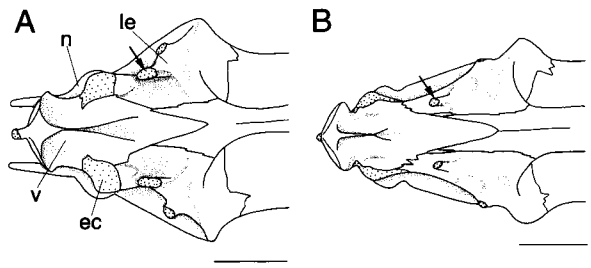

Fig. 8. Ventral view of anterior portion of neurocranium. A, *Mulloidichthys flavolineatus*, NSMT-P 19933; B, *Parupeneus indicus*, HUMZ 39671. Arrows show articular head of lateral ethmoid for articulating with lacrimal. Scales indicate 5 mm.

upeneus and *Pseudupeneus* the pterotic forms a thin crest, namely the fronto-pterotic crest, which is continued from the frontal. The crest is connected anteriorly with the fronto-parietal crest in *Parupeneus barberinus, P. bifasciatus, P. chrysonemus, P. cyclostomus, P. ciliatus, P. indicus, P. macronemus, P. multifasciatus, P. porphyreus* and *P. spilurus* (Fig. 11A).

The intercalar also lies on the postero-lateral region of the neurocranium. It joins the pterotic dorsally, the prootic anteriorly and the exoccipital postero-ventrally. It forms a facet for the connection with the ventral limb of the posttemporal.

The prootic occupies the postero-ventral wall of the orbit and is pierced by several foramina. It joins the sphenotic, pterotic, and intercalar dorsally, the exoccipital and basioccipital posteriorly, the parasphenoid ventrally, and the pterosphenoid and basisphenoid antero-medially. The trigeminofacial chamber, located in the antero-dorsal region of the bone, contains three foramina for cranial nerves III, V and VII (Fig. 12). There is a small carotid foramen on the prootic-parasphenoid suture line. The foramina for cranial nerves V, VII, IX and X are usually simple openings (Figs. 12A-E), but it is reticulated in *Parupeneus barberinoides, P. barberinus, P. forsskali, P. indicus* and *P. margaritatus* (Fig. 12F).

The exoccipital covers much of the lower posterior region of the neurocranium. It joins the supraoccipital, the epioccipital and intercalar dorsally, the prootic anteriorly and the basioccipital ventrally. It bears a condyle for articulation with the first vertebra. There are two foramina for cranial nerves IX and X on its lateral face.

The basioccipital occupies the postero-ventral region of the neurocranium. It is bordered by the prootic, parasphenoid and exoccipital, and has a condyle for articulation with the first vertebra.

The pterosphenoid forms the postero-dorsal wall of the orbit, and joins the frontal dorsally, the sphenotic

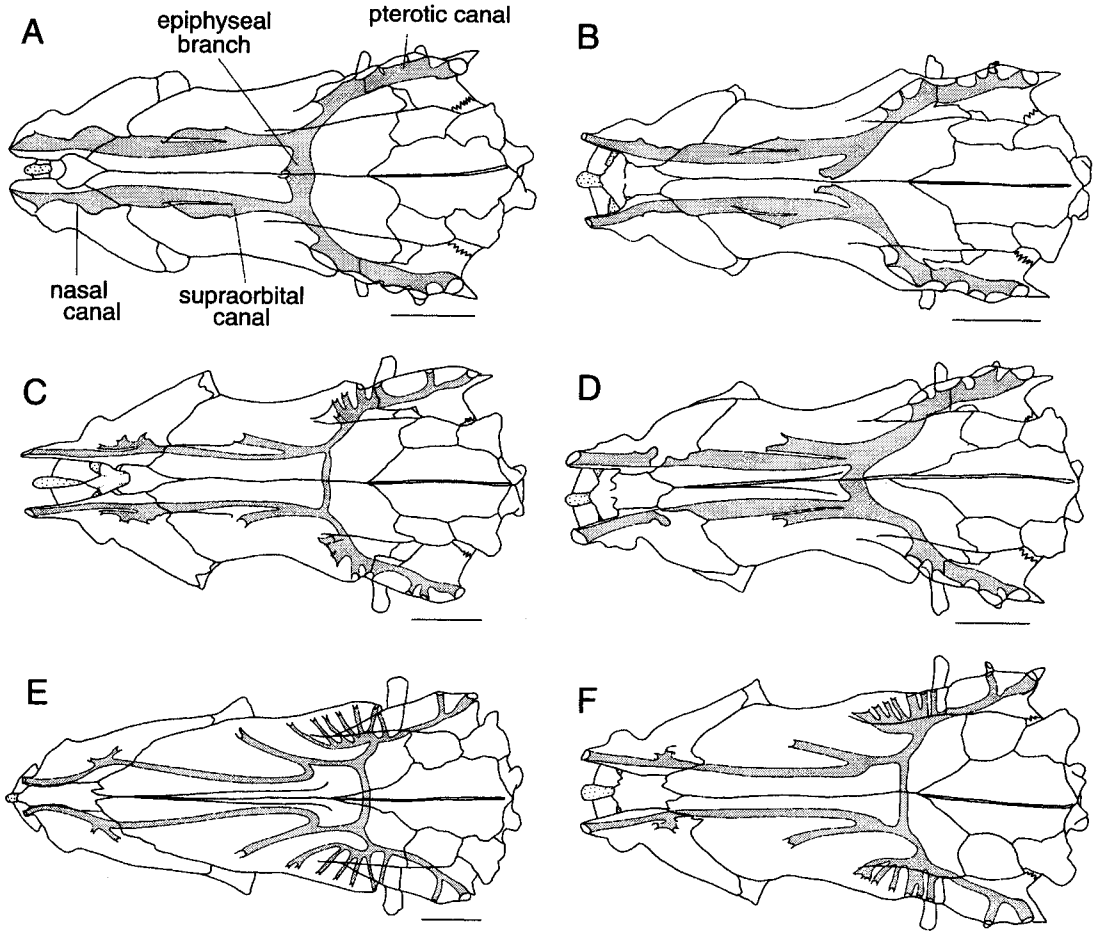

Fig. 9. Dorsal view of neurocranium. A, *Upeneus japonicus*, CNUC 23686 ; B, *Mullus surmuletus*, HUMZ 154868 ; C, *Mulloidichthys flavolineatus*, NSMT-P 19933 ; D, *Upeneichthys stotti*, AMS I. 130880-002 ; E, *Parupeneus barberinoides*, HUMZ 39651 ; F, *Pseudupeneus grandisquamis*, UW 022550. Dotted areas show supraorbital sensory canal system. Scales indicate 5 mm.

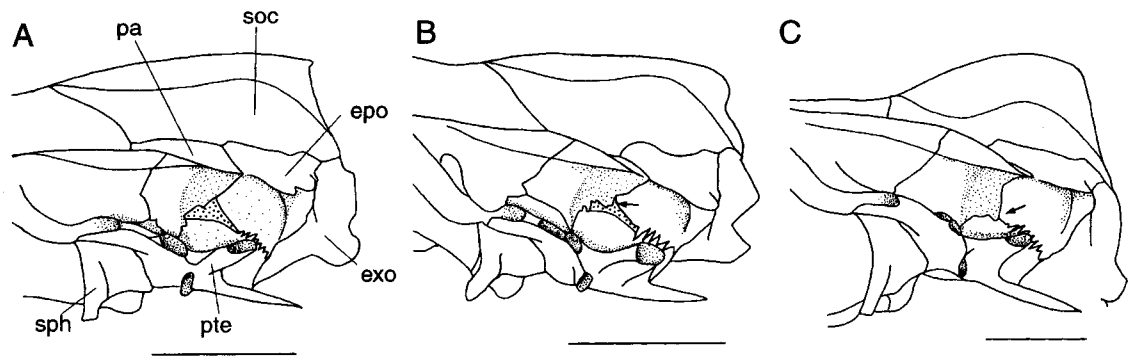

Fig. 10. Dorso-lateral view of posterior portion of neurocranium. A, *Mullus barbatus*, HUMZ 154853 ; B, *M. surmuletus*, HUMZ 154868 ; C, *M. argentinae*, NSMT-P 52642. Arrows show expansion of parietal. Scales indicate 5 mm.

laterally, and the prootic and basisphenoid ventrally.

The basisphenoid is located on the postero-ventral margin of the orbital and attached to the pterosphenoid dorsally and the prootic laterally. It has a small projection ventrally and is free from contacting with the parasphenoid (Fig. 12).

The parasphenoid occupies much of the ventral portion of the neurocranium. It joins the vomer and lateral ethmoid anteriorly and the prootic and basioccipital postero-dorsally.

The vomer is located on the antero-ventral region of the neurocranium. It is connected to the mesethmoid

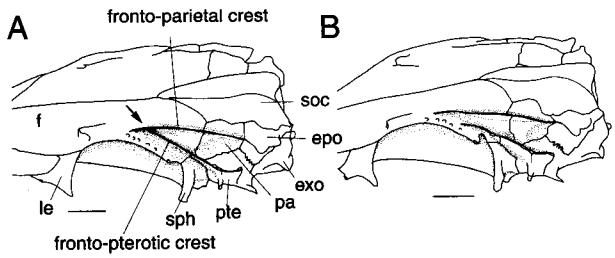

Fig. 11. Dorso-lateral view of posterior portion of neurocranium. A, *Parupeneus barberinus*, NSMT-P 30699; B, *P. forsskali*, HUJ 9977. Arrow shows connection of two crests. Scales indicate 2 mm.

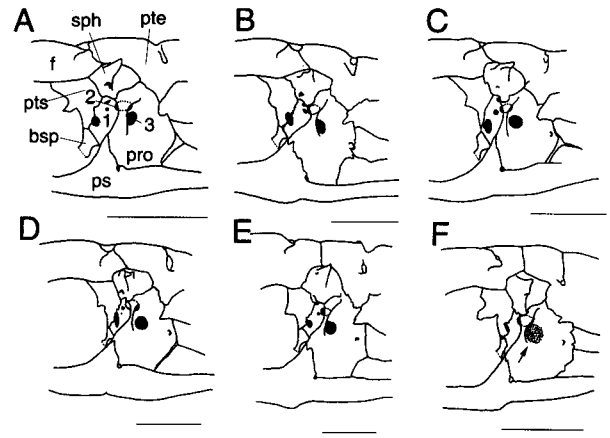

Fig. 12. Antero-lateral view of prootic and its neighboring parts of neurocranium. A, *Upeneus moluccensis*, BSKU 084674; B, *Mullus barbatus*, HUMZ 154853; C, *Mulloidichthys vanicolensis*, URM-P 26052; D, *Upeneichthys lineatus*, AMS I. 16879-006, E, *Pseudupeneus grandisquamis*, UW 022550; F, *Parupeneus forsskali*, HUJ 9977. 1, nervus oculomotorius (III); 2, nervus trigeminus (V); 3, nervus facialis (VII). Arrow shows reticular state. Scales indicate 5 mm.

and lateral ethmoid dorsally and the parasphenoid posteriorly. There is a thin cartilaginous portion in contact with the rostral cartilage of the premaxilla. Teeth on the vomer are present in *Upeneus, Mullus* and *Upeneichthys* (Figs. 13A-B, 14-15). The vomer in *Mullus* is notably expanded posteriorly and its teeth are modified and pebble-like (Fig. 13B). The vomer of *Mulloidichthys, Parupeneus* and *Pseudupeneus* is edentate (Fig. 13C). Each tooth plate of the vomer is deeply notched in *M. argentinae* (Fig. 14A) and *M. surmuletus* (Fig. 13B), while those in *Mullus barbatus* are nearly fused (Fig. 14B). Ventrally, the vomer has a well-developed crest on the ventral midline in *Upeneus asymmetricus, U. crosnieri, U. japonicus, U. luzonius, U. parvus, U. pori, U. taeniopterus* and *U. tragula* (Fig. 16B).

Characters

TS 1. Articulation of palatine with skull (Fig. 7)

0: with vomer; 1: with lateral ethmoid. In most genera of mullids the palatine articulates with the vomer (0), while in only *Mulloidichthys* it articulates with the lateral ethmoid (1).

TS 2. Articular head to receive palatine of lateral ethmoid (Fig. 8)

0: prominently projected; 1: not projected. The articular head of the lateral ethmoid to receive the palatine is prominently projected in *Upeneus, Mullus, Upeneichthys* and *Mulloidichthys* (0), whereas it is not projected but fused with the body of the lateral ethmoid in *Parupeneus* and *Pseudupeneus* (1).

TS 3. Nasal canal of supraorbital sensory canal (Fig. 4)

0: simple; 1: branched. The nasal canal is simple in *Upeneus, Mullus*, and *Upeneichthys* (0), while it is branched in *Mulloidichthys, Parupeneus* and *Pseudupeneus* (1).

TS 4. Crest on dorsal midline of frontal (Fig. 2)

0: absent; 1: present only on anterior portion of frontal; 2: well developed and connected with supraoccipital crest (ordered). The frontal in *Upeneus, Mullus, Mulloidichthys* and *Pseudupeneus* is relatively flat and without a crest-like projection (0). The crest, which is elevated on the anterior portion of the frontal,

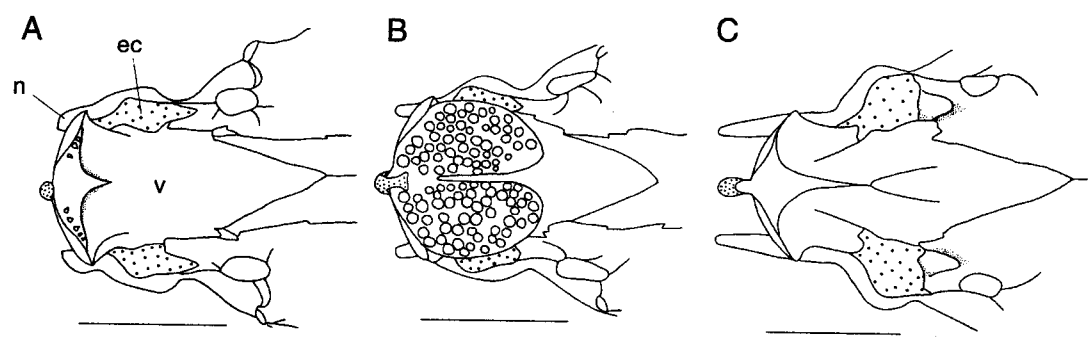

Fig. 13. Ventral view of antero-ventral region of neurocranium.. A, *Upeneichthys lineatus*, AMS I. 16879-006; B, *Mullus surmuletus*, HUMZ 154868; C, *Mulloidichthys flavolineatus*, NSMT-P 19933. Scales indicate 5 mm.

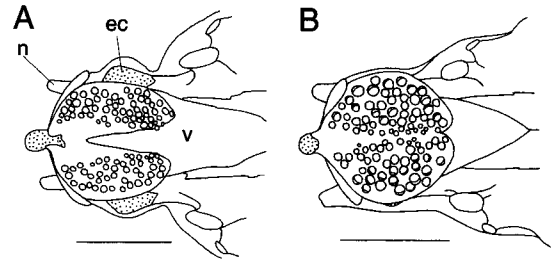

Fig. 14. Ventral view of antero-ventral region of neurocranium in *Mullus*. A, *M. argentinae*, NSMT-P 52642; B, *M. barbatus*, HUMZ 154853. Scales indicate 5 mm.

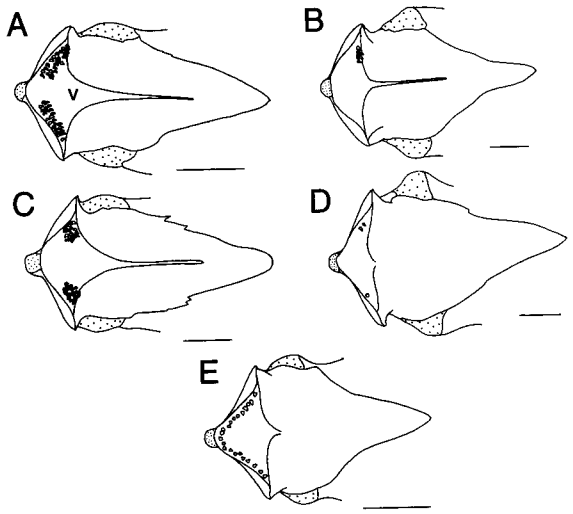

Fig. 15. Ventral view of vomer in *Upeneus*. A, *U. japonicus*, CNUC 23694; B, *U. parvus*, USNM 346105; C, *U. crosnieri*, USNM 306101; D, *U. vittatus*, HUMZ 46769; E, *U. sulphureus*, NSMT-P 54127. Scales indicate 2 mm.

is found in *Parupeneus* (1). The well-developed frontal crest, which is connected with the supraoccipital crest, is found in *Parupeneus* procerigena and *Upeneichthys* (2).

TS 5. Tooth plate of vomer (Fig. 14)

0: not expanded; 1; expanded and separated each other; 2: expanded and fused (ordered). In all mullid genera except *Mullus*, the tooth patch of the vomer is not expanded (0), but that of *Mullus* is expanded posteriorly. Right and left halves of the tooth plate of *M. surmuletus* and *M. argentinae* are separated (1), but those of *M. barbatus* are fused (2).

TS 6. Crest on ventral midline of vomer (Fig. 16)

0: absent or vestigial; 1: prominent. There is a well-developed crest on the ventral midline of the vomer only in *Upeneus asymmetricus, U. crosnieri, U. japonicus, U. luzonius, U. parvus, U. pori, U. taeniopterus* and *U. tragula* (1).

TS 7. Right and left epiphyseal branch of supraorbital sensory canal on frontal (Fig. 9)

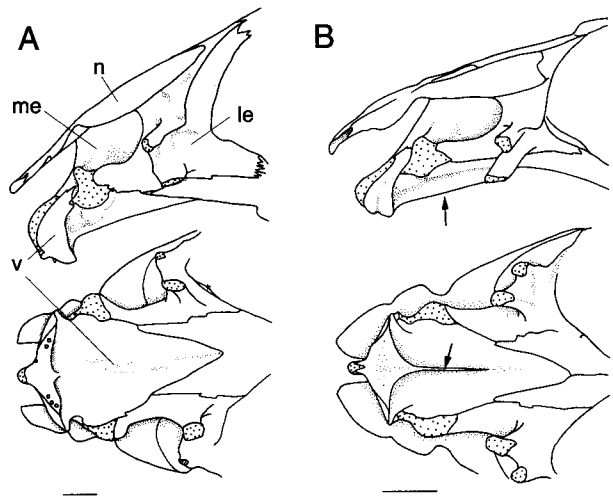

Fig. 16. Lateral (above) and ventral (below) views of anterior portion of neurocranium. A, *Upeneus vittatus*, HUMZ 46769; B, *U. luzonius*, AMS I. 34398-034. Arrows show ventral crest of vomer. Scales indicate 2 mm.

0: separated; 1: connected. Both epiphyseal branches of the supraorbital sensory canal on the frontal are separated from each other only in *Mullus* (0), whereas they are connected in the remaining genera (1).

TS 8. Supraorbital sensory canal on postero-lateral region of frontal (Fig. 9)

0: simple; 1: branched. In *Upeneus, Mullus* and *Upeneichthys* the supraorbital sensory canal situated on the postero-lateral region of the frontal is simple and not branched (0), whereas it is branched in *Mulloidichthys, Parupeneus* and *Pseudupeneus* (1).

TS 9. Foramina for cranial nerves V, VII, IX and X (Fig. 12)

0: simple opening; 1: reticulated. The foramina for cranial nerves V, VIII, IX, and X are simple openings in all genera except in several species of *Parupeneus* (0). The reticulated foramen is present in *P. barberinoides, P. barberinus, P. forsskali, P. indicus* and *P. margaritatus* (1).

Other variations

Teeth on vomer. Teeth on the vomer are a useful taxonomic character used by many authors (for example, Weber and Beaufort, 1931; Fowler, 1933, Lachner, 1954, 1960; Ben-Tuvia and Kissil, 1988) to classify the genera of mullids. In three genera, *Upeneus, Mullus* and *Upeneichthys* the vomer has small conical or pebble-like teeth. However, there are no teeth on the vomer in some individuals of several species of *Upeneus*, for example, *Upeneus doriae, U. luzonius* and *U. sundaicus*. Therefore, this character was not included in the analysis.

Posterior expansion of parietal. The parietal bone is not expanded posteriorly in *Mulloidichthys, Upeneichthys* and *Pseudupeneus*, while it is expanded posteriorly to overlap the epioccipital and pterotic bones in *Parupeneus*. However, intraspecific variation was found in *Mullus argentinae* and *Parupeneus chrysopleuron*, which have the two conditions.

1-2. Circumorbital bones (Figs. 17-19)

Description

The circumorbital bones (Fig. 17) comprise one lacrimal and five infraorbital bones, and form a serial tubular structure for the infraorbital sensory canal. The lacrimal is the largest bone among the circumorbitals, and partially overlies the anterior region of the maxilla. Its shape is relatively oval in *Upeneus, Mulloidichthys, Mullus* and *Upeneichthys* (Figs. 17A-D), and apparently elongated elliptical in *Parupeneus* and *Pseudupeneus* (Figs. 17E-F). The infraorbital sensory canal on the lacrimal is branched in *Mulloidichthys, Parupeneus* and *Pseudupeneus* (Fig. 18B), while it is simple in the remaining genera (Fig. 18A). The lacrimal is shifted anteriorly and articulated slightly with the lateral ethmoid postero-dorsally, and joins the first infraorbital posteriorly. The ventral margin of the bone is unossified and membranous. There are two ligaments on the lacrimal, one is branched from the nasal-maxillary ligament and connected to the antero-dorsal margin of the lacrimal (Fig. 5), and the other is between the lateral face of the anterior portion of the palatine and the medial face of the lacrimal.

The first infraorbital also shifts anteriorly and articulates with the lateral ethmoid antero dorsally by a strong connective tissue, the lacrimal anteriorly and the second infraorbital posteriorly. The bone has a well-developed subocular shelf medially and a simple ridge laterally. It also expands antero-ventrally to bear the branched sensory canals in *Parupeneus* and *Pseudupeneus* (Fig. 18B). The second infraorbital also has a well-developed subocular shelf, which is pointed postero-medially and connected to the suture line between the hyomandibula and the metapterygoid by a strong ligament. The remaining infraorbitals are tubular in shape with several sensory pores. Exceptionally, the third to fifth infraorbitals in *Upeneus sulphureus* have a shelf-like expansion along their entire length (Fig. 19). The fifth infraorbital (dermosphenotic) is loosely connected to the frontal and passes over the sphenotic; its canal is connected to the laterosensory canal of the frontal.

Characters

TS 10. Shape of lacrimal (Fig. 17)

0: oval; 1: elongated elliptical. In four mullid genera, except *Parupeneus* and *Pseudupeneus*, the lacrimal is not elongated and its shape is relatively oval (0). However, it is apparently elongated antero-ventrally in both *Parupeneus* and *Pseudupeneus* to form an elongated elliptical bone (1).

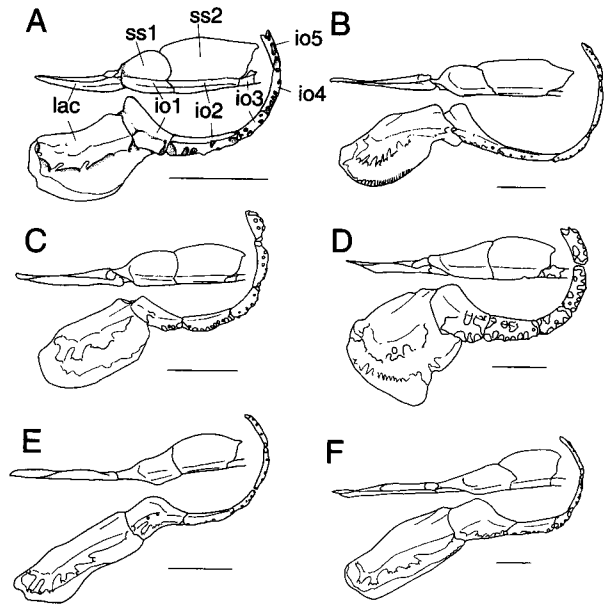

Fig. 17. Dorsal (above) and lateral (below) views of circumorbital bones. A, *Upeneus japonicus*, CNUC 23686; B, *Mulloidichthys flavolineatus*, UW 015145; C, *Mullus surmuletus*, HUMZ 154869; D, *Upeneichthys stotti*, WAM P. 30880.02; E, *Parupeneus barberinoides*, BSKU 015278; F, *Pseudupeneus prayensis*, NSMT-P 54121. Scales indicate 5 mm.

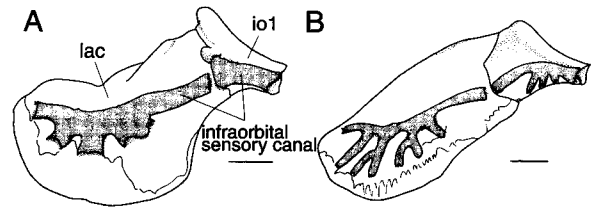

Fig. 18. Lacrimal and first infraorbital bones showing infraorbital sensory canal (dotted areas) in *Upeneus tragula*, HUMZ 62175 (A) and in *Parupeneus bifasciatus*, HUMZ 155960 (B). Scales indicate 2 mm.

Remarks. Although the shape of the lacrimal varies in the outgroups examined from oval to elliptical, the antero-ventral elongation the lacrimal is found in only *Lethrinus* in the present study. This elongation of the lacrimal is reported not only in *Scatophagus argus* (Smith and Bailey, 1962), but also in *Dentex, Pagrus, Argyrops, Evynnis, Sparus, Diplodus, Gymnocranius, Monotaxis* and *Lethrinus* (Akazaki, 1962).

TS 11. Infraorbital sensory canal on lacrimal (Fig. 18)

0: simple; 1: branched. The infraorbital sensory canal is simple and not branched in *Upeneus, Mullus* and *Upeneichthys* (0), while it is branched in *Mulloidi-*

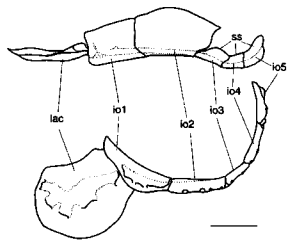

Fig. 19. Dorsal (above) and lateral (below) views of circumorbital bones in *Upeneus sulphureus*, NSMT-P 54127. Scales indicate 3 mm.

chthys, Parupeneus and *Pseudupeneus* (1).

TS 12. First infraorbital (Fig. 18)

0 : not expanded and lacking branched sensory canal ; 1 : expanded and bearing branched sensory canal. The first infraorbital is not expanded in *Upeneus, Mullus, Upeneichthys* and *Mulloidichthys* (0), whereas it is expanded antero-ventrally to bear branched infraorbital sensory canals in *Parupeneus* and *Pseudupeneus* (1).

Other variations

None.

1-3. Jaws (Figs. 20-25)

Description

The jaws consist of the premaxilla, maxilla and supramaxilla in the upper jaw (Fig. 20), and the dentary, anguloarticular, retroarticular and coronomeckelian in the lower jaw (Fig. 24). There are two cartilaginous elements, rostral cartilage and Meckel's cartilage, in the upper and lower jaws, respectively.

The premaxilla has four processes : ascending process, articular process, postmaxillary process and alveolar process (Fig. 20A). The rostral cartilage, being attached posteriorly to the ascending process, serves as a cushion between the premaxilla and the rostral region of the neurocranium. The articular process has a relatively large fossa in *Parupeneus*, and the postmaxillary process is projected dorsally or postero-dorsally except in *P. barberinoides, P. macronemus* and *P. multifasciatus*, which have an unprojected postmaxillary process (Fig. 21). The alveolar process bears villiform or conical teeth on its ventral surface, except in adult of *Mullus* (Fig. 22c). Teeth on the premaxilla are multiserial and villiform in *Upeneus* (Fig. 22A), biserial (rarely triserial in larger specimens), small, conical in *Mulloidichthys* and *Upeneichthys* (Figs. 22D, E), uniserial, large, conical in *Parupeneus* and *Mullus* (Figs. 22C, G), and irregular, biserial, large, conical in *Pseudupeneus* (Fig. 22F). The alveolar process is projected posteriorly in five genera (Figs. 20A, 20C-F), while it is shortened in *Mulloidichthys* (Fig. 20B).

The maxilla comprises a head, which bears the premaxillary condyle ventro-medially and cranial condyle dorsally, and has a long shaft, which is almost the same depth over its entire length in *Upeneus, Mullus, Upeneichthys* and *Mulloidichthys* (Figs. 20A-D), but expanded like a fan posteriorly in *Parupeneus* and *Pseudupeneus* (Figs. 20E-F). The premaxillary condyle articulates with the articular process of the premaxilla, and the cranial condyle articulates with the antero-

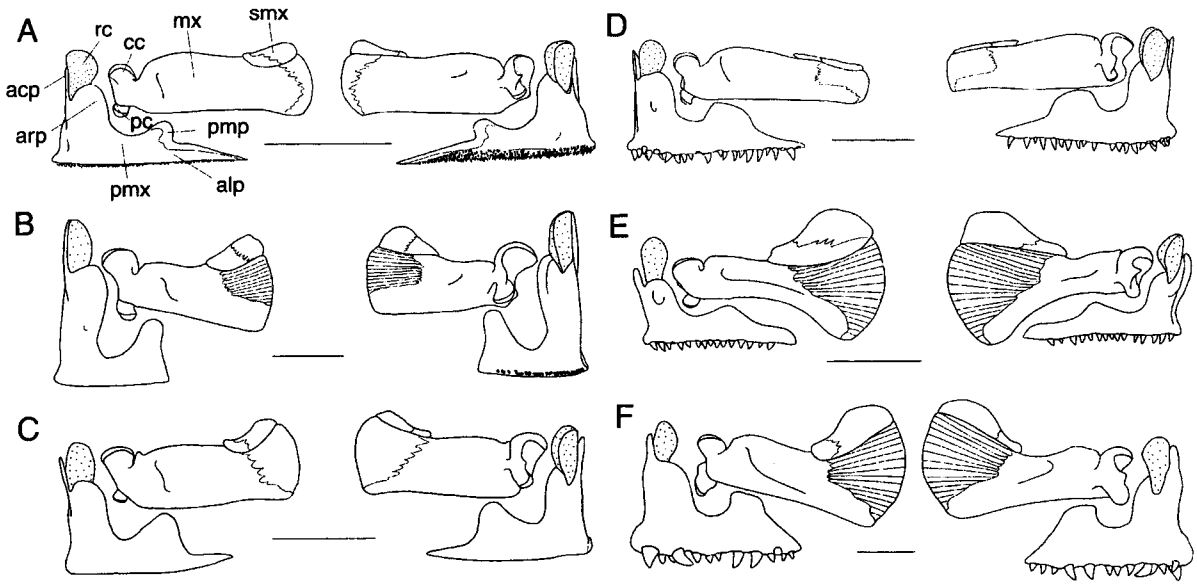

Fig. 20. Lateral (left) and medial (right) views of upper jaw. A, *Upeneus japonicus*, CNUC 23686 ; B, *Mulloidichthys flavolineatus*, UW 015145 ; C, *Mullus surmuletus*, HUMZ 154869 ; D, *Upeneichthys stotti*, WAM P. 30880.02 ; E, *Parupeneus barberinoides*, BSKU 015278 ; F, *Pseudupeneus prayensis*, NSMT-P 54121. Scales indicate 5 mm.

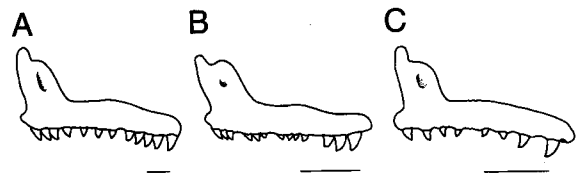

Fig. 21. Lateral view of premaxilla in *Parupeneus*. A, *P. multifasciatus*, HUMZ 48200; B, *P. macronemus*, HUMZ 89496; C, *P. barberinoides*, HUMZ 39251. Scales indicate 5 mm.

lateral face of the rostral region of the neurocranium. The ligamentum primordium is inserted onto the antero-dorsal surface of the shaft, and a tendon from the adductor mandibulae section 1 is inserted onto the ventro-medial surface of the maxilla (Fig. 5B).

The supramaxilla, lying on the postero-dorsal portion of the maxilla, is a thin leaf-like bone with membranous posterior margin. The bone of *Upeneichthys* is small and not expanded posteriorly (Fig. 20D), while it is expanded in the remaining genera, especially in *Parupeneus* and *Pseudupeneus* where it is much larger and nearly half the length of the maxilla (Figs. 20E-F). The bone is also connected to the maxilla by a maxillo-supramaxillary ligament in *Parupeneus* and *Pseudupeneus* (Fig. 23B).

The dentary is a toothed bone and is bifurcated to receive the anguloarticular posteriorly. The bone bears a mandibular sensory canal ventrally and is connected with the anguloarticular posteriorly and Meckel's cartilage medially (Fig. 24). The dentary bears more than two rows of villiform teeth in *Upeneus*, two irregular rows of small conical teeth in *Mulloidichthys* (rarely three rows in larger specimens) and *Upeneichthys*, one row of small conical teeth in *Mullus*, one row of large conical teeth in *Parupeneus*, and two irregular rows of relatively large conical teeth in *Pseudupeneus* (Fig. 22).

The anguloarticular is inserted into the deep notch of the dentary anteriorly. It also articulates with the condyle of the quadrate posteriorly and joins the retroarticular postero-ventrally and the coronomeckelian medially. The bone also bears the mandibular sensory canal, which comes from the preopercle along the ventral margin. This canal is almost open in *Upeneus* and *Upeneichthys* (except *Up. vlamingii*) (Fig. 25A), while it is closed with several pores in *Mulloidichthys, Mullus barbatus, Parupeneus* and *Pseudupeneus* (Fig. 25B). The coronomeckelian in *Mulloidichthys, Parupeneus* and *Pseudupeneus* is relatively larger than that of the remaining three genera (Figs. 24B, 24E-F).

The retroarticular, forming the postero-ventral angle

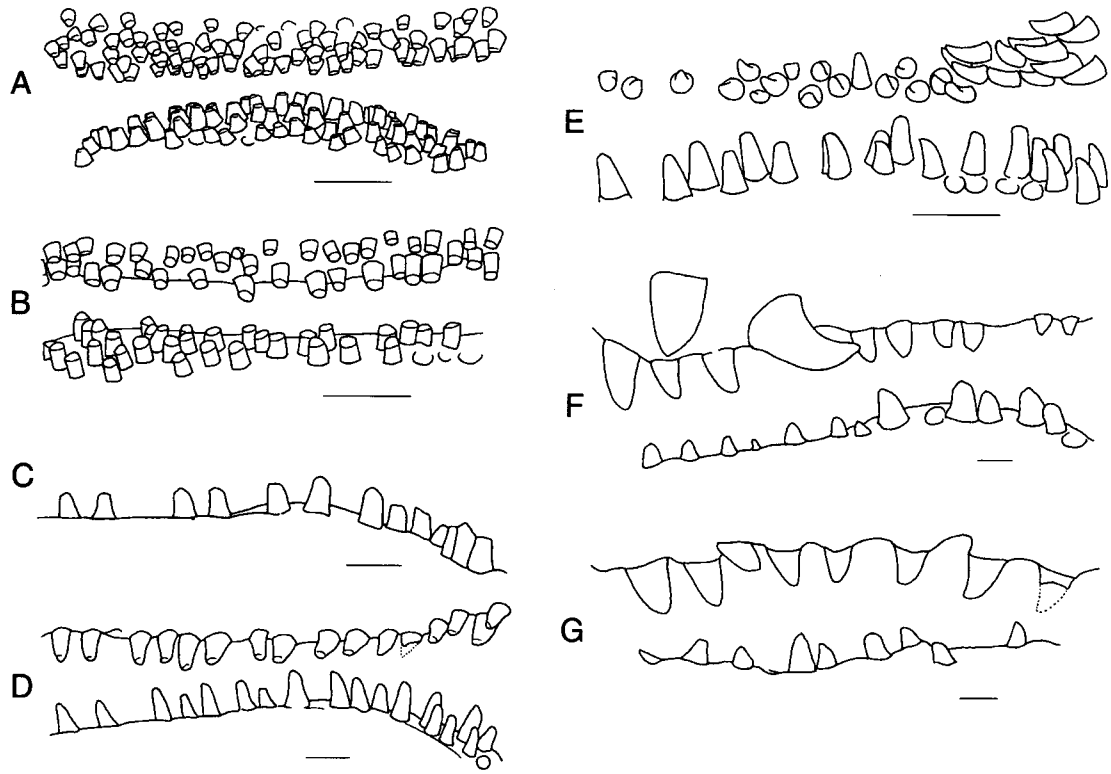

Fig. 22. Teeth on upper (above) and lower jaws (below). A, *Upeneus japonicus*, CNUC 23686; B, *U. sulphureus*, HUMZ 36345; C, *Mullus barbatus*, HUMZ 154868, teeth on upper jaw absent; D, *Upeneichthys lineatus*, AMS I. 16879-006; E, *Mulloidichthys flavolineatus*, NSMT-P 19933; F, *Pseudupeneus prayensis*, HUMZ 31015; G, *Parupeneus bifasciatus*, HUMZ 155960. Scales indicate 0.5 mm.

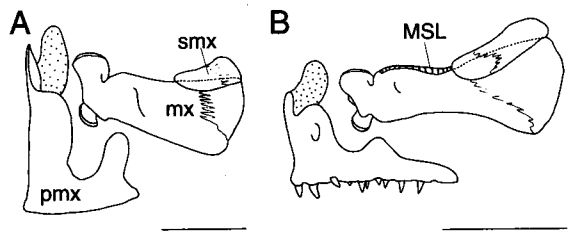

Fig. 23. Lateral view of upper jaw. A, *Mulloidichthys flavolineatus*, NSMT-P 19933; B, *Parupeneus barberinus*, NSMT-P 30698. Scales indicate 5 mm.

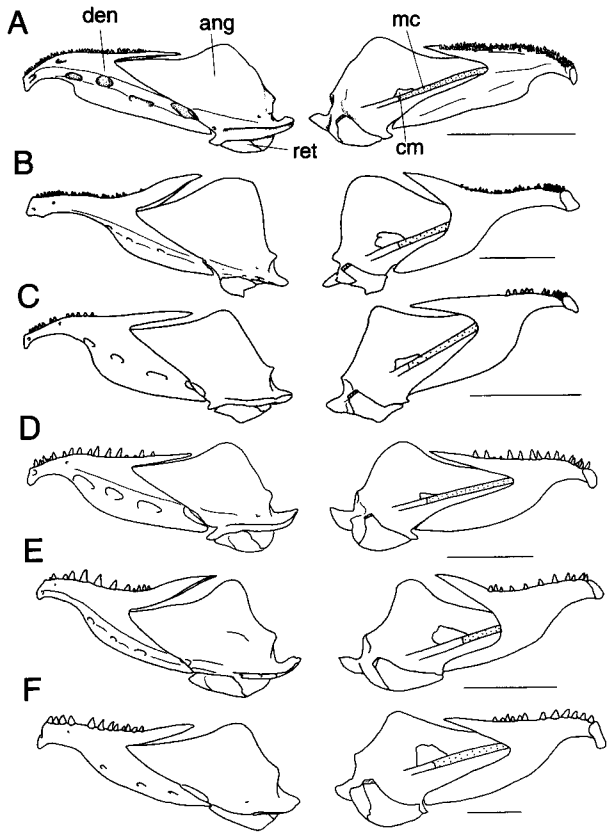

Fig. 24. Lateral (left) and medial (right) views of lower jaw. A, *Upeneus japonicus*, CNUC 23686; B, *Mulloidichthys flavolineatus*, UW 015145; C, *Mullus surmuletus*, HUMZ 154869; D, *Upeneichthys stotti*, WAM P. 30880.02; E, *Parupeneus barberinoides*, BSKU 015278; F, *Pseudupeneus prayensis*, NSMT-P 54121. Scales indicate 5 mm.

of the lower jaw, is attached to the anguloarticular postero-medially. It is also connected to the interopercle by a strong ligament.

Characters

TS 13. Supramaxilla (Fig. 20)

0: not expanded; 1: expanded. All genera of the mullids have a supramaxilla on the postero-dorsal region of the maxilla. It is small and not expanded posteriorly in *Upeneichthys* (0), however, those of the

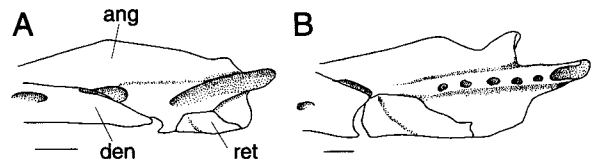

Fig. 25. Ventro-lateral view of posterior region in lower jaw. A, *Upeneus japonicus*, CNUC 23686; B, *Parupeneus bifasciatus*, HUMZ 155960. Scales indicate 1 mm.

remaining genera are expanded posteriorly like a fan (1).

Remarks. Gosline (1984) considered the supramaxilla as a supramaxillary scale because of its overlap with the maxilla, rather than riding on the upper rim, and having circuli on its anterior surface in *Upeneus parvus*. However, the circuli were not observed in all the specimens observed in the present study, and at least in *Upeneichthys*, the supramaxilla rides on the posterior upper rim of the maxilla (Fig. 20D), although in most genera of mullids the overlapping condition is observed. Accordingly, the bone is considered as a supramaxilla in the present study. The supramaxilla is also found in *Lates, Stereolepis*, and *Trachurus* among outgroups examined.

TS 14. Alveolar process of premaxilla (Fig. 20)

0: long; 1: shortened. The alveolar process is long in all genera of mullids (0), except *Mulloidichthys*. The shortened alveolar process of premaxilla is found only in *Mulloidichthys* (1).

TS 15. Teeth type on jaws (Fig. 22)

0: villiform teeth; 1: small conical teeth; 2: large conical teeth (unordered). Villiform teeth on both jaws were found in *Upeneus* (0) and small conical teeth in *Mullus, Upeneichthys* and *Mulloidichthys* (1). Large conical teeth were found in only *Parupeneus* and *Pseudupeneus* (2).

TS 16. Teeth on upper jaw in adult (Fig. 22)

0: present; 1: absent. All genera of the mullids, except *Mullus*, have teeth on upper jaw (0), but teeth are absent in adults of *Mullus* (1).

Remarks. The presence of premaxillary teeth in juveniles of *Mullus* is reported in several works, for example, *M. barbatus* by Wirszubski (1953). Caldwell (1962) also reported that *M. auratus* less than 50 mm has visible teeth in the upper jaw, and Aguirre (1997) described the loss of teeth from the premaxilla during the juvenile stage of *M. barbatus* and *M. surmuletus*.

TS 17. Enlarged conical teeth in upper jaw (Fig. 22)

0: absent; 1: present. Enlarged conical teeth in the outer row are absent in all genera (0), except *Pseudupeneus*, where they are present (1).

Remarks. Rosenblatt and Hoese (1968) reported on the sexual dimorphism in the dentition of *Pseudupeneus* based on observation of *Ps. grandisquamis* and *Ps.*

maculatus, that is, the enlarged outer row of conical teeth in the upper jaw is developed only in subadult and adult males. However, an enlarged outer row of conical teeth was found in the upper jaw of an adult female of *Ps. maculatus* (ANSP 133851, 227.2 mm SL) in the present study.

TS 18. Maxillo-supramaxillary ligament (Fig. 23)

0: absent; 1: present. The maxillo-supramaxillary ligament is present only in *Parupeneus* and *Pseudupeneus* among mullid genera (1).

Other variations.

Perforation of anguloarticular. Intraspecific variation is found in *M. argentinae* and *Up. vlamingii*, which have two conditions, opened and multi-perforated.

1-4. Suspensorium and opercular bones (Figs. 26-32)

Description

The suspensorium (Figs. 26-27) comprises the palatine, endopterygoid, ectopterygoid, metapterygoid, quadrate, symplectic and hyomandibula. The opercular bones include the preopercle, opercle, subopercle and interopercle.

The palatine occupies an anterior portion of the suspensorium. The anterior portion of the palatine expands and articulates with the head region of the maxilla antero-ventrally. There is a well-developed socket articulating with the ethmoid cartilage on the antero-dorsal region. In *Mulloidichthys*, the socket is expanded posteriorly to articulate not with the vomer but with the lateral ethmoid (Fig. 7B). Postero-dorsally the palatine articulates with the lateral ethmoid and joins the endopterygoid and ectopterygoid posteriorly. The posterior margin of the palatine has a well developed cartilage block articulating with the endopterygoid, although in *Upeneus* there is a weak overlap between the palatine and endopterygoid medially (Fig. 27A). The palatine is edentate in all genera (Figs. 27B-F) except in *Upeneus*, which has teeth on the ventro-medial face (Fig. 27A). Usually the teeth on the palatine do not form a tooth patch in *Upeneus* (Fig. 28A), but several species of the genus, e.g., *U. crosnieri, U. parvus, U. moluccensis* and *U. taeniopterus*, have a tooth patch (Fig. 28B).

The endopterygoid is a triangular bone in lateral view and bears a strong strut projecting dorsally to articulate with the lateral ethmoid. The strut is pointed and strengthened by a ligament in *Upeneus, Mulloidichthys, Mullus*, and *Upeneichthys* (Fig. 29A); it is widened to provide a stronger connection in *Parupeneus* and *Pseudupeneus* (Fig. 29B). The endopterygoid joins the palatine anteriorly, the ectopterygoid ventrally and the metapterygoid posteriorly. Medially, the bone is expanded ventrally to overlap the quadrate in *Mullus* (Fig. 27C), *Parupeneus* (Fig. 27E), *Pseudupeneus* (Fig. 27F), *Upeneus parvus*, and *U. sulphureus*. The endopterygoid does not overlap the quadrate owing to the intervention of the posterior expansion of the ectopterygoid in *Upeneus* (Fig. 27A) (except *U. parvus* and *U. sulphureus*), *Mulloidichthys* (Fig. 27B) and *Upeneichthys* (Fig. 27D). The endopterygoid has a relatively well-developed shelf for providing the adductor arcus palatini with an attachment site in *Upeneichthys*.

The ectopterygoid is a small boomerang-shaped bone in lateral view (Fig. 30A) except in *Parupeneus*, which has a dorsal projection on the postero-dorsal region (Fig. 30B). The bone articulates with the palatine anteriorly and joins the endopterygoid via a thin cartilaginous strip dorsally and to the quadrate postero-ventrally. The ectopterygoid teeth are present in only the following species of *Upeneus* (Fig. 28): *U. crosnieri, U. japonicus, U. moluccensis, U. parvus, U. quadrilineatus, U. sulphureus, U. taeniopterus* and *U. vittatus*. Among them, the ectopterygoid teeth form a patch in *U. crosnieri, U. parvus* and *U. taeniopterus* (Fig. 28B).

The metapterygoid is a roughly rectangular bone with a well-developed metapterygoid lamina in all the genera (Fig. 31A) except *Mulloidichthys* and *Upeneus vittatus* (Fig. 31B). The bone is overlapped by the endopterygoid anteriorly and is connected to the quadrate by a cartilaginous strip antero-ventrally, the symplectic ventrally and the hyomandibula postero-dorsally. Interdigitation between the endopterygoid and the metapterygoid is present in only *Mullus argentinae* and *M. barbatus*, while in the remaining mullid species the metapterygoid is smoothly overlapped by the endopterygoid.

The quadrate is a triangular bone having a large condyle for articulation with the anguloarticular antero-ventrally. It joins the ectopterygoid anteriorly, the endopterygoid, metapterygoid and symplectic dorsally, and the preopercle posteriorly.

The wedge-like symplectic (Fig. 27) has a cartilaginous cap on its ventral tip and a cartilaginous socket for articulation with the interhyal dorsally. It is overlapped by the quadrate laterally and interdigitated with the metapterygoid antero-dorsally. Posteriorly the symplectic is firmly attached to the preopercle.

The hyomandibula (Figs. 26, 27) is a large bone with a long shaft ventrally and three articular facets: the upper facet articulates with the sphenotic and prootic, the medial facet with the pterotic, and the posteriormost facet with the antero-dorsal corner of the opercle. It is sutured to the metapterygoid antero-ventrally and is firmly attached to the preopercle posteriorly. It is also

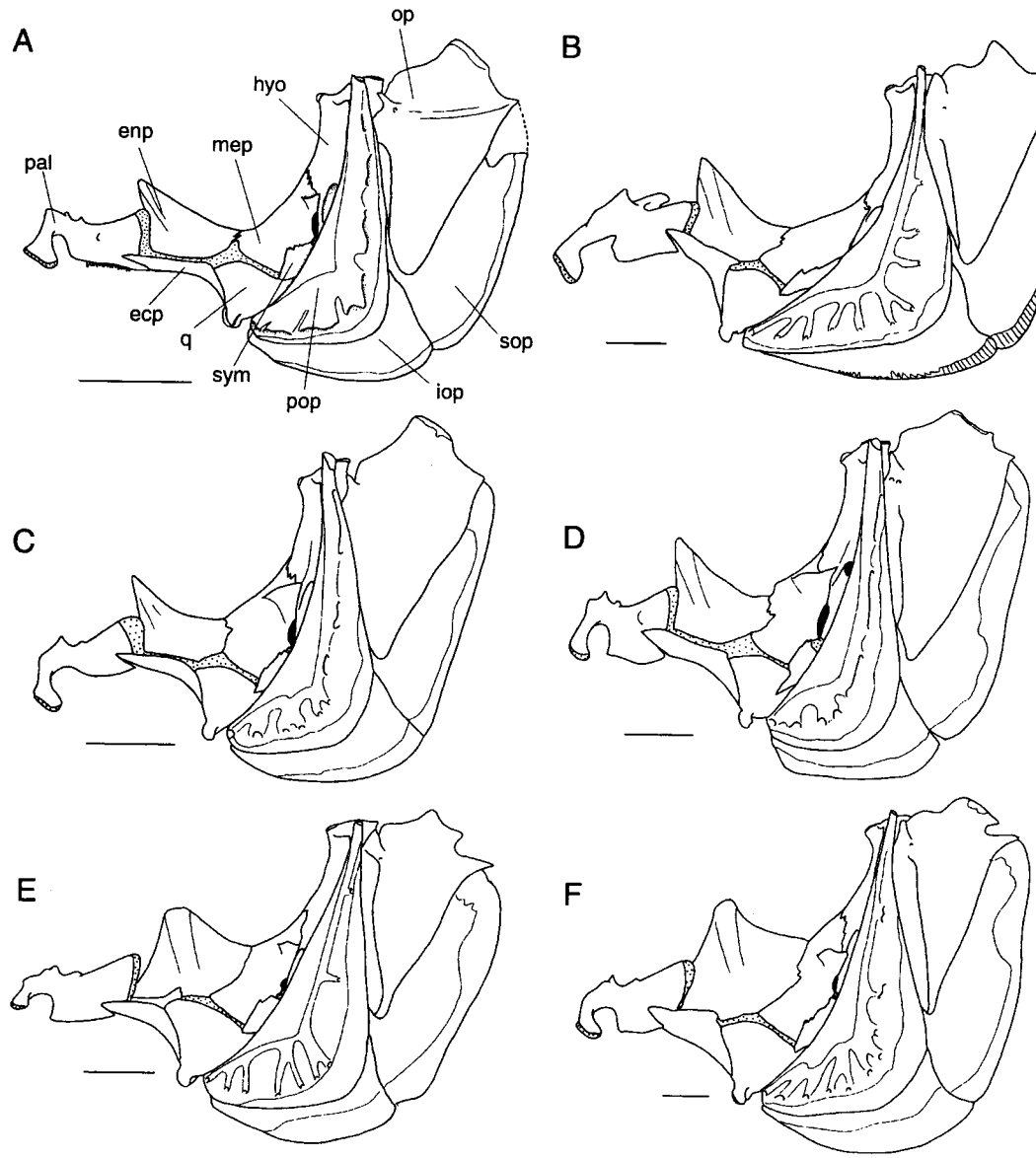

Fig. 26. Lateral view of suspensorium. A, *Upeneus japonicus*, CNUC 23686 ; B, *Mulloidichthys flavolineatus*, UW 015145 ; C, *Mullus surmuletus*, HUMZ 154869 ; D, *Upeneichthys stotti*, WAM P. 30880.02 ; E, *Parupeneus barberinoides*, BSKU 015278 ; F, *Pseudupeneus prayensis*, NSMT-P 54121. Scales indicate 5 mm.

attached to the symplectic and interhyal, intervened by cartilage ventrally.

The preopercle (Fig. 26) is a crescent-shaped bone housing the preopercular sensory canal of the laterosensory canal system. The canal is continuous with that of the anguloarticular antero-ventrally and that of the pterotic dorsally. The canal branches are broadly joined or anastomosed in *Upeneus, Mullus* and *Upeneichthys* (Figs. 26A, 26C-D), they are more strongly separated and better defined in *Mulloidichthys, Parupeneus* and *Pseudupeneus* (Figs. 26B, 26E-F). The posterior margin of the preopercle is membranous without any spine-like projection. It is attached to the hyomandibula and quadrate anteriorly, and the opercle, subopercle and interopercle posteriorly.

The opercle (Figs. 27, 32) is a large triangular bone joining the hyomandibula and preopercle anteriorly and the subopercle ventrally. There is a strong spine strengthened by a well-developed opercular medial strut on the posterior margin in *Mulloidichthys, Parupeneus* and *Pseudupeneus* (Fig. 32A), whereas in *Mullus* and *Upeneichthys* the opercle has a weak and flat projection owing to a weak medial strut (Fig. 32B). The genus *Upeneus* has two forms of opercular medial strut, that is, it is well-developed in *U. asymmetricus, U. japonicus, U. pori, U. crosnieri, U. luzonius* and *U. tragula*, whereas it is weak in *U. taeniopterus, U. moluccensis, U. parvus, U. quadrilineatus, U. sulphureus* and *U. vittatus*.

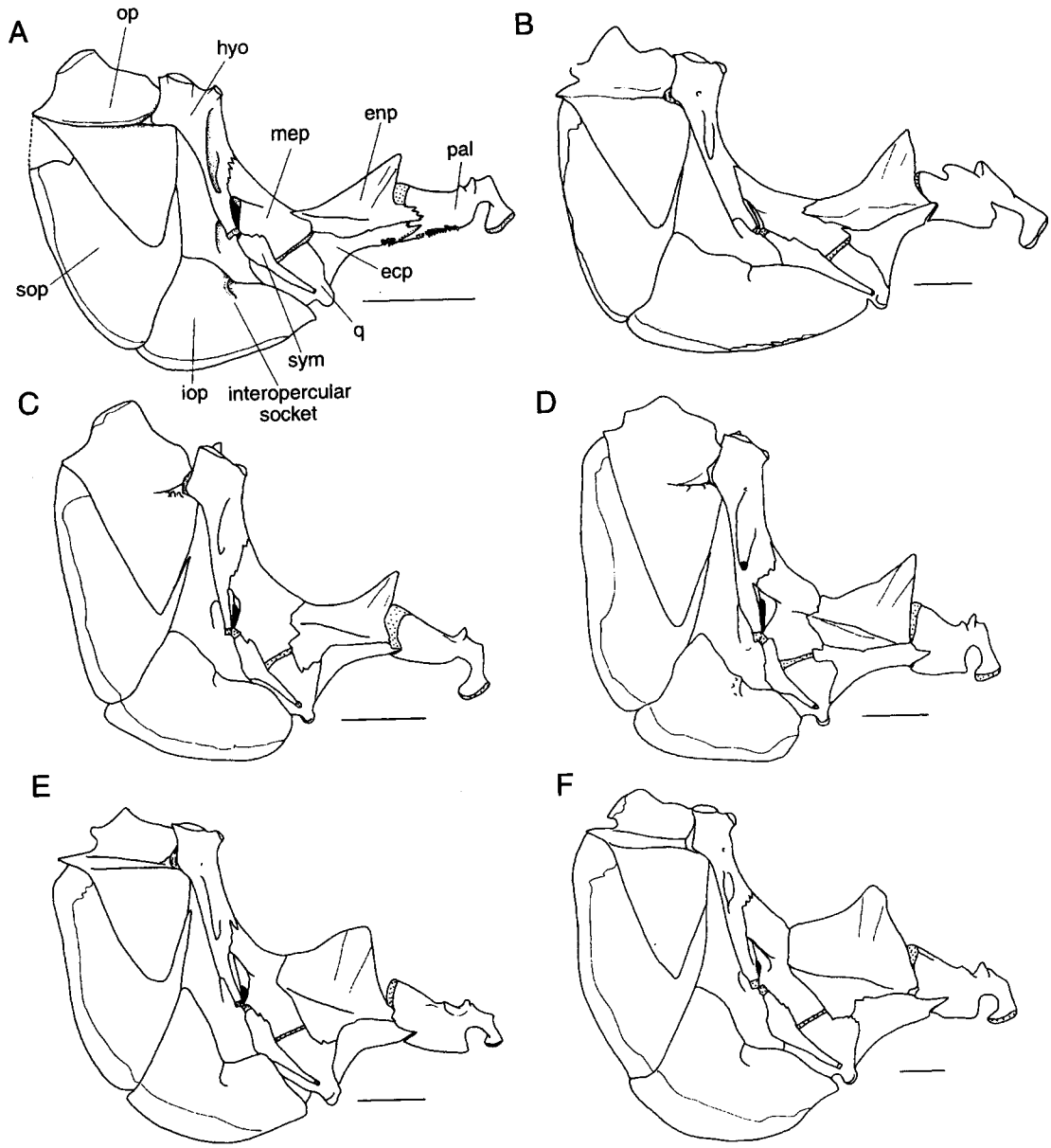

Fig. 27. Medial view of suspensorium. A, *Upeneus japonicus*, CNUC 23686; B, *Mulloidichthys flavolineatus*, UW 015145; C, *Mullus surmuletus*, HUMZ 154869; D, *Upeneichthys stotti*, WAM P. 30880.02; E, *Parupeneus barberinoides*, BSKU 015278; F, *Pseudupeneus prayensis*, NSMT-P 54121. Scales indicate 5 mm.

The L-shaped subopercle (Figs. 26, 27) joins the ventral part of the opercle dorsally, to the antero-ventral margin of the preopercle anteriorly, and the interopercle ventrally. The posterior margin of the bone is membranous and smooth.

The triangular interopercle is connected with the retroarticular by a strong ligament. It bears a well-developed articular socket that receives the posterior end of the posterior ceratohyal on its dorso-central region of the medial surface (Fig. 27).

Characters

TS 19. Teeth on palatine (Fig. 27)

0: absent; 1: present. Teeth on the palatine are absent in all genera (0) except in *Upeneus* (Fig. 27), where they are present (1).

TS 20. Palatine and endopterygoid (Fig. 27)

0: firmly attached; 1: incompletely articulated (overlapped); 2: completely articulated (ordered). A firm attachment between the palatine and the endopterygoid is found in all outgroups (0), and the palatine of *Upeneus* is articulated with the endopterygoid, except slight medial overlapping between them (1). However, in the remaining genera of mullids there is no direct connection between them, owing to the presence of a cartilaginous block on the posterior margin of the

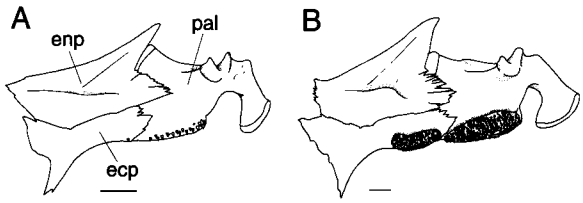

Fig. 28. Medial view of anterior portion of suspensorium. A, *Upeneus vittatus*, HUMZ 46773 ; B, *U. taeniopterus*, HUMZ 155966. Scales indicate 2 mm.

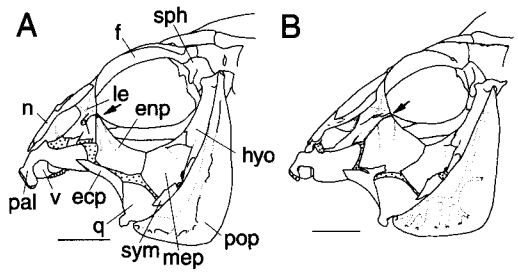

Fig. 29. Lateral view of articular portion between neurocranium and suspensorium. A, *Mullus surmuletus*, HUMZ 154869 ; B, *Parupeneus multifasciatus*, HUMZ 62786. Arrows show the articular portion between two bony structures. Scales indicate 5 mm.

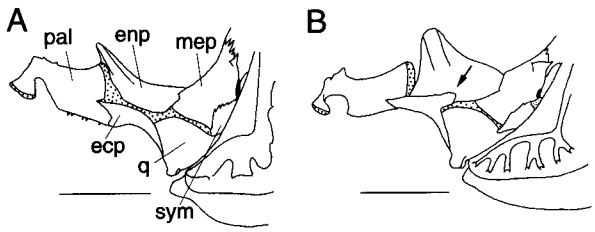

Fig. 30. Lateral view of anterior portion of suspensorium. A, *Upeneus moluccensis*, BSKU 084674 ; B, *Parupeneus pleurostigma*, UW 01330. Arrow shows the projection of ectopterygoid. Scales indicate 5 mm.

palatine (2).

TS 21. Articulation of endopterygoid with lateral ethmoid (Fig. 29)

0 : separated ; 1 : weak articulation ; 2 : strong articulation (ordered). The lateral ethmoid articulates with the palatine in all outgroups (0), but with the endopterygoid in the mullids. Among mullid genera, the articular portion of the endopterygoid in *Upeneus, Mullus, Upeneichthys* and *Mulloidichthys* is pointed, providing a relatively weak articulation (1), whereas in *Parupeneus* and *Pseudupeneus* it is blunt and provides a strong articulation (2).

TS 22. Ectopterygoid projection (Fig. 30)

0 : absent ; 1 : present. The ectopterygoid projection, which overlaps the endopterygoid dorsally, is absent in all mullid genera (0) except *Parupeneus*, where

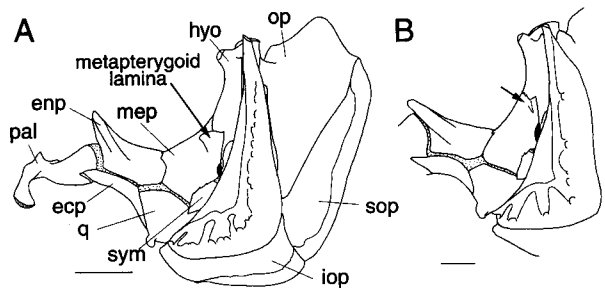

Fig. 31. Lateral view of suspensorium. A, *Mullus surmuletus*, HUMZ 154868 ; B, *Upeneus vittatus*, HUMZ 46769. Scales indicate 5 mm.

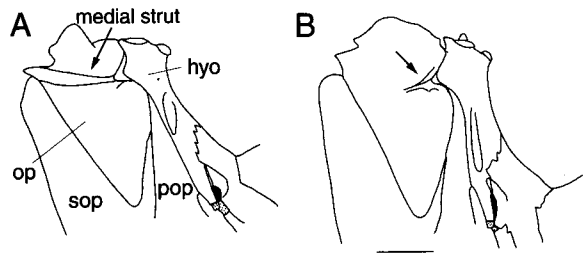

Fig. 32. Medial view of postero-dorsal portion of suspensorium. A, *Pseudupeneus prayensis*, HUMZ 31015 ; B, *Upeneichthys stotti*, WAM P. 30880.002. Scales indicate 5 mm.

there is such a projection (1).

TS 23. Metapterygoid lamina (Fig. 31)

0 : present ; 1 : minimized and modified into a narrow canal-like structure. Most genera of mullids have a well-developed metapterygoid lamina (0). However, it is modified into a narrow canal-like structure in *Mulloidichthys* and *Upeneus vittatus* (1).

TS 24. Preopercular sensory canal (Fig. 26)

0 : simple ; 1 : branched. The preopercular sensory canal is simple in *Upeneus, Upeneichthys* and *Mullus* (0), whereas it is branched in *Mulloidichthys, Parupeneus* and *Pseudupeneus* (1).

TS 25. Opercular medial strut (Fig. 32)

0 : extended backward ; 1 : reduced. The opercular strut is extended backwards to the posterior edge of the opercle in all examined species of *Upeneus* (except the ones mentioned below), *Mulloidichthys, Parupeneus* and *Pseudupeneus* (0). This medial strut is considerably reduced in *Mullus, Upeneichthys, U. taeniopterus, U. moluccensis, U. parvus, U. quadrilineatus, U. sulphureus* and *U. vittatus* (1).

Other variations

Ectopterygoid teeth. Teeth on the ectopterygoid are only found in several species of *Upeneus* (*U. japonicus, U. moluccensis, U. parvus, U. quadrilineatus, U. sulphureus, U. crosnieri, U. tragula, U. taeniopterus*). How-

ever, intraspecific variation (present or absent) is observed at least in *U. vittatus*.

Medial overlap of endopterygoid by quadrate. The endopterygoid is overlapped by the quadrate medially in *Mullus, Parupeneus, Pseudupeneus, Upeneus parvus, U. sulphureus* and *Upeneichthys stotti*, while it is separated from the quadrate in *Upeneus* (except *U. parvus* and *U. sulphureus*), *Mulloidichthys* and *Upeneichthys* (except *Up. stotti*). However, intraspecific variation is observed in this character in *U. sulphureus* and *Up. stotti*.

1-5. Hyoid arch (Figs. 33-36)

Description

The hyoid arch (Figs. 33-36) comprises the basihyal, dorsal and ventral hypohyals, anterior and posterior ceratohyals, interhyal, urohyal, and five branchiostegal rays, including the barbel, which is a modified first branchiostegal ray.

The basihyal, lying over the hypohyals, is a simple rod-like bone. It is usually detached from the hyoid arch except in *Upeneus parvus*. In *U. parvus* the basihyal is a narrow plate-like bone, being attached to

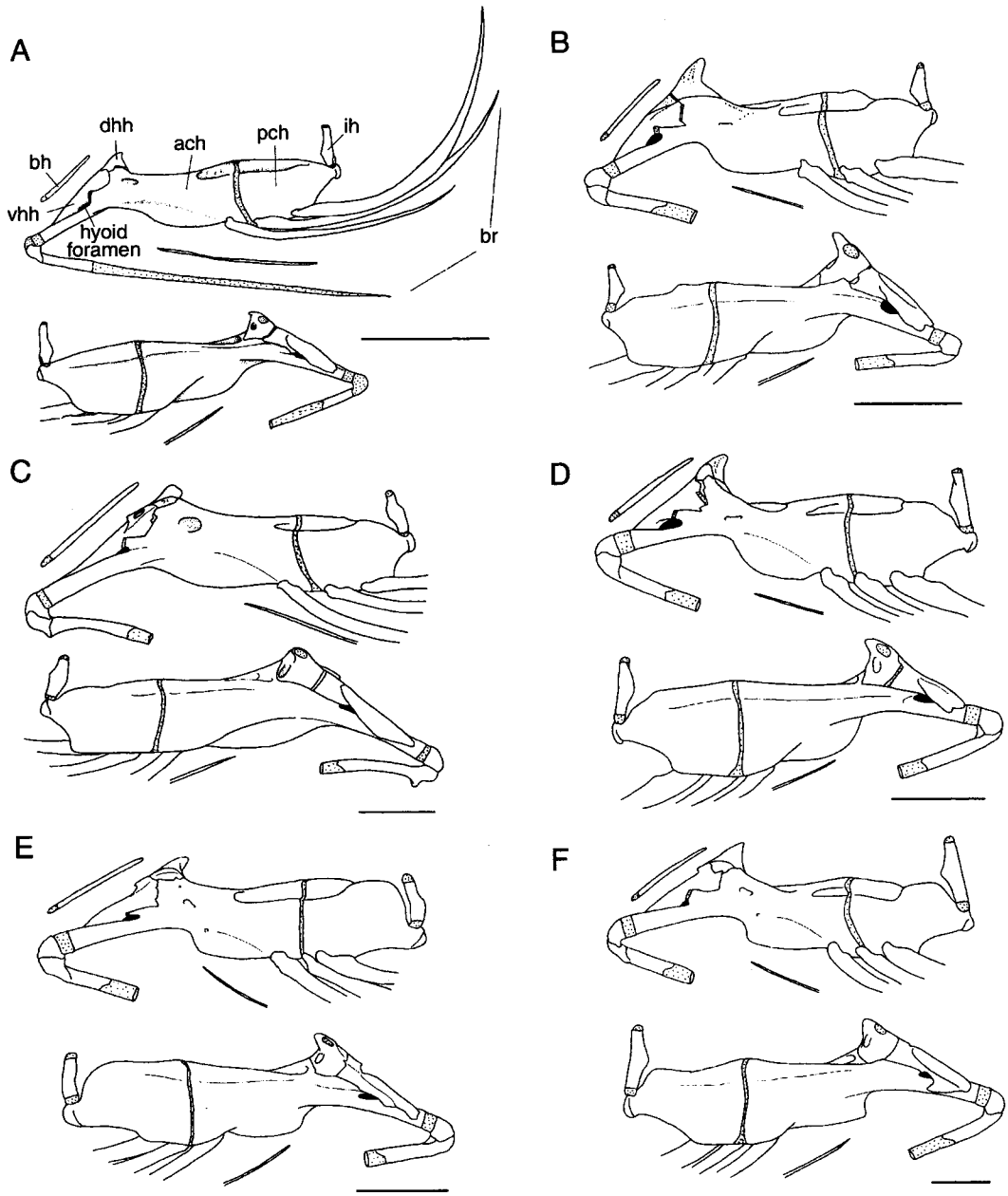

Fig. 33. Lateral (above) and medial (below) views of hyoid arch, except urohyal. A, *Upeneus japonicus*, CNUC 23686 (after Kim et al., 2001); B, *Mulloidichthys flavolineatus*, UW 015145; C, *Mullus surmuletus*, HUMZ 154869; D, *Upeneichthys stotti*, WAM P. 30880.02; E, *Parupeneus barberinoides*, BSKU 015278; F, *Pseudupeneus prayensis*, NSMT-P 54121. Medial view of basihyal is omitted. Scales indicate 5 mm.

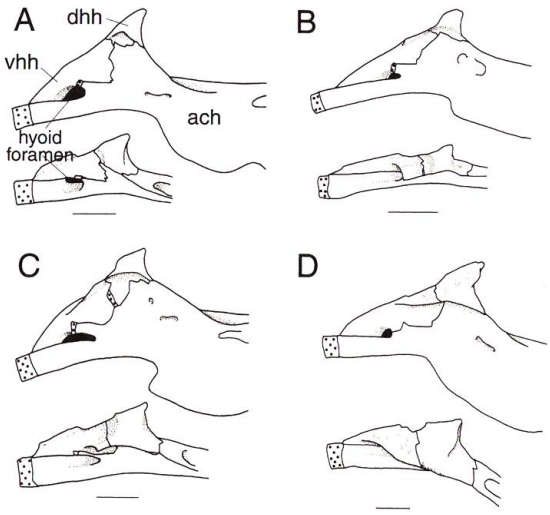

Fig. 34. Lateral (above) and dorsal (below) views of anterior region of hyoid arch. A, *Upeneichthys lineatus*, AMS I. 16879-006 ; B, *Mulloidichthys vanicolensis*, URM-P 26052 ; C, *Pseudupeneus grandisquamis*, UW 022550 ; D, *Mullus surmuletus*, HUMZ 154869. Scales indicate 2 mm.

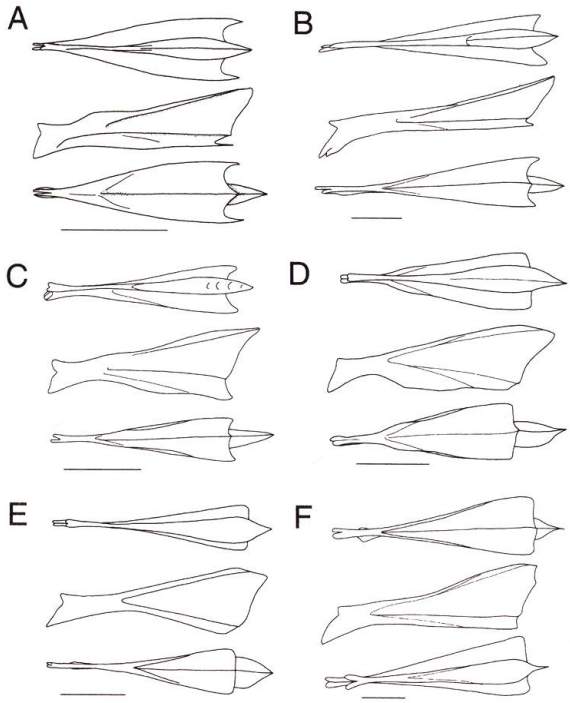

Fig. 35. Dorsal (top), lateral (center) and ventral (bottom) views of urohyal. A, *Upeneus japonicus*, CNUC 23686 ; B, *Mulloidichthys flavolineatus*, UW 015145 ; C, *Mullus surmuletus*, HUMZ 154869 ; D, *Upeneichthys stotti*, WAM P. 30880.02 ; E, *Parupeneus barberinoides*, BSKU 15278 ; F, *Pseudupeneus prayensis*, NSMT-P 54121. Scales indicate 5 mm.

the dorsal hypohyal by weak connective tissue.

The hypohyal, occupying the anterior portion of the hyoid arch, is composed of two elements of the dorsal and ventral hypohyals. These two elements take an oblique position caused by the anterior elongation of the anterior ceratohyal. The dorsal hypohyal is firmly attached to the anterior ceratohyal and the ventral hypohyal ventrally ; it is also connected to the first hypobranchial by a strong ligament posteriorly, and it bears a canal for the hyoid artery on its medial face. The ventral hypohyal firmly joins the anterior ceratohyal posteriorly and the dorsal hypohyal postero-dorsally, and is connected with the anterior tip of the urohyal by a strong ligament medially. There is no expansion or flat projection of the dorsal portion of the ventral hypohyal in *Upeneus asymmetricus, U. japonicus, U. luzonius, U. tragula* and *Upeneichthys* (Fig. 34A). The expanded projection, which is continuous with the dorsal hypohyal, is present in *U. moluccensis, U. parvus, U. quadrilineatus, U. sulphureus, U. taeniopterus, U. vittatus, Mulloidichthys, Mullus, Parupeneus* and *Pseudupeneus* (Figs. 34B-C). The ventral hypohyal is

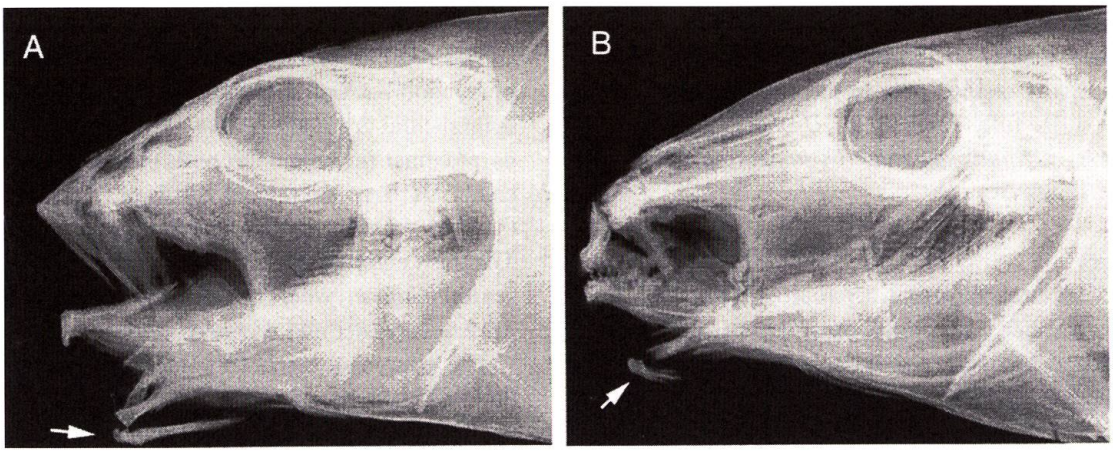

Fig. 36. Positive image of radiograph of anterior portion in *Upeneus moluccensis*, HUMZ 74102 (A) and *Parupeneus forsskali* (B), HUJ 57-262. Arrows indicate barbels.

especially expanded in *Mullus* (Fig. 34D). There is a relatively large hyoid foramen between the ventral hypohyal and the anterior ceratohyal for passage of the extensor tentaculi. It is formed by a forward elongation of the anterior ceratohyal.

The anterior ceratohyal is an elongated structure supporting the barbel on its anterior tip, intervened by a cap of fibro-cartilage. It makes contact with the hypohyals antero-dorsally, synchondrally joins the posterior ceratohyal on both sides posteriorly, and supports the third branchiostegal ray. The triangular posterior ceratohyal joins the anterior ceratohyal anteriorly and articulates with the interhyal postero-dorsally. It has a relatively well-developed condyle articulating with the interopercle on its posterior margin. It supports the posterior two branchiostegal rays. The anterior and posterior ceratohyals are convex laterally for providing attachment sites for the extensor tentaculi.

The rod-like interhyal connects the posterior ceratohyal with the suspensorium. It fits into the interspace between the lower shaft of the hyomandibula and the head of the symplectic dorsally, and articulates with the postero-dorsal corner of the posterior ceratohyal by cartilaginous tip ventrally.

The urohyal (Fig. 35), lying on the midline below the basibranchials, is connected to the ventral hypohyal by a strong ligament anteriorly. It has two expanded wings, a dorsal and a wider ventral one, and its shape in transverse section is a reclining H-shape (*sensu* Kusaka, 1974). The ventral face of the urohyal is concave, providing an attachment site for the sternohyoideus.

There are five branchiostegal rays including the barbel. The second branchiostegal ray is a very thin, thread-like bone. It does not articulate with the anterior ceratohyal and is embedded free in the hyohyoidei abductores section 2, which connects the third branchiostegal with the ventral face of the urohyal. The third branchiostegal ray is attached to the postero ventral region of the anterior ceratohyal, and the remaining two are attached mainly to the posterior ceratohyal. The barbel is usually ossified only in the basal portion (Fig. 36B), but it is fully ossified in *Upeneus parvus, U. moluccensis, U. quadrilineatus, U. sulphureus* and *U. vittatus* (Fig. 36A).

Characters

TS 26. First branchiostegal ray (barbel) (Fig. 36)

0: fully ossified; 1: partly ossified. In all mullid genera except *Upeneus*, the basal portion of the first branchiostegal ray (the barbel) is partly ossified (1). In *Upeneus*, five species, comprising *U. parvus, U. moluccensis, U. quadrilineatus, U. sulphureus* and *U. vittatus*, have a fully ossified barbel (0).

TS 27. Dorsal hypohyal (Fig. 34)

0: not expanded; 1: expanded. The dorsal hypohyal is not expanded in all mullid genera (0) except in *Mullus*, which has an expanded dorsal hypohyal (1).

Other variations

None.

1-6. Branchial arch (Figs. 37-39)

Description

The branchial arch (Figs. 37-39) comprises the basibranchial, hypobranchial, ceratobranchial, epibranchial and pharyngobranchial.

The basibranchials, occupying the median base of the branchial skeleton, consist of three thin plate-like bones and one cartilaginous element. The first basibranchial is a pointed rod-like bone being inserted into the lower portion between both dorsal hypohyals. The second basibranchial is sandwiched between the first and third hypobranchials, and the third by the second and fourth hypobranchials. The last basibranchial is bounded by the third hypobranchial and fourth ceratobranchial.

The hypobranchials, situated between the basibranchial and the ceratobranchial, are three paired bones decreasing in size posteriorly. The first hypobranchial is projected anteriorly on its lateral side and connected to the dorsal hypohyals by a strong ligament.

There are five ceratobranchials consisting of four rod-like bones and a toothed triangular bone. The first to third ceratobranchials articulate with corresponding hypobranchial facets anteriorly and epibranchials facets posteriorly. The fourth ceratobranchial is attached to the fourth basibranchial and its antimere anteriorly, and to the fourth epibranchial posteriorly. The fifth ceratobranchials on each side makes contact with each other along the midline. The fifth ceratobranchial usually bears small conical teeth except in *Upeneus vittatus* (Fig. 39A) and *Mulloidichthys flavolineatus* (Fig. 38E), which have a mixture of conical and molar teeth.

The rod-like epibranchials are situated between the pharyngobranchials and the ceratobranchials. The first epibranchial is a slender bone with a dorsal process, and its proximal tip articulates with the first pharyngobranchial. A large interarcual cartilage is present between the first epibranchial and second pharyngobranchial. The third epibranchial usually bears a tooth plate on the ventral surface, whereas the tooth-plate is absent in *Mullus barbatus* and *Upeneus parvus*.

The pharyngobranchials comprise one cartilage and three toothed bones (Figs. 37A-C, 37E-F). However, the first pharyngobranchial is a small, rod-like, toothless bone in *Upeneichthys, Upeneus parvus*, and *U. taeniopterus* (Fig. 37D). The first pharyngobranchial

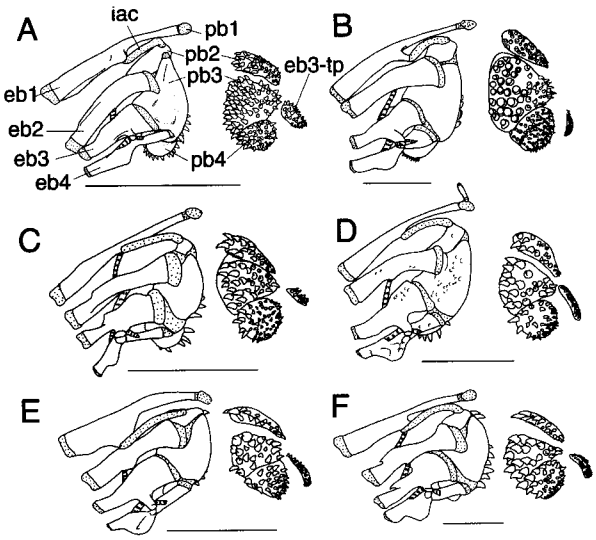

Fig. 37. Dorsal view of upper branchial arch and ventral view of its tooth-plate. A, *Upeneus japonicus*, CNUC 23686; B, *Mulloidichthys flavolineatus*, UW 015145; C, *Mullus surmuletus*, HUMZ 154869; D, *Upeneichthys stotti*, WAM P. 30880.02; E, *Parupeneus barberinoides*, BSKU 015278; F, *Pseudupeneus prayensis*, NSMT-P 54121. Scales indicate 5 mm.

makes contact with the parasphenoid anteriorly and with the first epibranchial posteriorly. The second is connected to the first epibranchial via the interarcual cartilage anteriorly, to the second epibranchial laterally, and to the third pharyngobranchial posteriorly. The largest third pharyngobranchial articulates with the second to fourth epibranchials laterally and with the fourth pharyngobranchial posteriorly. A mixture of conical and molar teeth was found in the third and fourth pharyngobranchials of *Upeneus vittatus* (Fig. 39A) and in the third pharyngobranchial of *Mulloidichthys flavolineatus*. Fusion between the third and fourth pharyngobranchial was found only in *Upeneus crosnieri* (Fig. 39B).

Characters

TS 28. First pharyngobranchial (Fig. 37)

0: ossified; 1: not ossified. In most genera of mullids the first pharyngobranchial is not ossified (1), while *Upeneichthys, Upeneus parvus* and *U. taeniopterus* have an ossified one (0).

Other variations

Tooth plate on third pharyngobranchial. Usually the third pharyngobranchial in the mullids has a tooth plate on its ventral surface, but it is absent in *Mullus barbatus* and *Upeneus parvus*. Intraspecific variation of the tooth plate on the third pharyngobranchial was also observed, at least in *Upeneus parvus*.

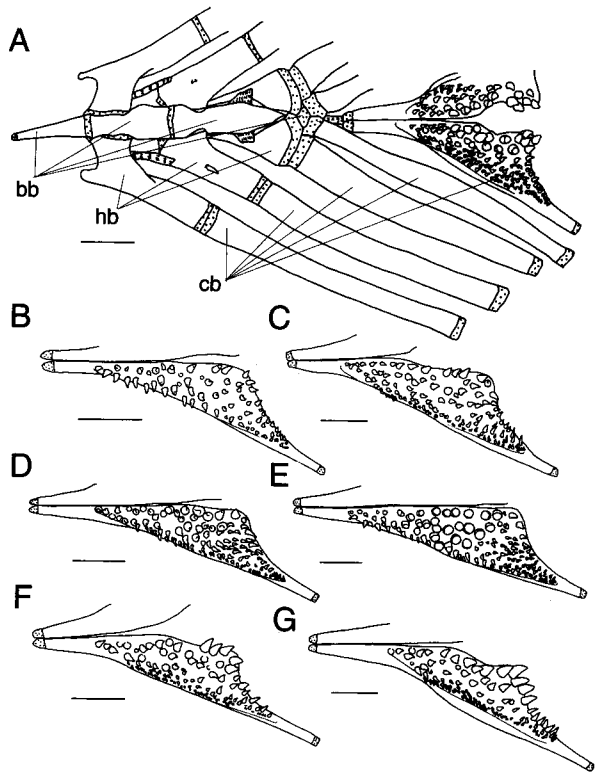

Fig. 38. Dorsal view of lower branchial arch (A) and fifth ceratobranchial (B-G). A, *Upeneus vittatus*, HUMZ 46773; B, *Mullus surmuletus*, HUMZ 154868; C, *Upeneichthys stotti*, WAM P. 30880.002; D, *Mulloidichthys flavolineatus*, NSMT-P, 19933; E, *Mu. flavolineatus*, UW 015145; F, *Parupeneus bifasciatus*, HUMZ 155960; G, *Pseudupeneus prayensis*, HUMZ 31015. Scales indicate 2 mm.

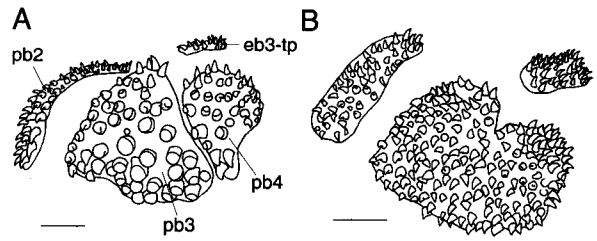

Fig. 39. Ventral view of tooth-plates of pharyngobranchial and of third epibranchial bones. A, *Upeneus vittatus*, HUMZ 46773; B, *U. crosnieri*, USNM 306101. Scales indicate 1 mm.

1-7. Pectoral girdle (Figs. 40-42)

Description

The pectoral girdle (Fig. 40) comprises the extrascapula, posttemporal, supracleithrum, cleithrum, dorsal and ventral postcleithra, scapula, coracoid and pectoral-fin radials.

The extrascapula is a single tube-like bone loosely applied to the postero-lateral region of the neurocranium. There are three main openings of the sensory

canal, with the anterior opening continuous with that of the pterotic, the posterior opening entering the posttemporal, and the dorsal opening connecting medially to its antimere.

The posttemporal is a forked bone with dorsal and ventral limbs. The dorsal limb of the bone is flat and slender, and firmly attached to the epioccipital by connective tissue. The ventral limb is slender, rod-shaped and connected to the intercalar by a strong ligament. The lateral-line canal on the posttemporal is directly connected to the first lateral-line scale.

The supracleithrum is a leaf-like bone attached to the posttemporal dorsally and the cleithrum ventrally. Baudelot's ligament connects from the lateral surface of the basioccipital to the medial face of this bone. The postero-dorsal margin of the supracleithrum is various in shape (Fig. 41). It is usually spined in *Upeneus* (except *U. parvus, U. taeniopterus* and *U. vittatus*), *Mulloidichthys* (except *Mu. flavolineatus*) and *Parupeneus heptacanthus*, is serrated in *Upeneichthys, Parupeneus* (except *P. heptacanthus*) and *Pseudupeneus prayensis*, and is smooth in *Mullus, U. parvus, U. taeniopterus, U. vittatus* and *Ps. grandisquamis*.

The cleithrum is the largest bone of the pectoral girdle and its antero-ventral region is expanded laterally like a shield. The bone makes contact with the supracleithrum dorsally, the coracoid ventrally and the scapula posteriorly. There is a round or pointed projection that receives the pharyngoclavicularis internus on the antero-medial margin of the cleithrum in *Upeneus* (except *U. parvus*), *Mulloidichthys* (except *Mu. martinicus*), *Parupeneus* (except *P. procerigena*) and *Pseudupeneus*. Usually the projection in *Mulloidichthys* and *Parupeneus* is pointed (Fig. 42C), and that in *Upeneus* is round (Fig. 42B). This cleithral projection is absent in *Mullus* and *Upeneichthys* as well as in the above exceptional species (Fig. 42A).

There are always two postcleithra. The dorsal postcleithrum is roughly crescent-shaped and attached medially to the postero-dorsal region of the cleithrum; the ventral postcleithrum is triangular, bearing a long slender process and attached to the dorsal postcleithrum.

The scapula is a roughly rectangular bone, being overlapped by the cleithrum anteriorly, and synchondrally joined to the coracoid ventrally. It articulates with the upper three pectoral-fin radials at its posterior margin. The postero-dorsal corner of the bone bears a prominent pectoral condyle for articulation with the uppermost pectoral fin ray. The number of scapular foramina varies from two to seven, but it is always two or more (Fig. 40, 42).

The coracoid is a relatively large triangular bone bearing large anterior and posterior processes, the first

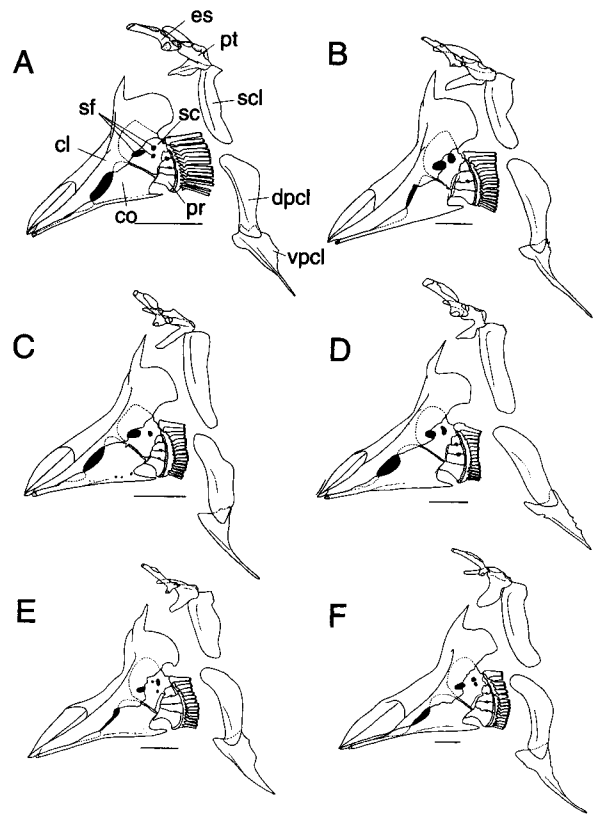

Fig. 40. Lateral view of pectoral girdle. A, *Upeneus japonicus*, CNUC 23686; B, *Mulloidichthys flavolineatus*, UW 015145; C, *Mullus surmuletus*, HUMZ 154869; D, *Upeneichthys stotti*, WAM P. 30880.02; E, *Parupeneus barberinoides*, BSKU 015278; F, *Pseudupeneus prayensis*, NSMT-P 54121. Scales indicate 5 mm.

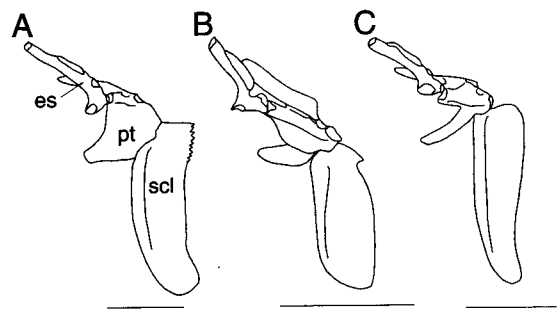

Fig. 41. Three types of postero-dorsal region on supracleithrum. A, serrate type, *Pseudupeneus prayensis*, HUMZ 31015; B, pointed type, *Upeneus moluccensis*, BSKU 084674; C, smooth type, *Mullus surmuletus*, HUMZ 154868. Scales indicate 5 mm.

nearly reaching the cleithrum, the second reaching the lowermost pectoral-fin radial. The interosseous space between the cleithrum and the coracoid is relatively narrow. There is a well-developed keel laterally in the postero-ventral region of the bone.

The number of pectoral-fin radials is always four, usually three and one-half articulating with the scapula

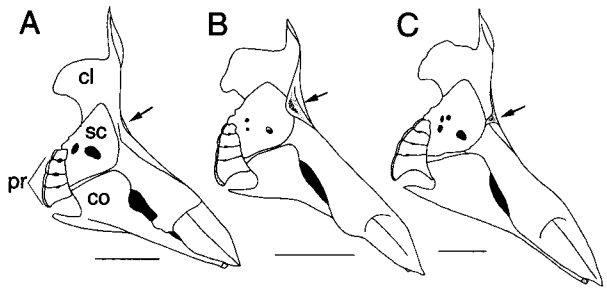

Fig. 42. Cleithral projection (arrow) for pharyngo-clavicularis internus. A, *Parupeneus pleurostigma*, HUMZ 48219; B, *Upeneus quadrilineatus*, HUMZ 35096; C, *Upeneichthys porosus*, AMS I. 17033-021. Scales indicate 5 mm.

and the lowermost one with the coracoid. They support all pectoral fin rays except the uppermost one.

Characters

None.

Other variations

Postero-dorsal shape of supracleithrum. Usually, the postero-dorsal portion of the supracleithrum is spined in *Upeneus* and *Mulloidichthys*, smooth in *Mullus*, and serrated in *Upeneichthys, Parupeneus* and *Pseudupeneus*. However, intraspecific variation is found in *U. vittatus*, with smooth or spined conditions, and also in *Mu. flavolineatus* with smooth and serrate conditions. This portion of the supracleithrum seems to be affected by the preserved condition or size of the specimen.

1-8. Pelvic girdle (Figs. 43-46)

Description

The pelvic girdle (Figs. 43-46) is composed of the

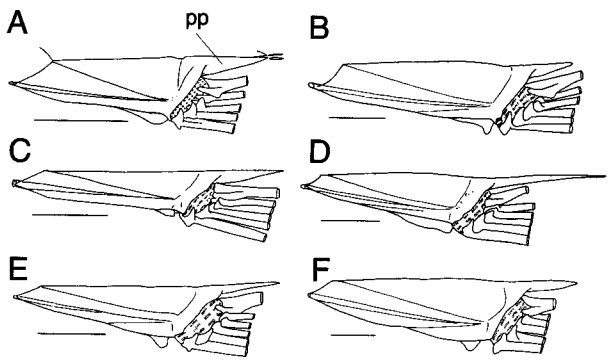

Fig. 43. Dorsal view of left pelvic girdle. A, *Upeneus japonicus*, CNUC 23686; B, *Mulloidichthys flavolineatus*, UW 015145; C, *Mullus surmuletus*, HUMZ 154869; D, *Upeneichthys stotti*, WAM P. 30880.02; E, *Parupeneus barberinoides*, BSKU 015278; F, *Pseudupeneus prayensis*, NSMT-P 54121. Scales indicate 5 mm.

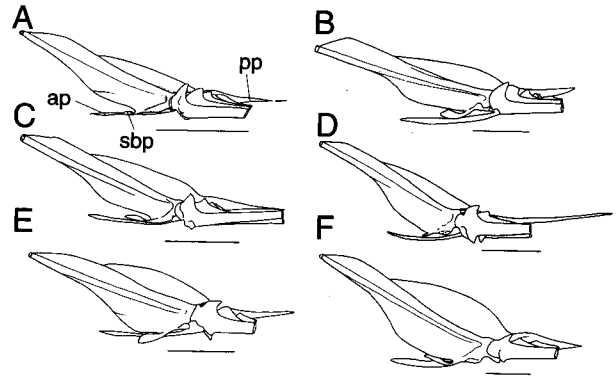

Fig. 44. Lateral view of left pelvic girdle. A, *Upeneus japonicus*, CNUC 23686; B, *Mulloidichthys flavolineatus*, UW 015145; C, *Mullus surmuletus*, HUMZ 154869; D, *Upeneichthys stotti*, WAM P. 30880.02; E, *Parupeneus barberinoides*, BSKU 015278; F, *Pseudupeneus prayensis*, NSMT-P 54121. Scales indicate 5 mm.

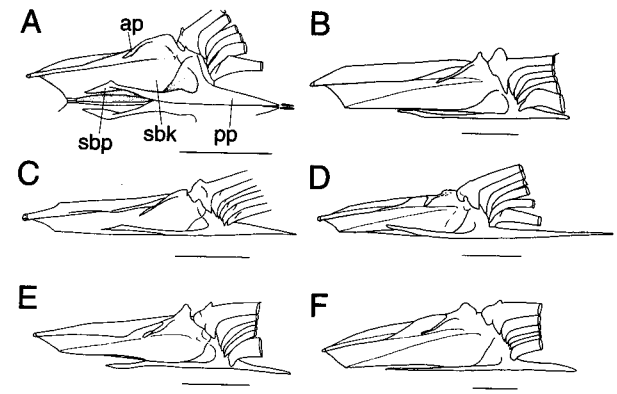

Fig. 45. Ventral view of left pelvic girdle. A, *Upeneus japonicus*, CNUC 23686; B, *Mulloidichthys flavolineatus*, UW 015145; C, *Mullus surmuletus*, HUMZ 154869; D, *Upeneichthys stotti*, WAM P. 30880.02; E, *Parupeneus barberinoides*, BSKU 015278; F, *Pseudupeneus prayensis*, NSMT-P 54121. Scales indicate 5 mm.

paired basipterygia which are elongated triangular bones. It is attached to the cleithrum at its antero-dorsal portion. There are two processes ventrally, one is the subpelvic process and the other the postpelvic process. There is a leaf-like additional process projected antero-medially near the lateral process of the basipterygium. Both basipterygia are separated from each other at their anterior tip, forming V-shape, and the accessory subpelvic keels are expanded medially nearly to meet each other along the midline. There are three types of postpelvic processes in the mullids. One is a blunt type, represented by *Upeneus moluccensis, U. parvus, U. quadrilineatus, U. sulphureus* and *U. vittatus* (Fig. 46A), the other is a pointed type, represented by *U. asymmetricus, U. japonicus, U. luzonius, U. pori, U.*

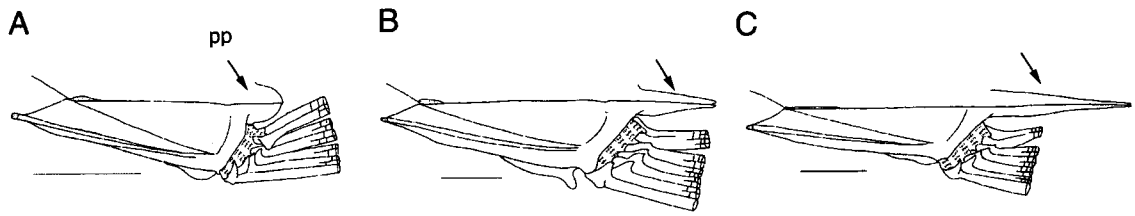

Fig. 46. Three types of postpelvic process (arrow). A, blunt type, *Upeneus moluccensis*, BSKU 084674; B, pointed type, *Parupeneus barberinoides*, HUMZ 39651; C, elongated type, *Upeneichthys stotti*, WAM P. 30880.002. Scale bars indicate 5 mm.

taeniopterus, U. tragula, Mullus, Mulloidichthys, Parupeneus and *Pseudupeneus* (Fig. 46B). The third is an elongated type found in *Upeneichthys* (Fig. 46C). The elongated type is prominently elongated posteriorly, and its length is nearly half that of the entire basipterygium.

Characters

TS 29. Postpelvic process (Fig. 46)

0: blunt; 1: pointed; 2: elongated (ordered). A blunt postpelvic process is found in *U. moluccensis, U. parvus, U. quadrilineatus, U. sulphureus* and *U. vittatus* (0). The pointed type is found in *U. asymmetricus, U. japonicus, U. luzonius, U. pori, U. taeniopterus, U. tragula, Mullus, Mulloidichthys, Parupeneus*, and *Pseudupeneus* (1). In only *Upeneichthys* the postpelvic process is prominently elongated (2).

Other variations

None.

1-9. Caudal skeleton (Figs. 47-48)

Description

The caudal skeleton (Fig. 47) is composed of the second and third preural centra and their neural and haemal spines, uroneural, epurals, urostyle-hypural complex (which is formed by fusion of the urostyle and hypurals 3-4), hypurals and parhypural bone.

The second preural centrum is located anterior to the urostyle-hypural complex. It bears dorsally a short neural spine, projected postero-dorsally, and an autogenous haemal spine ventrally. The third preural centrum lies anterior to the second preural centrum and bears a long neural spine dorsally and an autogenous haemal spine ventrally.

The urostyle is fused with hypurals 3-4 to form the urostyle-hypural complex. It tightly joins the uroneural dorsally and articulates with the lower two hypurals postero-ventrally and the parhypural ventrally.

The uroneural is a crescent-shaped bone lying on the antero-dorsal region of the urostyle-hypural complex. There is a second uroneural between the posteriormost epural and the uppermost hypural in *Parupeneus* (except in *P. margaritatus* and *P. procerigena*), *Upeneichthys porosus* and *Pseudupeneus grandisquamis*, while it is absent in most *Upeneus, Mulloidichthys, Mullus*, and *Up. lineatus, Up. vlamingii* and *Ps. prayensis*.

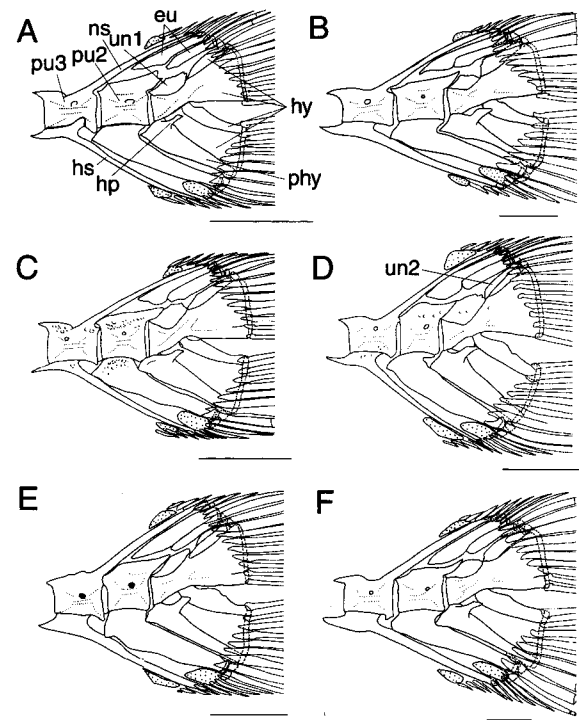

Fig. 47. Lateral view of caudal skeleton. A, *Upeneus japonicus*, CNUC 23686; B, *Mulloidichthys flavolineatus*, UW 015145; C, *Mullus surmuletus*, HUMZ 154869; D, *Upeneichthys stotti*, WAM P. 30880.02; E, *Parupeneus barberinoides*, BSKU 015278; F, *Pseudupeneus prayensis*, NSMT-P 54121. Scales indicate 5 mm.

The epurals are broad plate-like bones, and there are always two. The anterior epural is larger than the posterior one, and its lower tip lies over the neural spine of the second preural centrum. They are tightly joined to each other.

The hypurals are plate-like bones consisting of four elements. The first and second hypurals articulate with the postero-ventral region of the urostyle-hypural complex. The third and fourth hypurals are fused to each other and also with the urostyle at its base to form the urostyle-hypural complex. The fifth hypural is situated

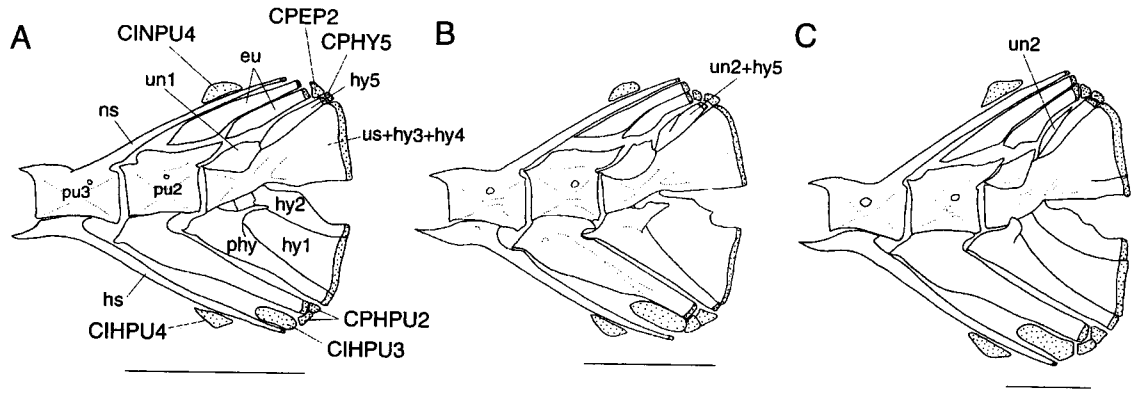

Fig. 48. Lateral view of caudal skeleton after caudal fin rays removed. A, *Upeneus asymmetricus*, USNM 267584; B, *U. quadrilineatus*, HUMZ 35096; C, *Pseudupeneus grandisquamis*, UW 022550. Scales indicate 5 mm.

on the urostyle-hypural complex. Hypural 1 and hypural 2 are usually separated from each other, while they are fused completely with each other in *Upeneus vittatus* and *U. quadrilineatus* (Fig. 48B), and are incompletely fused in *Parupeneus procerigena* and *Mulloidichthys martinicus*. Hypural 3 and hypural 4 are completely fused to each other in *Upeneus* (Fig. 47A), *Mulloidichthys* (Fig. 47B), *Upeneichthys* (except *Up. lineatus*) (Fig. 47D), *Parupeneus ciliatus, P. heptacanthus* and *P. procerigena*, whereas these bones are incompletely fused in *Mullus* (Fig. 47C), *Up. lineatus, Parupeneus* (except for above three species) (Fig. 47E) and *Pseudupeneus* (Fig. 47F).

The parhypural is a plate-like bone bearing a hypurapophysis. It articulates with the urostyle-hypural complex antero-dorsally and with the lowermost hypural dorsally.

The branched caudal rays are seven and six in the upper lobe and lower lobe, respectively. The segmented rays are three or four in both lobes.

There are usually six cartilage components: interneural spine cartilage of PU4 (CINPU4, its number 1); post-epural 2 cartilage (CPEP2, 1); post-hypural 5 cartilage (CPHY5, 1); post-haemal spine cartilage of PU2 (CPHPU2, 2); interhaemal spine cartilage of PU3 (CIHPU3, 1); interhaemal spine cartilage of PU4 (CIHPU4, 1) (Fig. 48).

Characters.

TS 30. Third hypural and fourth hypural (Fig. 47)

0: separated; 1: fused incompletely; 2: fused completely (ordered). The third and fourth hypurals are separated in all outgroups examined (0). Incomplete fusion between them is found in *Mullus, Upeneichthys lineatus, Parupeneus* (except *P. ciliatus, P. heptacanthus* and *P. procerigena*) and *Pseudupeneus* (1), while their complete fusion is found in *Upeneus, Mulloidichthys, Upeneichthys* (except *Up. lineatus*), *P. ciliatus, P. heptacanthus* and *P. procerigena* (2).

Other variations

Second uroneural. A second uroneural is found in *Parupeneus* (except *P. margaritatus* and *P. procerigena*), *Upeneichthys porosus* and *Pseudupeneus grandisquamis*, while it is absent in most *Upeneus, Mulloidichthys, Mullus*, and *Up. lineatus, Up. vlamingii*, and *Ps. prayensis*. However, intraspecific variation (present or absent) of the bone is observed in at least *U. parvus, P. chrysopleuron, P. cyclostomus, P. pleurostigma* and *Up. stotti*.

1-10. Axial skeleton and median fin supports (Figs. 49-53)

Description

The axial skeleton (Fig. 49) consists of the vertebrae, and pleural and epipleural ribs. The median fin supports include the supraneural, pterygiophore and stay. The vertebrae are composed of abdominal and caudal elements, and their number is always 24. The first vertebra bears a condyle on both sides for articulation with the exoccipital. The neural spines are well developed except for those on the last two centra. All the abdominal vertebrae and anteriormost two or three caudal vertebrae have the epipleurals on their respective parapophyses or lateral faces. The eight slender pleural ribs are attached to the posterior face of the parapophysis of their respective abdominal vertebrae, except for the first two. Each caudal vertebra bears a haemal arch and a haemal spine.

The supraneural bones are leaf-like bones, and their dorsal portion is various in shape. The anteriormost supraneural is inserted anterior to the first neural spine, the middle between the first and second neural spines, the posteriormost when present between the second and third neural spines along with the first dorsal proximal pterygiophore. There are three supraneurals in

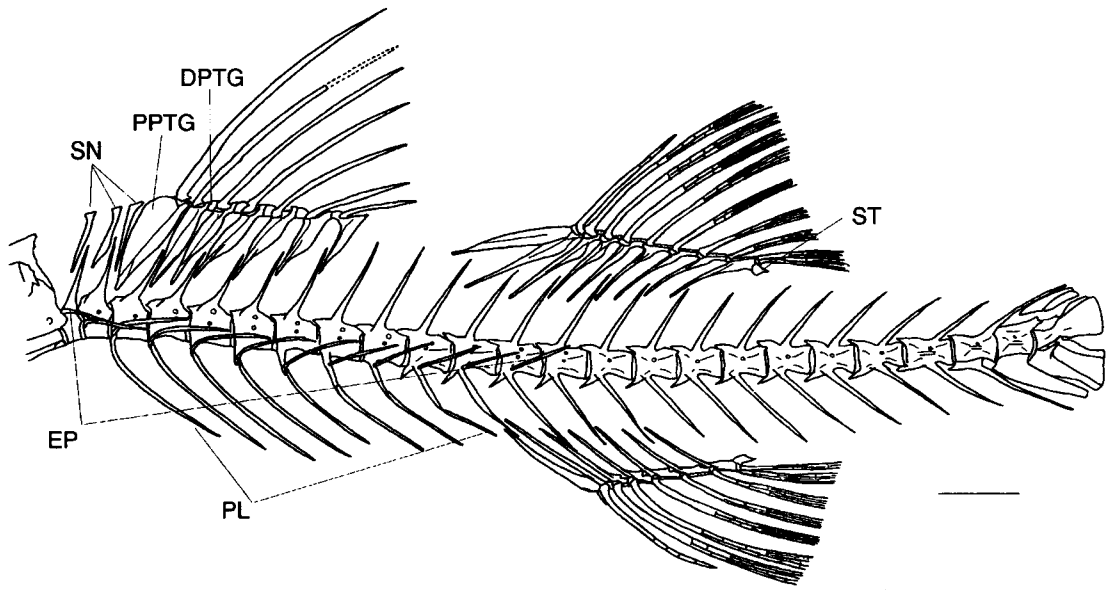

Fig. 49. Lateral view of axial skeleton and median fin supports of *Upeneus japonicus*, CNUC 23686. Scale indicates 5 mm.

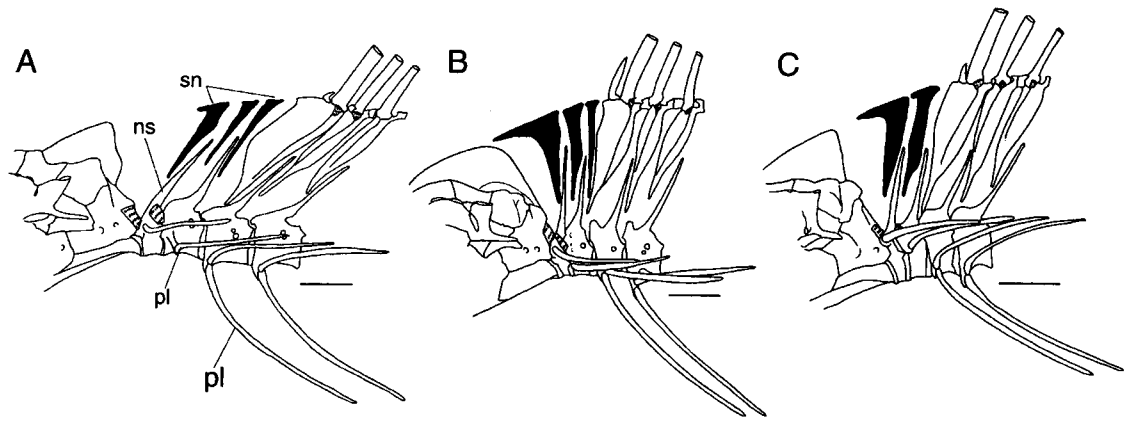

Fig. 50. Lateral view of anterior portion of axial skeleton and median fin supports. A, *Mulloidichthys flavolineatus*, UW 015145; B, *Upeneichthys stotti*, WAM P. 30880.02; C, *Parupeneus barberinoides*, BSKU 015278. Scales indicate 5 mm.

Upeneus (except *U. luzonius*, which has two), *Mulloidichthys* (Fig. 50A), *Mullus* and *Upeneichthys* (Fig. 50B), whereas there are two in *Parupeneus* (except *P. spilurus*) (Fig. 50C) and *Pseudupeneus*, which lack the posteriormost one. The dorsal portion of the anteriormost supraneural is prominently projected anteriorly in *Parupeneus, Pseudupeneus* and *Upeneichthys*. The anteriormost supraneural is especially elongated and lies over the supraoccipital crest in *P. bifasciatus* and *Upeneichthys* (Fig. 50B). The pterygiophores supporting the dorsal and anal fin rays are bipartite (proximal and distal) and lack medial elements. The ossified stay is always present. The dorsal pterygiophores are divided into two portions: the first-dorsal-fin set is supported by seven or eight spines, the second-dorsal-fin set by soft rays. The first dorsal proximal pterygiophore inserts between the second and third neural spines. It bears two spines in all genera of mullids, except *Upeneus asymmetricus, U. crosnieri, U. japonicus* and *U. pori* (Fig. 51A), where they bear only one spine by lacking the minute anterior one. The first dorsal spine, when present, is bifurcate ventrally to articulate with the proximal pterygiophore, the second spine articulates with the first pterygiophore ventrally, and the third has a perforation in its lower portion (Fig. 51A). The distal pterygiophore of the first dorsal fin is firmly attached to the proximal pterygiophore, and it is expanded laterally in its dorsal region. The distal radials of the first dorsal fin are posteriorly pointed to insert into the foramen of subsequent dorsal spines. The pterygio-

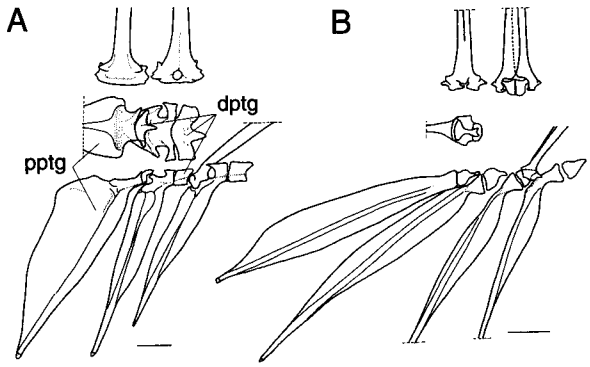

Fig. 51. Dorsal (center) and lateral (top) views of anterior three and four pterygiophores of first and second dorsal fins, respectively in *Upeneus pori* (HUJ 13549). First two fin rays (top) are viewed anteriorly. Scales indicate 5 mm.

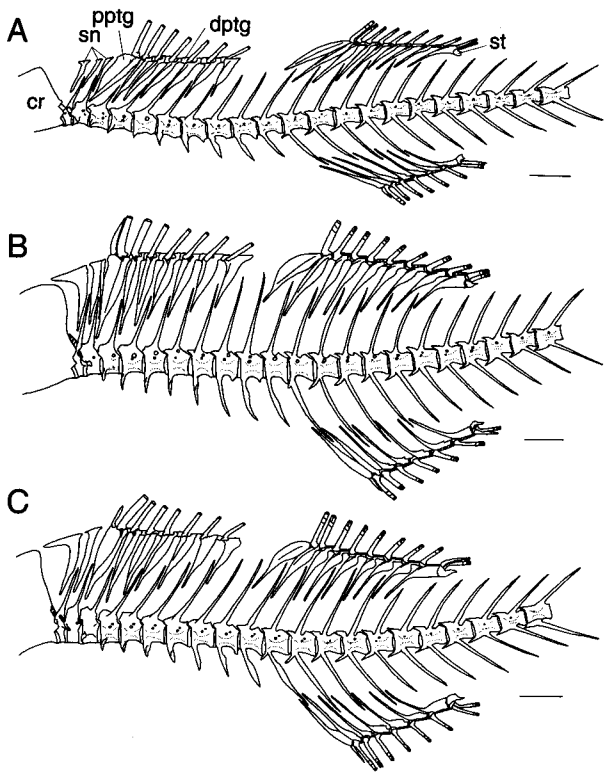

Fig. 52. Lateral view of axial skeleton and median fin supports. A, *Upeneus pori*, HUJ 13549; B, *Upeneichthys porosus*, AMS I. 20194-028; C, *Parupeneus multifasciatus*, HUMZ 62786. Scales indicate 5 mm.

phores of the second dorsal fin consist of two elements, and each distal pterygiophore is articulated with the proximal pterygiophore anteriorly (Fig. 51B). There is a gap between the two sets of dorsal fin pterygiophores (Fig. 52). The dorsal pterygiophore formula is 1/2/1/1/1/1/0/1/1/1/2/2/2 in *Upeneus* (except for *U. vittatus, U. moluccensis*, and *U. quadrilineatus*) and *Mulloidichthys*, whereas the formula is 1/2/1/1/1/1/0/

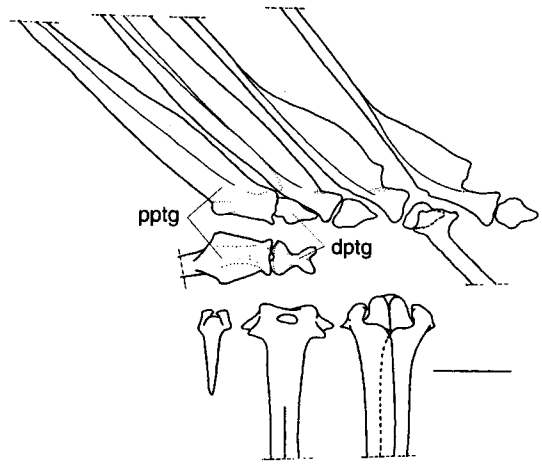

Fig. 53. Lateral (top) and ventral (center) views of anterior four pterygiophores of anal fin in *Upeneus pori* (HUJ 13549). First three fin rays (top) are viewed anteriorly. Scales indicate 5 mm.

1/1/2/1/2/2 in *Mullus, Upeneichthys, Parupeneus* (except for *P. heptacanthus*) and *Pseudupeneus*. The anal pterygiophores are located in the interhaemal spaces, and the first proximal pterygiophore is inserted into the front of the first haemal spine. The first anal pterygiophore bears a small spine and a segmented ray; the second anal pterygiophore bears a branched soft ray. The first small anal spine is bifurcate to articulate with the proximal pterygiophore at its base; second soft ray has a perforation like that in the second dorsal spine (Fig. 53). The distal pterygiophores of the anal fin also consist of two elements, except for the anteriormost one, as in the second dorsal fin. The anal pterygiophore formula is 1/2/1/2/1 in all mullid genera examined except *U. parvus* (mainly 1/1/2/2/1).

Characters

TS 31. Number of spines on the first dorsal proximal pterygiophore (Figs. 49, 50)

0: two; 1: one (first minute one lacking). The number of spines on the first dorsal pterygiophore is only one in *Upeneus asymmetricus, U. japonicus, U. pori, U. crosnieri* (1).

Remarks. Although Lachner (1954) has reported only one spine on the first dorsal pterygiophore in *U. parvus*, that species has two spines on the first dorsal pterygiophore based on the present study. The first spine of *U. parvus* is too minute to observe by naked eye, and is covered with the epidermis.

Other variations

Third supraneural bone. Usually, there are three supraneural bones in *Upeneus* (except *U. luzonius*), *Mullus, Upeneichthys* and *Mulloidichthys*, while in

Parupeneus and *Pseudupeneus* there are two supraneurals. However, intraspecific variation is found in *P. spilurus*, where three supraneurals are occasionally encountered, although the species usually has only two.

2. Myology

2-1. Muscles of cheek (Figs. 54-55)

Description

The muscles of the cheek (Fig. 54) consist only of the adductor mandibulae, which is a large muscle composed of four sections: A1, A2, A3 and Aw.

Section A1 is a large and robust muscle mass, lying on A2. It originates from the hyomandibula and antero-dorsal surface of the preopercle and inserts onto the ventro-medial surface of the maxilla by a strong tendon. This section is connected with A3 by a thin tendon medially (Figs. 54B-C). The connection of A1 with the hyomandibula and preopercle is by muscle fibers in *Upeneus* and *Mullus*, whereas it is by a tendinous tissue in *Upeneichthys, Mulloidichthys, Parupeneus* and *Pseudupeneus*. In addition, the postero-dorsal portion of A1 is fused with that of A2 in the latter four genera. In *Parupeneus* and *Pseudupeneus* especially, the antero-dorsal part of A1 also originates from the ventral surface of the subocular shelves of the first and second infraorbitals (Fig. 55). There is a small muscular mass on the postero-medial surface of A1, which is connected to the ventral surface of the subocular shelf of the second infraorbital (Fig. 55B).

Section A2 lies on the largest section A3. It originates from the anterior margin of the preopercle and is usually connected with the antero-dorsal portion of A3. In *Upeneus parvus*, A2 is quite expanded dorsally to cover the original point of A1 and is also connected with A1 tendinously (Fig. 56A). In *Mulloidichthys flavolineatus*, the A2 is expanded ventrally to cover the A3 (Fig. 56B).

Section A3 originates from the lateral surface of the

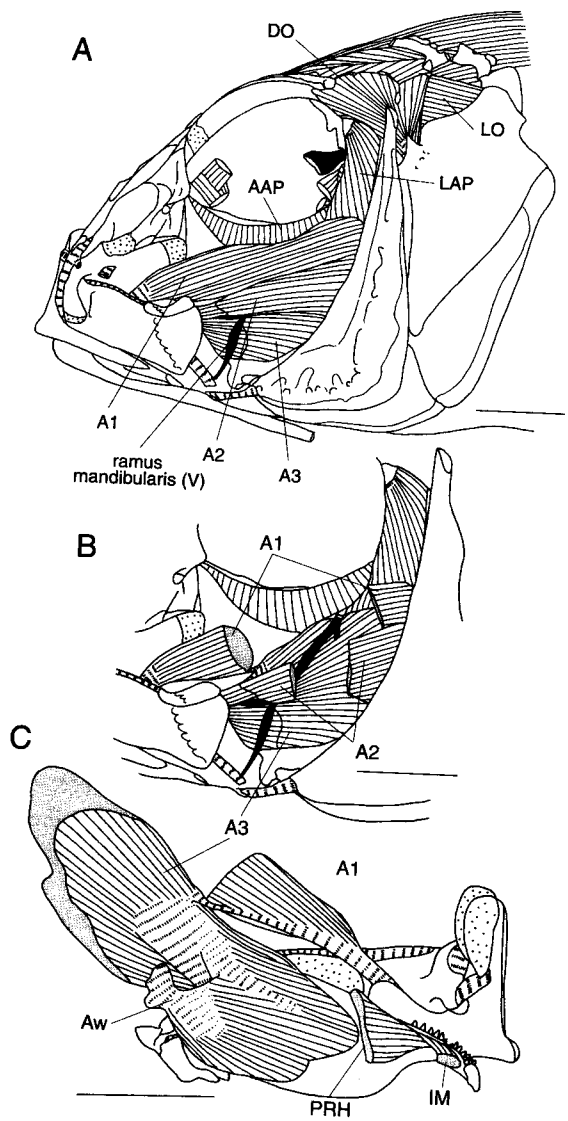

Fig. 54. Lateral view of cheek and other cephalic muscles in *Mullus surmuletus* (HUMZ 154869). A, superficial view; B, lateral view after removal of A1 and A2; C, medial view of adductor mandibulae. Scales indicate 5 mm.

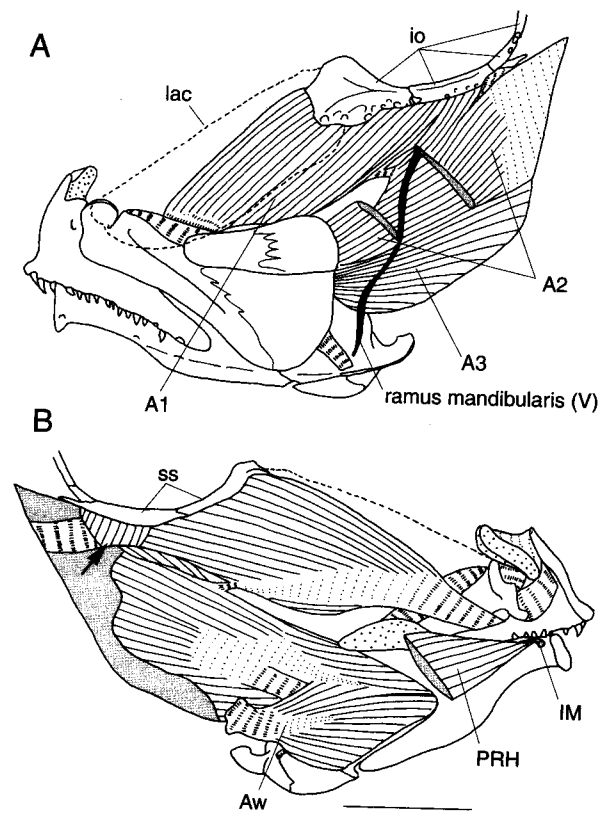

Fig. 55. Lateral (above) and medial (below) views of adductor mandibulae of *Parupeneus cyclostomus* (HUMZ 39286). Scale indicates 5 mm.

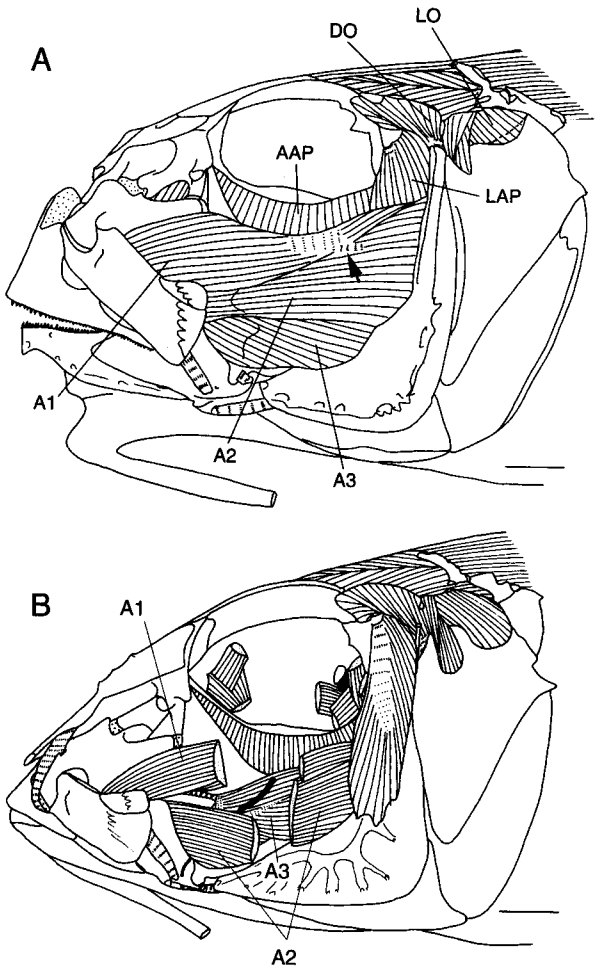

Fig. 56. Lateral views of cheek and other cephalic muscles in *Upeneus parvus*, USNM 1346104 (A) and *Mulloidichthys flavolineatus*, UW 015145, after removal of A1 and A1 (B). Arrow shows the connection of A1 and A2. Scales indicate 5 mm.

posterior region of the palatal arch, including the metapterygoid, hyomandibula, symplectic and quadrate and the anterior margin of the preopercle beneath A2. It inserts onto the medial surfaces of the anguloarticular and the coronomeckelian by a strong tendon.

Section Aw originates from the Meckelian fossa on the medial surfaces of the dentary and anguloarticular and inserts tendinously onto the medial surface of the quadrate, although the origin of the muscles on the lower jaw varies (Fig. 57).

Characters

TS 32. Connection between adductor mandibulae section 1 and infraorbitals (Fig. 55)

0 : absent ; 1 : present. In most genera of mullids, the A1 is not connected with the infraorbital (0). The A1 is partly connected with the subocular shelves of the first and second infraorbitals in only *Parupeneus* and *Pseudupeneus* (1).

TS 33. Small muscular mass on adductor mandibulae section 1 medially (Fig. 55B)

0 : absent ; 1 : present. The small muscular mass of A1 is present in *Parupeneus* and *Pseudupeneus* (1). Other mullid genera do not have this muscular mass (0).

Other variations

None.

2-2. Cephalic muscles between neurocranium and suspensorium-opercular bones (Figs. 58-61)

Description

The cephalic muscles are composed of the levator arcus palatini, adductor arcus palatini, dilatator operculi, levator operculi and adductor operculi.

The levator arcus palatini is located on the posterodorsal region of the suspensorium. It originates from the ventral surface of a projection on the sphenotic and inserts onto the preopercle, hyomandibula and metapterygoid. This muscle overlies the posterior portion of the adductor mandibulae and extends to the lower portion of the preopercle in *Upeneichthys, Mulloidichthys, Parupeneus* and *Pseudupeneus* (Figs. 58C-F). It also inserts onto the medial surface of the metapterygoid through the metapterygoid lamina when it is present (Fig. 59).

The adductor arcus palatini, situated on the lower region of the orbit, connects the neurocranium with the suspensorium. It extends to the ventral surface of the vomer and to the medial surface of the palatine anteriorly (Fig. 60).

The dilatator operculi is conical in shape, with the

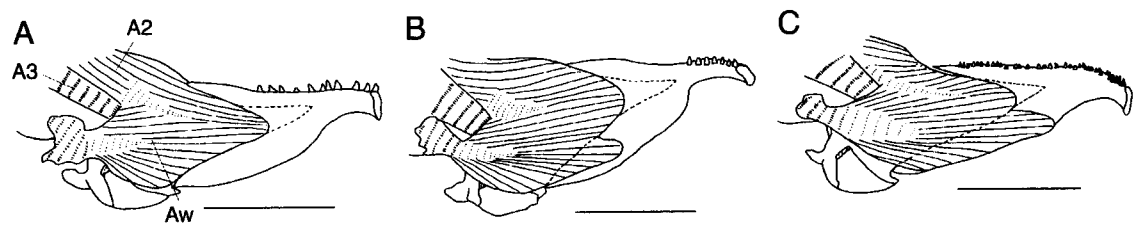

Fig. 57. Medial view of adductor mandibulae section w. A, *Parupeneus heptacanthus*, BSKU 084326 ; B, *Mullus barbatus*, HUMZ 154853 ; C, *Upeneus parvus*, HUMZ 31349. Scales indicate 5 mm.

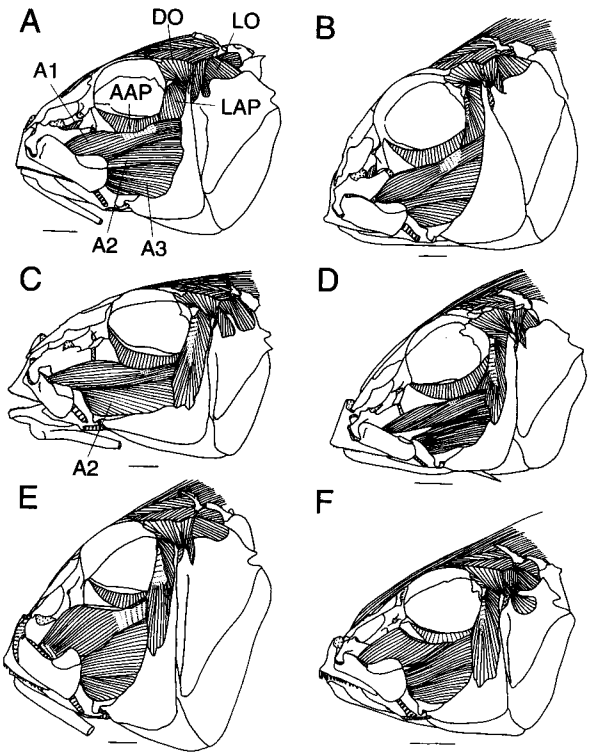

Fig. 58. Lateral view of cheek and other cephalic muscles of six mullids genera. A, *Upeneus tragula*, HUMZ 62175; B, *Mullus argentinae*, NSMT-P 52642; C, *Mulloidichthys flavolineatus*, UW 013326; D, *Upeneichthys porosus*, AMS I. 17033-021; E, *Pseudupeneus grandisquamis*, UW 022550; F, *Parupeneus heptacanthus*, BSKU 084326. Scales indicate 5 mm.

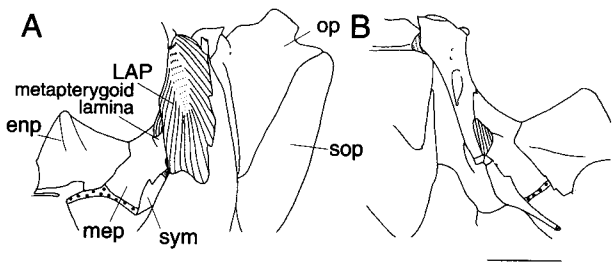

Fig. 59. Lateral (A) and medial (B) view of levator arcus palatini in *Parupeneus cyclostomus*, HUMZ 39268. Scale indicates 5 mm.

apex pointing ventrally, and comprises two sections (Fig. 61). The anterior section of this muscle originates from the frontal, sphenotic, pterotic and hyomandibula, and inserts onto the antero-dorsal corner of the opercle. The smaller posterior section originates on the pterotic and inserts onto the antero-dorsal portion of the opercle. It also expands fan-like posteriorly in *Upeneus luzonius, U. moluccensis, U. sulphureus, U. crosnieri, U. tragula, U. vittatus, Mulloidichthys, Parupeneus* (except *P. bifasciatus*), *Pseudupeneus grandisquamis* (Fig. 61B).

The levator operculi, situated behind the dilatator

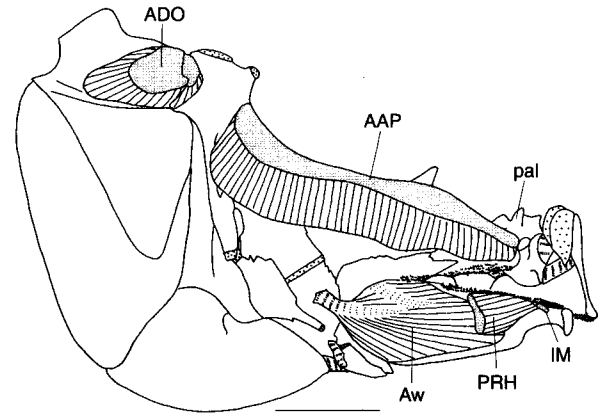

Fig. 60. Medial view of suspensorium and its related muscles in *Upeneus japonicus*, CNUC 23697. Scale indicates 5 mm.

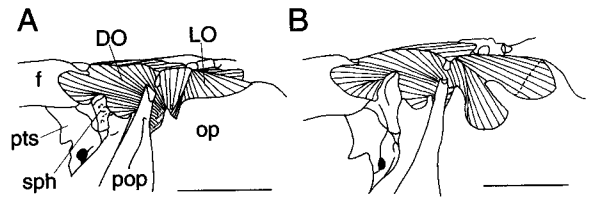

Fig. 61. Antero-lateral view of muscles relating connection between skull and opercle. A, *Mullus surmuletus*, HUMZ 154869; B, *Mulloidichthys flavolineatus*, NSMT-P 19933. Scales indicate 5 mm.

operculi, originates on the pterotic and usually inserts onto the dorso-medial surface of the opercle. The insertion of the muscle extends to the dorso-lateral surface of the opercle in *Mulloidichthys* (Fig. 61B).

The adductor operculi connects the dorso-medial surface of the opercle to the lateral skull wall in the auditory region. Its origin includes the pterotic, prootic, exoccipital and intercalar. The muscle inserts on the dorso-medial surface of the opercle just behind the articulation of the bone with the hyomandibula, and occasionally the insertion portion includes the hyomandibula (Fig. 60).

Characters

TS 34. Ventral extension of levator arcus palatini (Fig. 58)

0: absent; 1: present. The levator arcus palatini does not extend to the lower portion of the preopercle in *Upeneus* and *Mullus* (0). The ventral portion of the levator arcus palatini extends to the lower portion of the preopercle in *Mulloidichthys, Upeneichthys, Parupeneus* and *Pseudupeneus* (1).

TS 35. Insertion of levator operculi on opercle (Fig. 61)

0: only dorso-medial surface; 1: dorso-medial and lateral surfaces. In most mullids the levator operculi

inserts onto only the dorso-medial surface of the opercle (0), while in *Mulloidichthys* its insertion also includes the dorso-lateral surface of the opercle (1). Although the muscle is slightly inserted onto the dorso-lateral surface of the opercle in *Upeneus asymmetricus, U. parvus* and *U. quadrilineatus*, it is regarded as inserting onto only the dorso-medial surface (0) because its insertion is much weaker than that of *Mulloidichthys*.

Other variations

Posterior expansion of dilatator operculi on antero-dorsal portion of opercle. The posterior expansion of the dilatator operculi on the opercle was found in several species of *Upeneus, Mulloidichthys* and most *Parupeneus*, but it is impossible to determine the degree of expansion objectively. Therefore, this character was not employed in the present analysis.

2-3. Ventral muscles of head (Figs. 62-67)

Description

The ventral head muscles (Figs. 62-63) comprise the intermandibularis, protractor hyoidei, hyohyoidei abductores, hyohyoidei adductores and four muscles associated with the barbel.

The intermandibularis is a small cylindrical-shaped muscle lying between the antero-medial surface of both dentaries.

The protractor hyoidei is a robust muscle that connects the hyoid arch with the lower jaw. It originates from the postero-lateral surface of the anterior ceratohyal and inserts onto the dorso-medial surface just behind the intermandibularis of the dentary. Right and left components of the muscle are separated by dislocation of the first branchiostegal ray (barbel).

The hyohyoidei abductores are divided into two sections (Fig. 64C). The diminished section 1 lies between the third branchiostegal ray and the ventro-medial surface of the anterior ceratohyal. Section 2 lies between the second branchiostegal ray and the ventral surface of the urohyal.

The hyohyoidei adductores are developed as sheets of muscle fibers lying between the distal portions of the branchiostegal rays. They continue dorsally above the postero-dorsalmost ray to attach the medial surfaces of the opercle and subopercle (Fig. 62).

There are four muscles associated with movement of the barbel on each hyoid arch : the extensor tentaculi, retractor tentaculi and two sections of the rotator tentaculi (Fig. 64).

The extensor tentaculi originates from the medial surfaces of the anterior and posterior ceratohyals, and inserts tendinously onto the anterior surface of the barbel base, passing through the hyoid foramen between

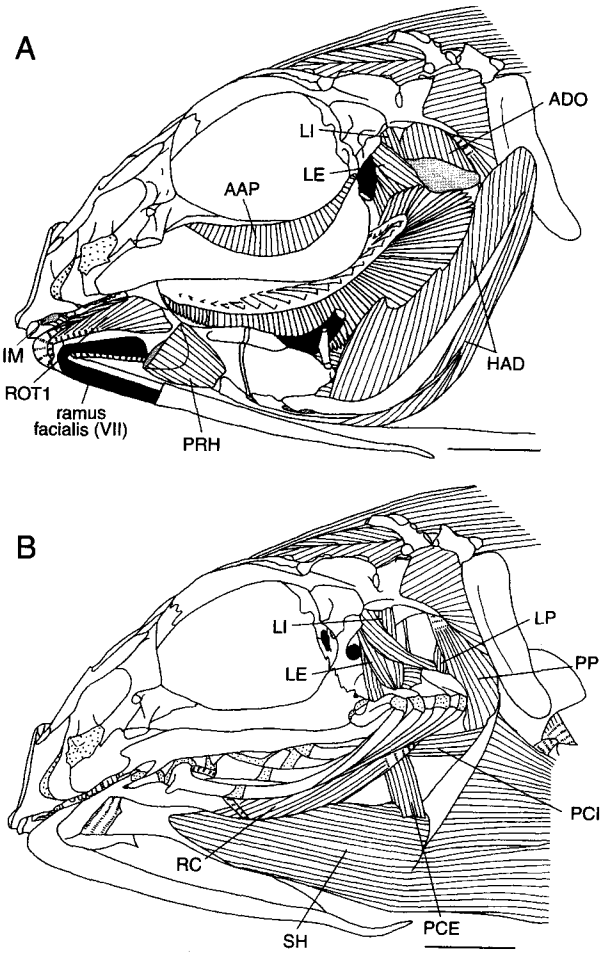

Fig. 62. Lateral view of head region after removal of jaw and suspensorium (A) and hyoid arch, except urohyal (B) in *Mullus surmuletus*, HUMZ 154869. Scales indicate 5 mm.

the ventral hypohyal and the anterior ceratohyal. It is extended posteriorly and connected to the medial surface of the interhyal in *Upeneus moluccensis, U. quadrilineatus, Pseudupeneus prayensis* and *Parupeneus barberinoides* (Fig. 65B).

The retractor tentaculi originates on the medial surfaces of the fourth and fifth branchiostegal rays, and inserts onto the posterior surface of the barbel base by a strong tendon (Fig. 65B). The origin of the muscle is sometimes restricted only to the fifth branchiostegal rays in *Upeneus asymmetricus, U. parvus* (Fig. 65A), *U. sulphureus, Mulloidichthys* (except *Mu. martinicus*), *Mullus argentinae, M. barbatus, Parupeneus bifasciatus* and *Pseudupeneus grandisquamis*.

The rotator tentaculi consists of two sections. Section 1 originates on the antero-dorsal surfaces of the anterior ceratohyal and hypohyals, and inserts tendinously onto the lateral surface of the barbel base (Fig. 66). The rotator tentaculi section 1 is relatively short in *Upeneus*, the posterior limit of the muscle does not

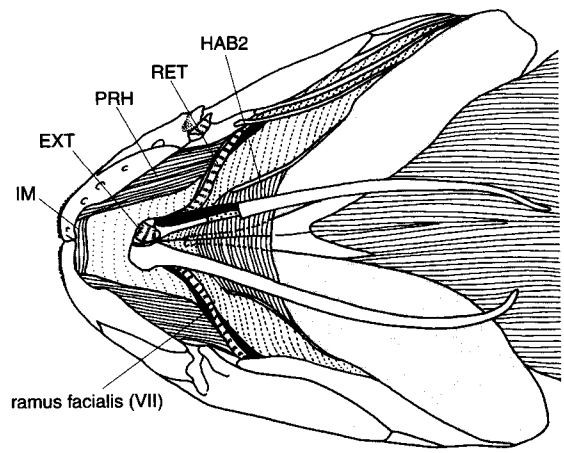

Fig. 63. Ventral view of head region and its related muscles in *Upeneus japonicus*, HUMZ uncatalog (after Kim et al., 2001). Scale indicates 5 mm.

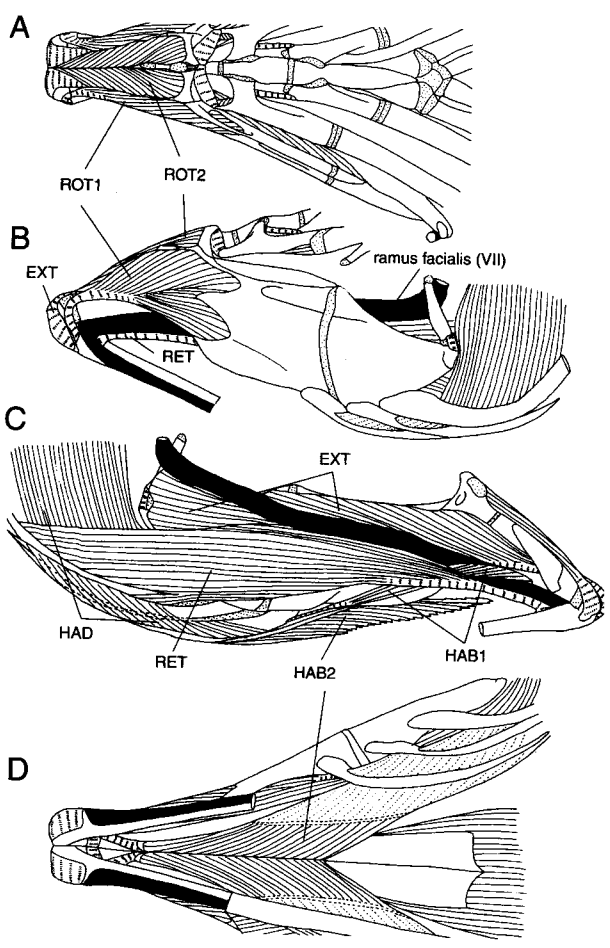

Fig. 64. Dorsal (A), lateral (B), medial (C) and ventral (D) views of hyoid muscles related in *Upeneus moluccensis*, BSKU 084674. Scale indicates 5 mm.

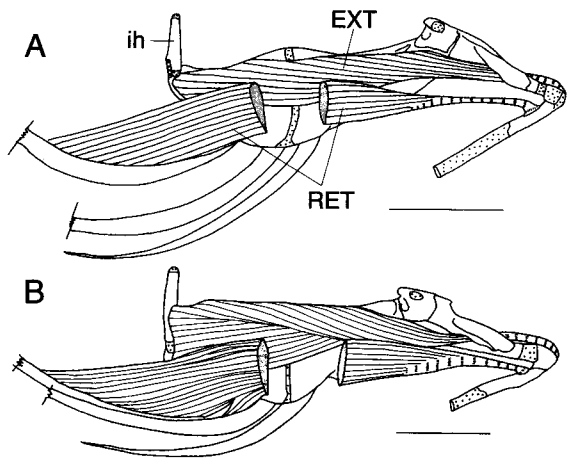

Fig. 65. Medial view of hyoid muscles related to barbel. A, *Upeneus parvus*, HUMZ 31349; B, *Parupeneus forsskali*, HUJ 9977. Scales indicate 5 mm.

extend beyond a vertical through the posterior tip of the dorsal hypohyal (Fig. 66A). In the remaining genera of mullids, it extends posteriorly beyond a vertical through the posterior tip of the dorsal hypohyal. In *Mullus* and *Upeneichthys* it is relatively short, while those of *Mulloidichthys, Parupeneus* (Fig. 66B) and *Pseudupeneus* are relatively long. Section 1 of *Mulloidichthys* is especially long, reaching the junction of anterior and posterior ceratohyals (Fig. 66C). Section 1 is branched in *Upeneus moluccensis, U. quadrilineatus* and *U. vittatus* (Fig. 64B). Section 2 lies on the dorsal surfaces of the hypohyals and comprises two subsections: one (subsection 2a) originates on the lateral surfaces of the anterior ceratohyal and ventral hypohyal under the rotator tentaculi section 1, the other (subsection 2b) originates on the dorsal surfaces of the hypohyals (Fig. 67). The common insertion of these two subsections is onto the medial surface of the barbel base by a relatively weak tendon. Dorsally, the rotator tentaculi section 2 originates on the dorsal hypohyal (except in *Mullus*), and ventrally on the lateral surfaces of the hypohyals and anterior ceratohyal (except in *Upeneus*). Subsection 2b of rotator tentaculi section 2 in *Mullus* is absent; it originates from the lateral surfaces of the hypohyals and the antero-dorsal portion of the anterior ceratohyal (Fig. 67B). In all species of *Upeneus* except *Upeneus japonicus* (Fig. 66A), the origin of subsection 2a does not include the anterior ceratohyal (Figs. 67A, 67C).

Remarks. Although Kim et al. (2001) described the barbels and related muscles of the Mullidae and compared with those of the Polymixiidae, I described again the muscles related to barbels of the mullids more detail on the basis of much more mullid specimens covering all genera in the present study.

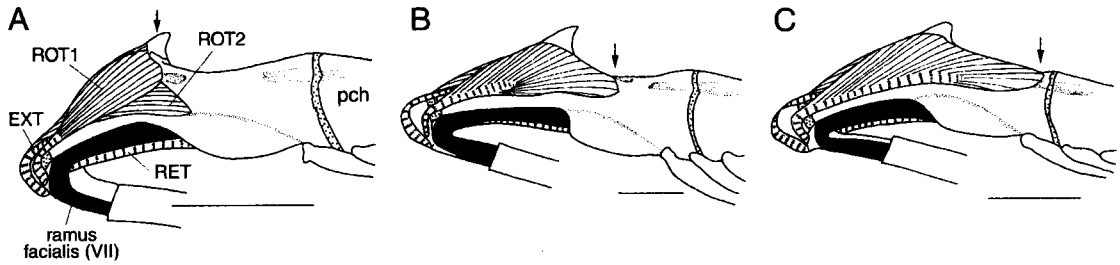

Fig. 66. Lateral view of hyoid muscles related to barbel on anterior portion of hyoid arch. A, *Upeneus japonicus*, CNUC 23694 (after Kim et al., 2001); B, *Pseudupeneus prayensis*, NSMT-P 54121; C, *Mulloidichthys flavolineatus*, NSMT-P 19933. Arrows show the posterior end of each ROT1. Scales indicate 5 mm.

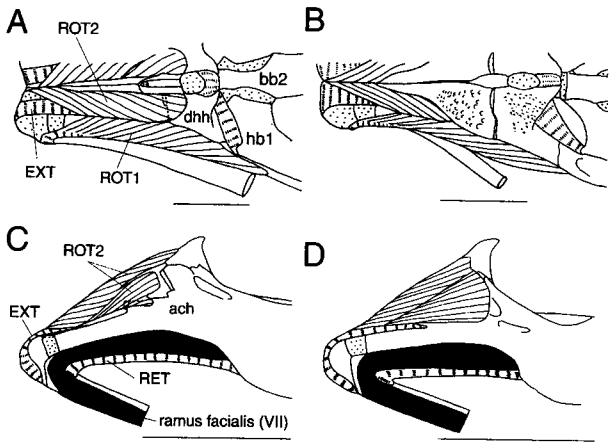

Fig. 67. Dorsal (A, B) and lateral (C, D) views of hyoid muscles related to barbel on anterior portion of hyoid arch. A, *Upeneus parvus*, HUMZ 31349; B, *Mullus surmuletus*, HUMZ 154868. Scales indicate 3 mm.

Characters

TS 36. Rotator tentaculi section 1 (Figs. 64, 67)

0: absent; 1: present and unbranched; 2: present and branched (unordered). The rotator tentaculi is absent in all outgroups (0). In all mullid genera, except below, the muscle is present, but unbranched (1). *Upeneus moluccensis, U. quadrilineatus, U. sulphureus* and *U. vittatus* have branched rotator tentaculi section 1 (2).

TS 37. Rotator tentaculi section 2 (Figs. 67A-B)

0: absent; 1: present and originating on the dorsal hypohyal; 2: present and not originating on the dorsal hypohyal (unordered). The rotator tentaculi is absent in all outgroups (0). In almost all genera of mullids, the origin of the muscle includes the dorsal surface of the dorsal hypohyal (1), while in *Mullus* it excludes the dorsal surface of the dorsal hypohyal (2).

TS 38. Rotator tentaculi subsection 2a (Figs. 67C-D)

0: absent; 1: present and originating on the hypohyals and anterior ceratohyal; 2: present and originating on the hypohyal (unordered). The rotator tentaculi is absent in all outgroups (0). The origin of the rotator tentaculi subsection 2a is expanded and originates on the hypohyals and anterior ceratohyal in *Upeneus japonicus, Mullus, Upeneichthys, Mulloidichthys, Pseudupeneus* and *Parupeneus* (1), but in *Upeneus* (except *U. japonicus*) the muscle is not expanded and originates only from the hypohyal (2).

Other variations

Insertion of retractor tentaculi. Insertion of the muscles is usually on the fourth and fifth branchiostegal rays. The origin of the muscle is sometimes restricted to the only fifth branchiostegal rays, as mentioned above. In addition, intraspecific variation occurs in *U. asymmetricus* and *U. parvus*, showing two conditions of their origin.

2-4. Muscles of branchial arches (Figs. 62, 68)

Description

The muscles associated with the branchial arches (Fig. 68) include the levator externus, levator internus, levator posterior, transversus dorsalis, obliquus dorsalis, retractor dorsalis, obliquus ventralis, rectus ventralis, rectus communis, transversus ventralis, obliquus posterior, sphincter oesophagi and adductor.

The levator externus, comprising four elements, originates from the prootic just below the pterotic groove for the hyomandibula articulation of the skull. It inserts onto the dorsal surface of each epibranchial.

The levator internus comprises two elements and originates from the prootic and pterotic just medially to the origin of the levator externus. The anterior element of this muscle inserts onto the dorsal surface of the second pharyngobranchial, and the posterior element inserts onto the third pharyngobranchial.

The levator posterior originates from the lateral surface of the intercalar, and inserts onto the dorsal surface of the fourth epibranchial.

The transversus dorsalis consist of two elements, the transversus dorsalis anterior and transversus dorsalis posterior. The transversus dorsalis anterior is divided into two parts, the musculus cranio-pharyngobranchialis 2 and the musculus transversus epibranchialis 2 (*sensu*

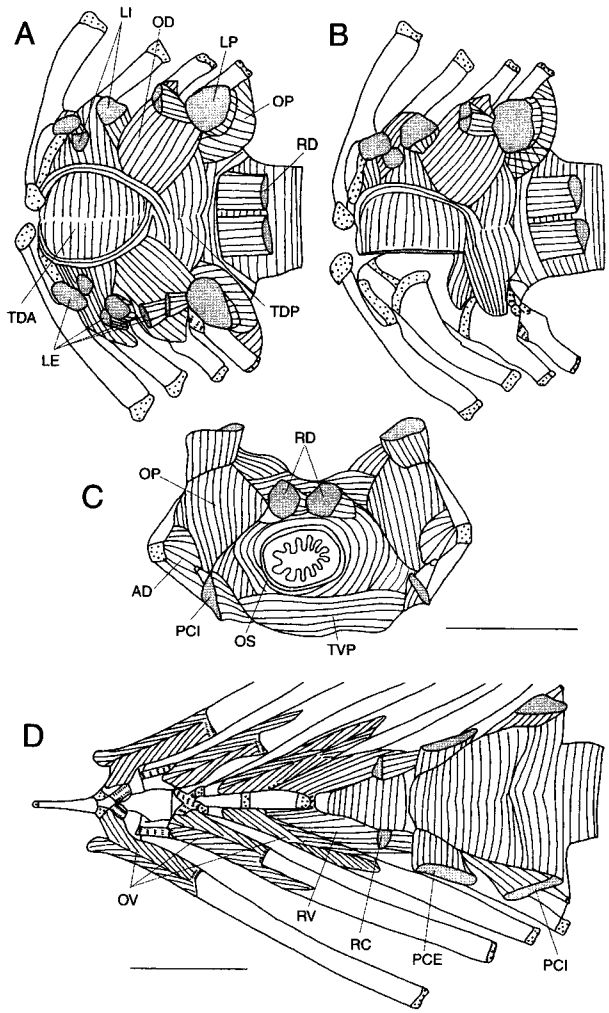

Fig. 68. Dorsal (A, B) and posterior (C) views of branchial muscles related to upper branchial arch and ventral view (D) of branchial muscles related to lower branchial arch in *Upeneus vittatus*, HUMZ 46773. Scales indicate 5 mm.

Anker, 1978) (Fig. 68A). The transversus dorsalis anterior originates from the dorsal surfaces of the second epibranchial and interarcual cartilage, and fuses with its antimere on the dorsal midline by a median raphe. The transversus dorsalis posterior, lying under the obliquus dorsalis, interconnects the third pharyngobranchial and third epibranchial of each side.

The obliquus dorsalis connects the postero-dorsal surface of the third pharyngobranchial to the dorsal surfaces of the third and fourth epibranchials. The anterior portion of this muscle is covered by the transversus dorsalis anterior.

The retractor dorsalis is bilaterally paired and connects the postero-medial surfaces of the third and fourth pharyngobranchials (mainly the third pharyngobranchial) to the lateral surface of the second abdominal vertebra.

The obliqui ventrales connect ventral surfaces of the first to third hypobranchials and their respective ceratobranchials.

The rectus ventralis originates from the ventral surface of the fourth ceratobranchial, and inserts onto the ventral process of the third hypobranchial by a long thin tendon. They are usually connected to each other by a thin tendon on the midline.

The rectus communis connects the fifth ceratobranchial with the dorsal surface of the urohyal. The dorsal portion of this muscle grades into an aponeurotic fascia, and attaches to the ventro-lateral margin of the fifth ceratobranchial.

Transversus ventralis consists of two elements, the transversus ventralis anterior and transversus ventralis posterior. The transversus ventralis anterior lies between both fourth ceratobranchials, and the transversus ventralis lies posterior between both fifth ceratobranchials.

The obliquus posterior connects the posterior surface of the fourth epibranchial with the postero-medial surface of the fifth ceratobranchial.

The sphincter oesophagi encircles the oesophagus in the posterior region of the branchial arch.

The adductor comprises two elements, adductor 4 and 5. The former interconnects between the fourth epibranchial and the fourth ceratobranchial; the latter interconnects between the fourth epibranchial and fifth ceratobranchial.

Characters

No derived character suitable for the analysis was recognized.

Other variations

None.

2-5. Muscles between pectoral girdle and skull, hyoid, and branchial arches (Fig. 62B)

Description

The muscles associated with this part include the protractor pectoralis, pharyngoclavicularis and sternohyoideus.

The protractor pectoralis, lying between the skull and the pectoral girdle, originates from the posterior process of the pterotic and is weakly connected to the antero-dorsal margin of the cleithrum.

The pharyngoclavicularis, comprising two elements of the pharyngoclavicularis internus and pharyngoclavicularis externus, connects the fifth ceratobranchial with the cleithrum. The internus element originates from the antero-medial surface of the cleithrum, dorsal to the origin of the externus element, and inserts onto the

ventral surface of the fifth ceratobranchial. The externus element originates from the antero-ventral surface of the cleithrum, and inserts onto the ventral surface just anterior to the insertion of the internus element on the fifth ceratobranchial. The origin of the latter is sandwiched by the posterior portion of the sternohyoideus.

The robust sternohyoideus originates from the antero-ventral surface of the cleithrum and is connected with the anterior portion of the obliquus inferioris posteriorly. It inserts onto the postero-dorsal, lateral, and ventral surfaces of the urohyal.

Characters

No derived character suitable for the analysis was recognized.

Other variations

None.

2-6. Muscles of pectoral fin (Figs. 69-72)

Description

The pectoral fin muscles (Fig. 69) comprise the abductor superficialis, abductor profundus, arrector ventralis, adductor superficialis, adductor medius, adductor profundus, arrector dorsalis, adductor radialis and coracoradialis.

The abductor superficialis is situated on the lateral surface of the pectoral girdle. It originates from the posterior surface of the shield-like flange of the cleithrum and inserts onto the base of each pectoral fin ray, except the uppermost one, by a strong tendon.

The abductor profundus, lying under the abductor superficialis, originates from the postero-ventral surface of the cleithrum below the origin of the abductor superficialis and anterior region of the coracoid. Insertion of this muscle is onto the base of each pectoral fin ray by a strong tendon.

The arrector ventralis lies on the dorso-lateral surface of the cleithrum between the abductor superficialis and the abductor profundus. It originates from the postero-ventral surface of the cleithral flange and inserts onto the antero-medial base of the uppermost pectoral fin ray by a strong tendon.

The adductor superficialis is situated on the medial surface of the pectoral girdle. It originates from the dorso-medial surface of the cleithrum and tendinously inserts on the medial surface of each pectoral fin ray, except the uppermost one. The superficial portion of the muscle covers the upper portion of which is inserted onto the upper several pectoral fin rays.

The adductor medius lies between the adductor superficialis and the adductor profundus. It originates from the antero-medial margin of the cleithrum and

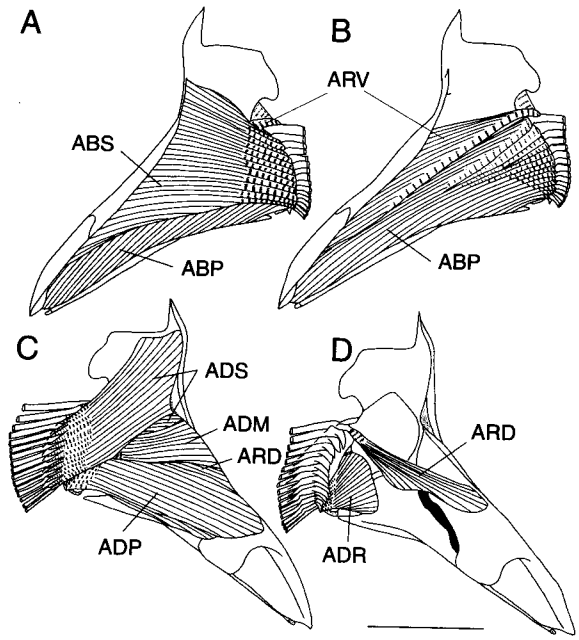

Fig. 69. Lateral (A, B) and medial (C, D) views of pectoral fin muscles in *Upeneus vittatus*, HUMZ 46773. B, after removal of ABS; D, after removal of ADS, ADM and ADP. Scale indicates 5 mm.

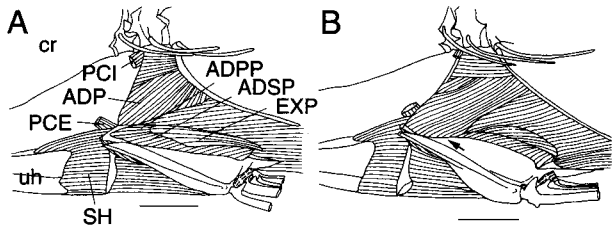

Fig. 70. Dorso-lateral view of pelvic girdle and its related muscles. A, *Upeneus parvus*, HUMZ 31349; B, *Parupeneus cyclostomus*, HUMZ 39268. Arrow shows the pelvic origin of ADP. Scales indicate 5 mm.

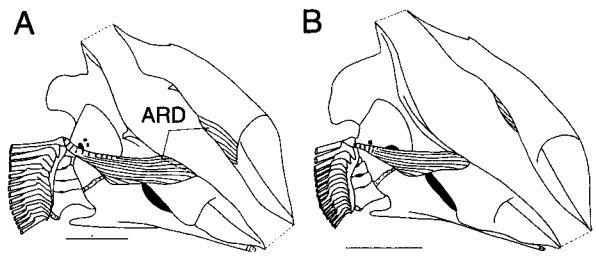

Fig. 71. Medial (left) and anterior (right) views of arrector dorsalis. A, *Parupeneus pleurostigma*, BSKU 025978; B, *Upeneus parvus*, HUMZ 31349. Scales indicate 5 mm.

inserts tendinously onto several middle pectoral fin rays.

The adductor profundus is located below the adductor superficialis on the medial surface of the pectoral girdle. It originates from the ventro-medial surface of the cleithrum, coracoid and the antero-dorsal surface of

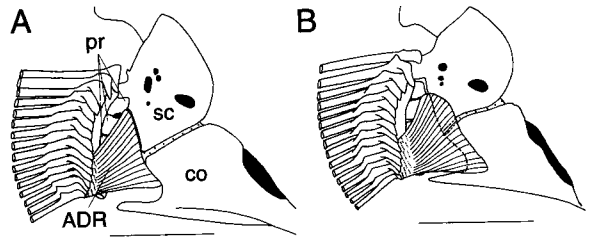

Fig. 72. Medial view of posterior portion of pectoral girdle and its related muscles. A, *Parupeneus pleurostigma*, BSKU 025978; B, *Upeneus vittatus*, HUMZ 46773. Scales indicate 5 mm.

the pelvic bone (Fig. 70B), except in *Upeneus parvus*. The muscle in *U. parvus* is not connected with the pelvic bone (Fig. 70A). Insertion of this muscle is onto the base of each pectoral fin ray, except the uppermost one.

The arrector dorsalis lies on the dorso-medial surface of the cleithrum under the adductor superficialis and adductor medius. It originates from the medial surface of the cleithrum and the adjoining area of the coracoid. Insertion of this muscle is tendinously onto the base of the uppermost pectoral fin ray. The origin of the muscle includes the anterior surface of the cleithrum in *Upeneichthys vlamingii, Up. stotti, Pseudupeneus prayensis* and *Parupeneus* (Fig. 71A).

The adductor radialis is a small muscle between the pectoral fin radials and several lower pectoral fin rays. Its origin involves the lower three pectoral fin radials in *Mulloidichthys, Upeneichthys, Parupeneus* and *Pseudupeneus* (Fig. 72A), while it is anteriorly extended to include the posterior portions of the scapula and coracoid in both *Upeneus* and *Mullus* (Fig. 72B).

The coracoradialis, lying between the posterior process of the coracoid and the ventro-medial surface of the lowermost pectoral fin radial, is usually absent or is vestigial when present.

Characters

TS. 39. Origin of adductor radialis (Fig. 72)

0: involving only pectoral fin radials; 1: involving pectoral fin radials, scapula and coracoid. The origin of the adductor radialis includes only the pectoral fin radials in *Mulloidichthys, Upeneichthys, Parupeneus* and *Pseudupeneus* (0), while it involves the scapula and coracoid as well as pectoral fin radials in *Upeneus* and *Mullus* (1).

Other variations

None.

2-7. Muscles of pelvic fin (Figs. 73-74)

Description

The pelvic muscles (Fig. 73) comprise the abductor superficialis pelvicus, abductor profundus pelvicus, arrector ventralis pelvicus, extensor proprius, adductor superficialis pelvicus, adductor profundus pelvicus and arrector dorsalis pelvicus.

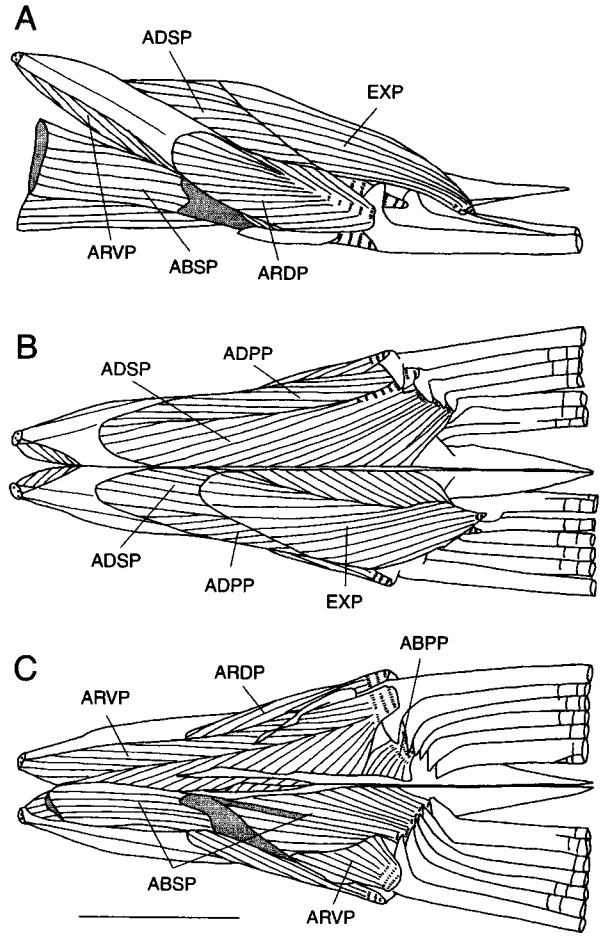

Fig. 73. Lateral (top), dorsal (center) and ventral (bottom) views of pelvic fin muscles in *Mullus surmuletus*, HUMZ 154869. Scale indicates 5 mm.

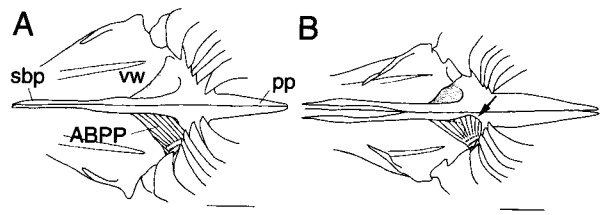

Fig. 74. Ventral view of pelvic girdle showing insertion of abductor profundus pelvicus on the base of subpelvic process (arrow). A, *Parupeneus cyclostomus*, HUMZ 39268; B, *Mullus surmuletus*, HUMZ 154869. Scales indicate 2 mm.

The abductor superficialis pelvicus, lying on the arrector ventralis pelvicus, originates from the ventral region of the basipterygium and the joint region between both cleithra of the pectoral girdle. It inserts tendinous-

ly onto all the pelvic fin rays.

The abductor profundus pelvicus originates from the ventral surface of the basipterygium and inserts tendinously on the first three soft pelvic fin rays. It is separated from the other ventral pelvic muscles by intervening the expanded accessory subpelvic keel. The origin of this muscle also includes the basal portion of the subpelvic process in *M. surmuletus* (Fig. 74B), *Upeneichthys lineatus, Up. vlamingii, Parupeneus spilurus* and *Pseudupeneus*.

The arrector ventralis pelvicus, which is covered by the abductor superficialis pelvicus, originates from the ventral surface of the accessory subpelvic keel and inserts onto the lateral surface of the base of the pelvic spine.

The extensor proprius is a superficial muscle located on the adductor superficialis pelvicus and adductor profundus pelvicus. Insertion is onto the two innermost pelvic fin rays.

The adductor superficialis pelvicus lies between the extensor proprius and the adductor profundus pelvicus. It originates from the dorso-medial surface of the basipterygium and inserts tendinously onto all the pelvic fin rays except the innermost pelvic soft ray.

The adductor profundus pelvicus originates from the dorsal surface of the pelvis, and inserts onto all the pelvic soft rays.

The arrector dorsalis pelvicus originates from the lateral surface of the basipterygium and inserts laterally onto the base of the pelvic spine.

Characters

No derived character that could be used in the analysis was found.

Other variations

Origin of the abductor profundus pelvicus. Usually the muscle originates from the ventral surface of the basipterygium, but it is expanded onto the basal portion of the subpelvic process in several species as above mentioned. However, intraspecific variation in the origin of the muscle is found in *M. surmuletus, Upeneus japonicus, U. asymmetricus, U. pori, Upeneichthys stotti* and *Up. porosus*.

2-8. Muscles of caudal fin (Fig. 75)

Description

The caudal fin muscles (Fig. 75) consist of the interradialis, hypochordal longitudinalis, flexor dorsalis, flexor dorsalis superior, flexor ventralis externus, flexor ventralis and flexor ventralis internus. The adductor dorsalis is lacking in all mullid fishes.

The interradialis consists of a number of bundles of muscle fibers interconnecting each branched and unbranched caudal segmented ray. They lie between adjacent rays, and extend over more than one ray. The muscle fibers are attached to the ray nearest the midlateral line and pass from the base of the rays upwards and downwards. There are additional bundles of the muscle fibers separated from the main bundle dorsally and ventrally; each interconnects two rays in both caudal lobes.

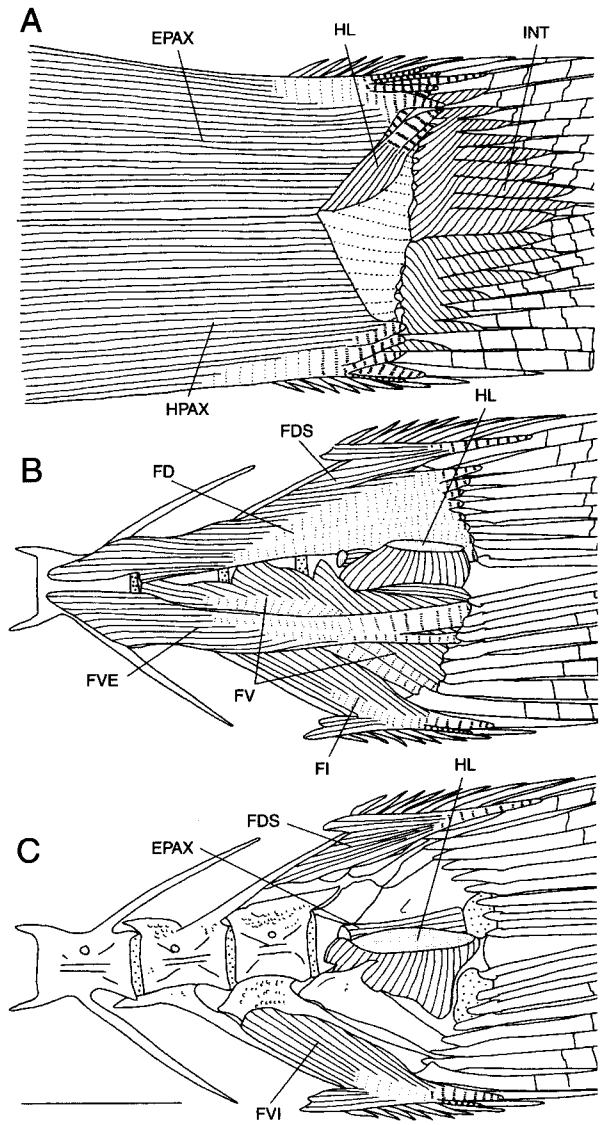

Fig. 75. Lateral view of caudal fin muscles in *Mullus surmuletus*, HUMZ 154869. A, superficial view; B, after removal of EPAX and HYPX; C, after removal of FD, FVE and FV. Scale indicate 5 mm.

The hypochordal longitudinalis originates from the antero-ventral portion of urostyle-hypural complex, the parhypural, and the lower two hypurals, and passes postero-dorsally to insert tendinously onto the two lowermost unbranched segmented rays and two or three branched rays below them.

The flexor dorsalis, lying under the posterior portion of the epaxialis, originates from the second to fourth preural centra, the urostyle-hypural complex, the uroneural, and the lower portion of two epurals. It inserts onto the lowermost unbranched segmented ray and all the branched rays of the upper caudal lobe.

The flexor dorsalis superior, situated higher than the flexor dorsalis, originates from the neural spine of the third preural centrum and inserts tendinously onto the second unbranched segmented ray of the upper caudal lobe.

The flexor ventralis externus, lying on the flexor ventralis, originates mainly from the fourth preural centrum and inserts tendinously onto several branched caudal rays in the lower caudal lobe. Although the range of insertion of the muscle shows no order by number of ray, the insertion of this muscle includes more branched rays in *Upeneus* and *Mulloidichthys* (upper four (only in *U. japonicus, U. luzonius* and *U. tragula*) or five branched rays) than in *Mullus, Upeneichthys, Parupeneus* and *Pseudupeneus* (three (only in *Parupeneus* sp., *P. porphyreus*, and *P. chrysonemus*) or four branched rays). There is individual variation in the number of fin rays involved in *Mu. flavolineatus* (three or four), *P. barberinoides* (three or four), and *P. chrysopleuron* (three or four).

The flexor ventralis originates from the second and third preural centra (including the haemal spine), urostyle-hypural complex, parhypural and hypurals. It inserts onto the anterior tip of all branched rays and two unbranched segmented rays in the lower caudal lobe.

The flexor ventralis inferior originates from the haemal spines of the second and third preural centra and inserts onto the one or two unbranched caudal rays that are below the insertion of the flexor ventralis.

Characters

No derived character that could be used in the analysis was found.

Other variations

None.

2-9. Muscles of median fins and their supportive elements (Fig. 76)

Description

Three muscle categories (inclinator, erector, and depressor) are attached to the fin base of the dorsal and anal fins.

The muscles of the dorsal fin comprise the inclinatores dorsales, erectores dorsales, and depressores dorsales.

The inclinatores dorsales originate from the fascia between the skin and the epaxialis. These muscles insert onto the lateral base of the spines or fin rays. The fibers of these muscles attach to the bases of the first to third dorsal spines and to the dorso-lateral surfaces of the pterygiophores in the first dorsal fin. These muscles are also present between both dorsal fins. In the second dorsal fin, they insert onto the bases of all fin rays. The erectores dorsales originate from the antero-lateral surfaces of the proximal pterygiophores of the dorsal fins and insert tendinously onto the antero-lateral bases of the fin rays. The depressores dorsales originate from the postero-lateral surfaces of the proximal pterygiophor-

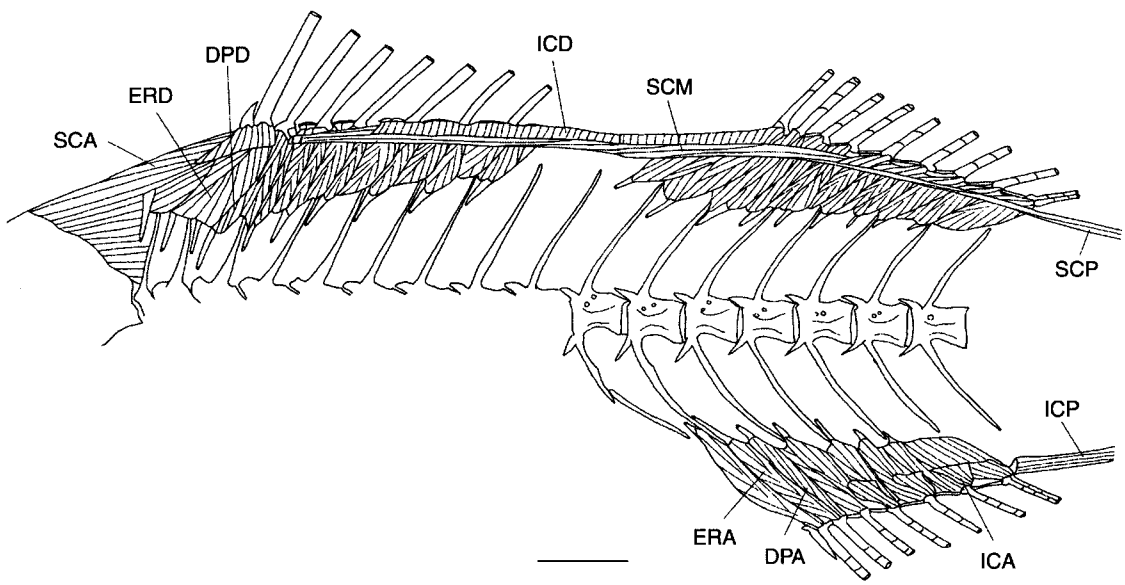

Fig. 76. Lateral view of muscles of median fins and their supportive elements in *Mullus surmuletus*, HUMZ 154869. Anterior portions of inclinatores dorsales and inclinatores anales removed, and infracarinalis anterior and infracarinalis medius are removed. Scale indicates 5 mm.

es of the dorsal fins and insert tendinously onto the postero-lateral bases of the fin rays.

The muscles of the anal fin comprise the inclinatores anales, erectores anales, and depressores anales.

The inclinatores anales originate from the fascia between the skin and the hypaxial, and insert onto the midregion of the bases of the anal fin rays. The erectores anales arise from the lateral surfaces of the proximal pterygiophores of the anal fin and insert onto the antero-lateral bases of the fin rays. The depressores anales originate from the lateral surfaces of the proximal pterygiophores and insert on the postero-lateral bases of the anal fin rays.

The carinal muscles comprise the supracarinalis anterior, supracarinalis medius, supracarinalis posterior, infracarinalis anterior, infracarinalis medius and infracarinalis posterior.

The supracarinalis anterior lies almost on the dorsal midline and interconnects the skull to the anterior tip of the first proximal pterygiophore of the dorsal fin. It also attaches to the intervening supraneurals. The supracarinalis medius, situated between both dorsal fins, connects the dorso-lateral surface of the last proximal pterygiophore of the first dorsal fin to the dorso-lateral surface of the first proximal pterygiophore of the second dorsal fin. It is connected to the supracarinalis posterior, and both fibers are passed anteriorly to insert onto the lateral wing of the second proximal pterygiophore of the first dorsal fin. The supracarinalis posterior connects the stay of the second dorsal fin to the anteriormost procurrent ray of the caudal fin. It also lies below the second dorsal fin and connects to the supracarinalis medius. The infracarinalis anterior lies on the ventral midline and interconnects the postero-ventral tip of the cleithrum to the antero-ventral surface of the pelvis. The infracarinalis medius connects the postero-dorsal surface of the postpelvic process of the pelvic fin to the ventro-lateral surface of the first proximal pterygiophore of the anal fin. The infracarinalis posterior connects the stay of the anal fin to the anteriormost procurrent ray.

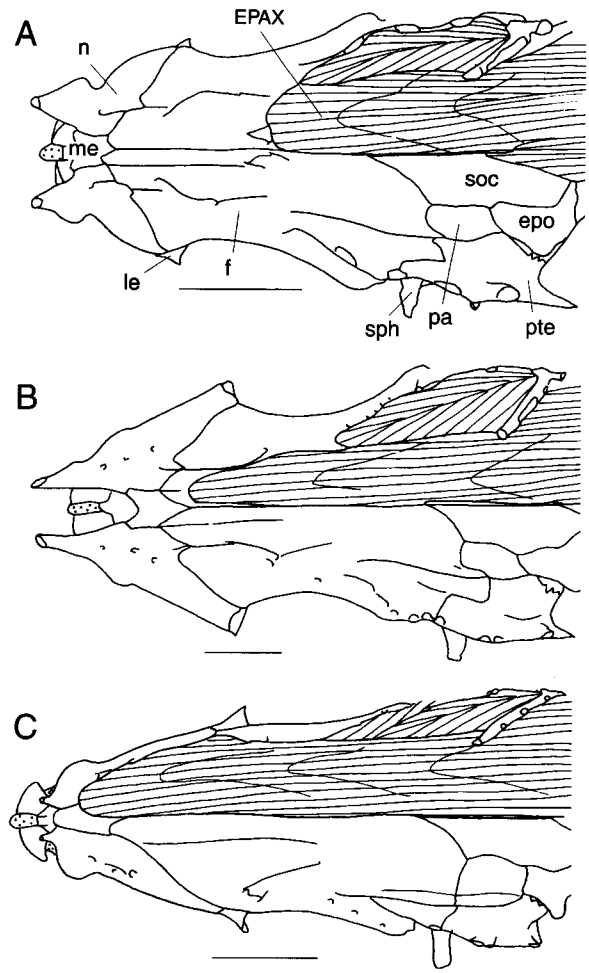

Fig. 77. Dorsal view of epaxialis on skull. A, *Mullus surmuletus*, HUMZ 154869; B, *Mulloidichthys flavolineatus*, UW 013326; C, *Parupeneus multifasciatus*, HUMZ 62786. Left epaxialis removed. Scales indicate 5 mm.

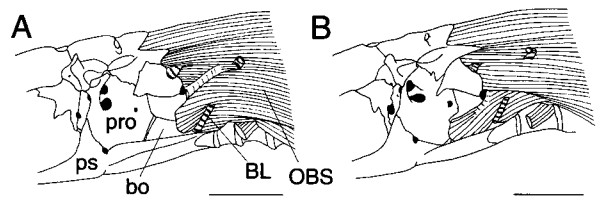

Fig. 78. Ventro-lateral view of obliquus superioris. A, *Upeneus parvus*, HUMZ 31349; B, *Mullus surmuletus*, HUMZ 154869. Scales indicate 5 mm.

Characters

No derived character that could be used in the analysis was found.

Other variations

None.

2-10. Body muscles (Figs. 77-78)

Description

The body muscles, forming the main musculature of the body, comprise segmentally arranged myomeres separated by myocommata. They are separated into three divisions: the epaxialis, the lateralis superficialis and the hypaxialis.

The epaxialis forms the dorsal component of the body musculature and lies above the lateral septum. It anteriorly attaches to the neurocranium and the dorsal elements of the pectoral girdle. The muscle extends anter-

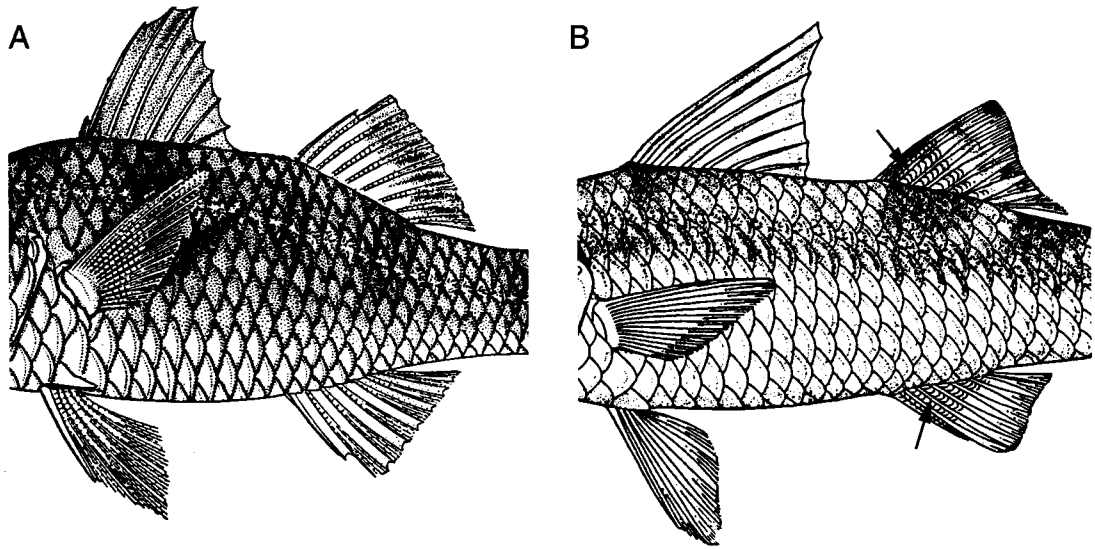

Fig. 79. Scales on second dorsal and anal fins. A, *Parupeneus porphyreus*, after Jenkins, 1903 ; B, *Upeneus luzonius*, after Jordan and Seale (1907).

iorly to the nasal and mesethmoid in *Parupeneus* (except *P. spilurus, P. signatus* and *P. chrysopleuron*) and *Pseudupeneus*. It reaches the anterior portion of the frontal in *Mulloidichthys* and *Upeneichthys* and the mid-portion of the frontal in *Mullus* (Fig. 77). However, two distributional patterns of the muscle are present in *Upeneus*. The epaxialis reaches the anterior portion of the frontal in *U. asymmetricus, U. japonicus, U. luzonius, U. crosnieri, U. tragula, U. pori* and *U. taeniopterus*, while it reaches the mid-portion of the frontal in *U. moluccensis, U. parvus, U. quadrilineatus, U. sulphureus* and *U. vittatus*.

The lateral superficialis consists of a sheet of fibers on either side of the lateral midline.

The hypaxialis occupies the ventral component of the body musculature, lying below the lateral septum, and consists of two elements, the obliquus superioris and the obliquus inferioris. The obliquus superioris, lying just below the horizontal septum, originates from the postero-lateral region of the neurocranium, cleithrum and postcleithrum. The muscle also attaches to the intercalar and the ventral side of the pterotic in *U. asymmetricus, U. japonicus* and *U. pori*. The lower portion of the obliquus superior attaches to the lateral surfaces of the exoccipital and basioccipital. In *U. asymmetricus, U. japonicus, U. pori* and *U. tragula*, the muscle extends anteriorly to cover almost the entire basioccipital (Fig. 78B).

Characters

TS 40. Anterior limit of epaxialis on frontal (Fig. 77)

0 : posterior portion ; 1 : middle portion ; 2 : anterior portion near nasal and mesethmoid (ordered). The epaxialis is extended anteriorly to the middle portion of the frontal in *Upeneus moluccensis, U. parvus, U. quadrilineatus, U. sulphureus, U. vittatus* and *Mullus* (1). In *Upeneichthys, Mulloidichthys, Pseudupeneus* and *Parupeneus*, as well as the remaining species of *Upeneus* except the above five, the muscle reaches the anterior portion of the frontal near the nasal and mesethmoid (2).

Other variations

None.

3. External morphology

TS 41. Scales on fin membranes of second dorsal and anal fins (Fig. 79)

0 : absent ; 1 : present. In most of mullid genera as well as in the outgroups, the scales on the second dorsal and anal fins are absent (0). These scales were found in only *Upeneus* (1).

V. Phylogeny

1. Monophyly of the family Mullidae

All genera of the family Mullidae share many osteological and myological characters as listed Table 1. From that list, characters 1 to 13 seem to be autapomorphies unique to the family Mullidae, among the percoids, and support strongly the monophyly of the family. The remaining characters (14 to 27) are synapomorphies for all mullids, although they also were found in several percoids. Four characters (24 to 27) were proven as synapomorphies of the Mullidae after phylogenetic analysis employing DELTRAN optimization of character evolution. In addition, two characters (22 and 23)

Table 1. List of autapomorphic characters of the family Mullidae and apomorphic characters shared by whole mullids and other percoids

1. Articulation of first infraorbital with lateral ethmoid
2. Presence of expanded subocular shelf on first infraorbital
3. Articulation of endopterygoid with lateral ethmoid
4. Cartilaginous articulation of palatine with endopterygoid
5. Interdigitation of symplectic with metapterygoid
6. Presence of interopercular medial socket
7. Osteological differentiation of hyoid arch
   7-1. Modification of first branchiostegal ray into barbel
   7-2. Diminishment of branchiostegal rays
   7-3. Forward projection of anterior ceratohyal
   7-4. Lateral convex of ceratohyals
8. Medial expansion of accessory subpelvic keel
9. Presence of additional process on basipterygium
10. Rigid attachment of nasal with neurocranium
11. Myological differentiation of hyoid muscles
   11-1. Presence of four muscles related to barbel
   11-2. Separation of protractor hyoidei of both sides
   11-3. Diminished insertion of hyohyoidei abductores section 1
   11-4. Insertion of hyohyoidei abductores section 2 onto urohyal
12. Insertion of transversus dorsalis anterior onto interarcual cartilage
13. Forward extension of supracarinalis medial and supracarinalis posterior
14. Origin of adductor profundus from basipterygium
15. Presence of additional scapular foramina
16. Diminishment of branched caudal fin rays
17. Diminishment of epural bone
18. Diminishment of anal spine
   18-1. Segment of second fin ray on anteriormost anal pterygiophore
   18-2. Branch of fin ray on second anal pterygiophore
19. Fusion of urosytle and fused third and fourth hypurals
20. Origin of dilatator operculi from frontal
21. Absence of crescent expansion on endopterygoid
22. Anterior expansion of adductor arcus palatini
23. Fan-like expansion of supramaxilla
24. Presence of weak opercular medial strut
25. Fusion of third and fourth hypurals
26. Anterior expansion of epaxialis on frontal

were considered as a valid relationship indicator inferring the sister groups of the mullids (see chapter VIII).

Character 1. Articulation of first infraorbital with lateral ethmoid (Fig. 80)

The first infraorbital of the mullids is located posterior to the lacrimal and is shifted forward to articulate with the lateral ethmoid. The lateral ethmoid has usually two surfaces for articulation with the lacrimal and the palatine. The dorso-lateral surface is for articulation with the lacrimal and the ventral one is for the palatine. In teleosts, the lacrimal usually articulates with the lateral ethmoid, and the infraorbital bone behind it is well free from articulating with the lateral ethmoid (Gosline, 1984). Smith and Bailey (1962) suggested that the lacrimal in the mullids is shifted forward to contact weakly with the lateral ethmoid, while the first infraorbital situated posterior to the lacrimal is mainly in contact with the lateral ethmoid. This forward dislocation of the lacrimal also has been reported in the pentacerotids as well as in the mullids (Gosline, 1984).

In the present study the lacrimal of all the percoids examined is articulated with the lateral ethmoid dorsally, and the first infraorbital is free from articulating with the lateral ethmoid (Fig. 80A), except in *Pentaceros* and all

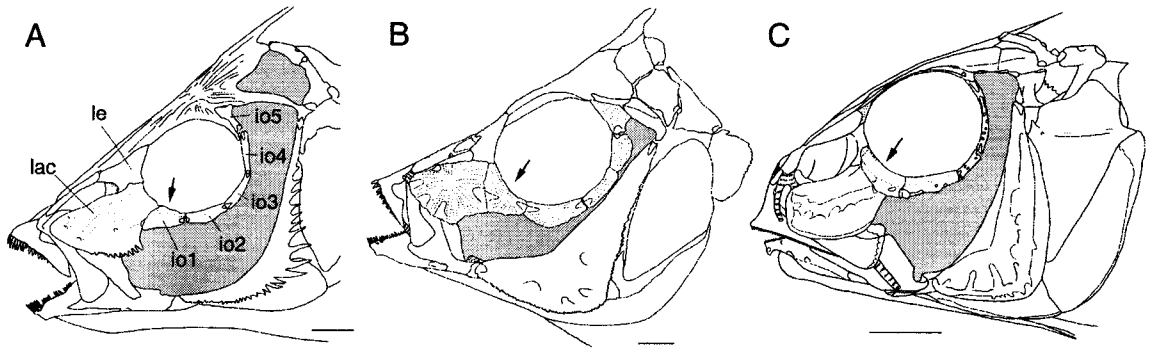

Fig. 80. Lateral view of head region showing relation between lateral ethmoid and circumorbital bones. A, *Rhyncopelates oxyrhynchus*, HUMZ 39480; B, *Pentaceros japonicus*, HUMZ 90278; C, *Upeneus japonicus*, HUMZ 105764. Arrows show first infraorbital bone. Scales indicate 5 mm.

genera of the mullids. As suggested by both Smith and Bailey (1962) and Gosline (1984), the articulation between the circumorbital bones and lateral ethmoid is via the first infraorbital in both *Pentaceros* and the mullids. However, in *Pentaceros* the main articulation between two bones is made by the lacrimal (Fig. 80B), while it is by the first infraorbital bone in the mullids (Fig. 80C).

Character 2. Presence of expanded subocular shelf on first infraorbital (Fig. 81)

The first infraorbital of the mullids articulates with the lateral ethmoid dorsally and bears an expanded subocular shelf medially. This subocular shelf supports the strong articulation between the lateral ethmoid and the infraorbital bone, and is also continued with the shelf of the second infraorbital. The subocular shelf is a bony lamina that extends inward from the infraorbital bones, and it is possessed by several beryciforms and many percoids among perciforms (Smith and Bailey, 1962). It is also suggested that the second infraorbital (the third infraorbital of Smith and Bailey, 1962, who included the lacrimal in the count) alone contributes to the subocular shelf in most members of the percoids, and that exceptionally, both the first and second infraorbital bones have subocular shelves in the mullids (Smith and Bailey, 1962; Gosline, 1984).

In the present study most of the percoids, including *Lates, Stereolepis, Niphon, Chelidoperca, Sacura, Banjos, Priacanthus, Apogon, Branchiostegus, Lutjanus, Etelis, Macolor, Pterocaesio, Pristipomoides, Girella, Hapalogenys, Acanthopagrus, Dentex, Scolopsis, Nemipterus, Polydactylus, Pempheris, Microcanthus, Rhyncopelates, Oplegnathus* and *Goniistius*, have a subocular shelf only on the second infraorbital (Fig. 81A). However, in both *Pentaceros* and all genera of the mullids the subocular shelves are present not only on the first infraorbital but also on the second one (Figs. 81B-C). Furthermore, the subocular shelf on the first

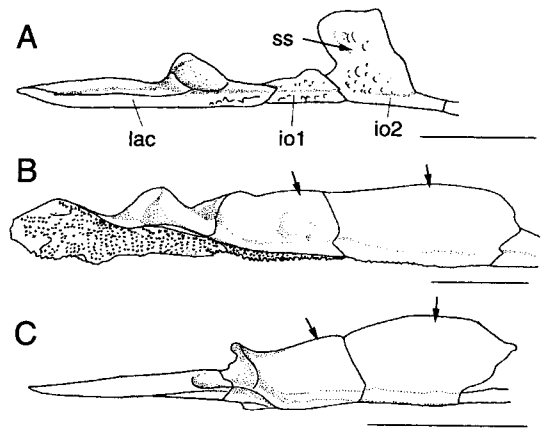

Fig. 81. Dorsal view of anterior portion of circumorbital bones showing subocular shelf. A, *Rhyncopelates oxyrhynchus*, HUMZ 39480; B, *Pentaceros japonicus*, HUMZ 90278; C, *Parupeneus heptacanthus*, BSKU 084326. Arrows show subocular shelves. Scales indicate 5 mm.

infraorbital is as well developed as the one on the second infraorbital in both groups. However, there is no major articulation between the first infraorbital and the lateral ethmoid in *Pentaceros*, while the subocular shelf of the first infraorbital in the mullids articulates with the lateral ethmoid on its antero-dorsal margin via connective tissue.

Character 3. Articulation of endopterygoid with lateral ethmoid (Fig. 82)

The endopterygoid of the mullids has an antero-dorsal projection to articulate with the lateral ethmoid (see TS 21). As mentioned in character 1, the ventral surface of the lateral ethmoid is for articulation with the palatine, in other words, the palatine usually articulates with the lateral ethmoid in the percoids.

The forward dislocation of the palatine is reported in the mullids and *Pentaceros* by Gosline (1984). Because of the forward shift of the palatine, the endopterygoid behind it is articulated with the lateral ethmoid in both

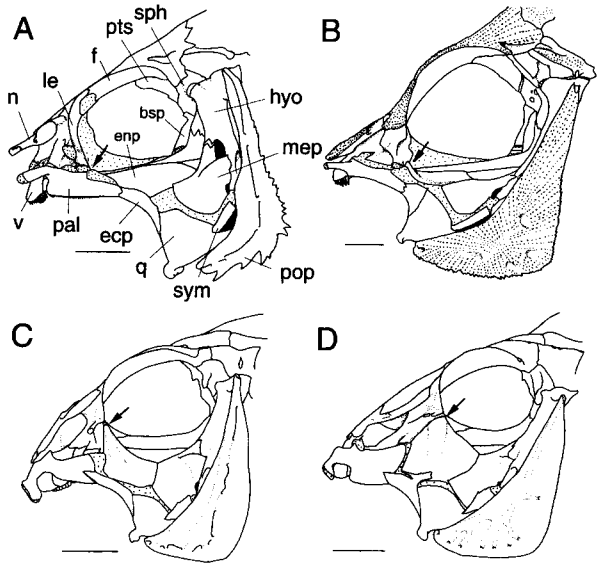

Fig. 82. Lateral view of head region showing articulation between neurocranium and suspensorium. A, *Stereolepis doederleini*, HUMZ 71230; B, *Pentaceros japonicus*, HUMZ 90278; C, *Mullus surmuletus*, HUMZ 154869; D, *Parupeneus multifasciatus*, HUMZ 62786. Arrows show the articular portion between lateral ethmoid and endopterygoid. Scales indicate 5 mm.

groups. However, although the endopterygoid of the two groups meets the lateral ethmoid (Figs. 82B-D), there is a distinct difference in articulation pattern. The endopterygoid of *Pentaceros* has a small projection on its antero-dorsal region which is in contact slightly with the lateral ethmoid by the tip only (Fig. 82B). In the mullids, however, the endopterygoid is expanded and projected antero-dorsally to form a triangular shape and is mainly articulated with the lateral ethmoid (Figs. 82C-D).

Character 4. Cartilaginous articulation of palatine with endopterygoid (Fig. 83)

The palatine of the mullids has a well-developed cartilaginous block to articulate with the endopterygoid posteriorly, although the bone is overlapped and weakly attached medially to the endopterygoid in only *Upeneus* (see TS 20). The palatine is firmly attached (for example, pentacerotids, Gosline, 1984) or joined (girellids, Johnson and Fritzsche, 1989) with the endopterygoid posteriorly by connective tissue in most percoids. Gosline (1984) pointed out that the palatine of the mullids is joined to the endopterygoid by a flexible area of cartilage on its posterior margin, and that such a joint is common in the percoids.

The palatine is firmly attached posteriorly with the endopterygoid to form a single unit of the suspensorium in all percoids examined (Fig. 83A) except *Priacanthus*,

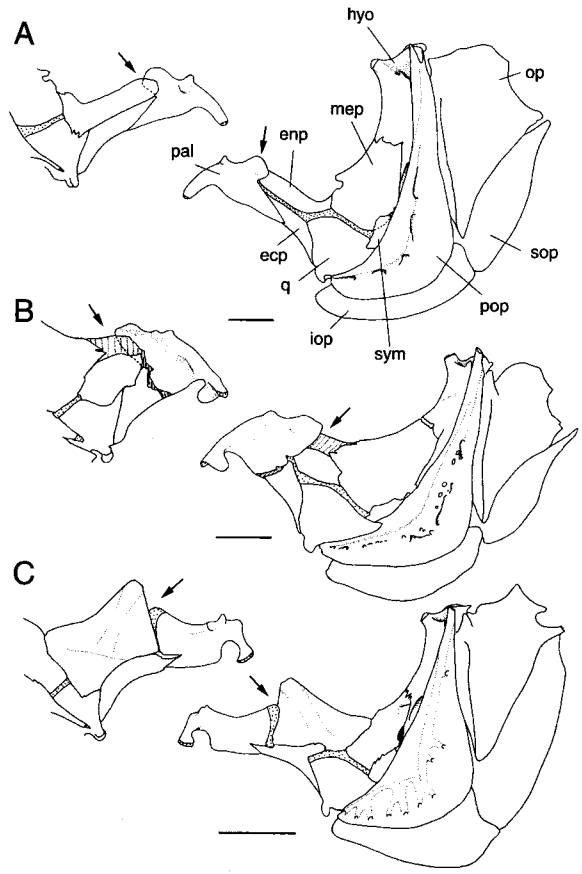

Fig. 83. Medial (left) and lateral (right) views of suspensorium showing relation between palatine and endopterygoid. A, *Dentex caeruleopunctatus*, HUMZ 73314; B, *Lethrinus xanthochilus*, HUMZ 41408; C, *Parupeneus heptacanthus*, BSKU 084326. Arrows show articular portion between palatine and endopterygoid. Scales indicate 5 mm.

Lethrinus, *Scolopsis*, *Nemipterus*, *Polydactylus*, *Larimichthys* and *Goniistius*. The palatine in these exceptional genera is connected with the endopterygoid by a ligament or connective tissue; therefore, it makes the palatine move right and left (Fig. 83B). However, in the mullids the palatine has a well-developed cartilaginous portion on its posterior margin to provide flexibility, and there is neither firm attachment nor overlap (except in *Upeneus*) between the palatine and the endopterygoid (Fig. 83C).

Character 5. Interdigitation of symplectic with metapterygoid (Fig. 84)

The symplectic of the mullids is expanded dorsally and also interdigitated with the metapterygoid on both sides. In most generalized percoids the symplectic is a simple strut-like bone not extending beyond the lower arm of the hyomandibula. The bone of the sparoids (*sensu* Johnson, 1980) has a laminar projection dorsally and ventrally to articulate with the metapterygoid and

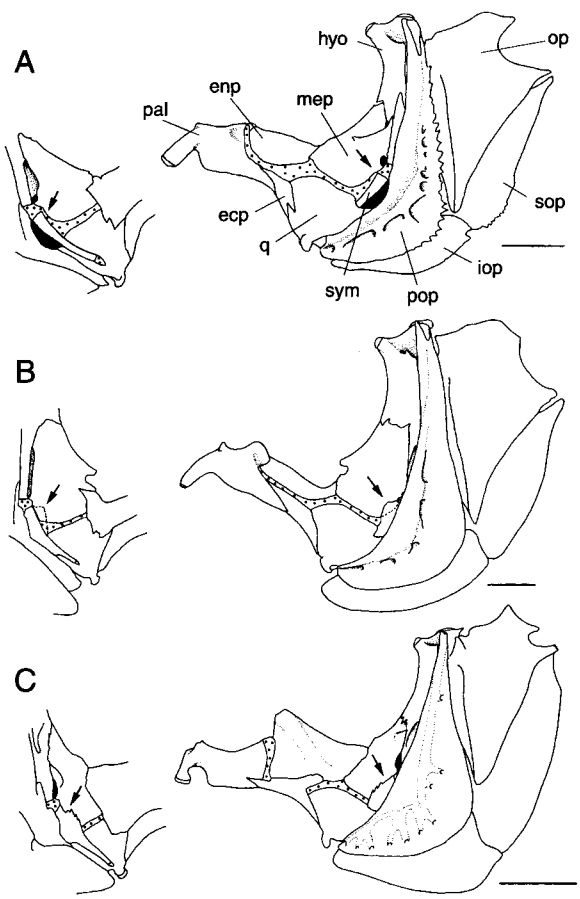

Fig. 84. Medial (left) and lateral (right) views of suspensorium showing relation between metapterygoid and symplectic (arrow). A, *Hapalogenys mucronatus*, HUMZ 143107; B, *Dentex caeruleopunctatus*, HUMZ 73314; C, *Parupeneus heptacanthus*, BSKU 084326. Scales indicate 5 mm.

the preopercle, and this condition of the symplectic is said to be a unique character to the sparoids (Johnson, 1980). A similar expansion of the symplectic is reported in Sciaenidae by Sasaki (1989). This distal expansion of the symplectic was considered by Gosline (1984) as one of the common characters of the sparoids and the mullids.

In the present study most of the percoids examined have a simple strut-like symplectic (Fig. 84A). The expansion of the symplectic is found in the sparoid genera *Acanthopagrus, Dentex, Lethrinus, Scolopsis* and *Nemipterus*, as well as in all genera of the mullids. Although the symplectic of the mullids is expanded distally like those of the sparoids, there is a distinct difference in the relationship between the symplectic and the metapterygoid. The symplectic of the sparoids is merely overlapped by the metapterygoid laterally (Fig. 84B), while that of the mullids is interdigitated with the metapterygoid in both sides (Fig. 84C).

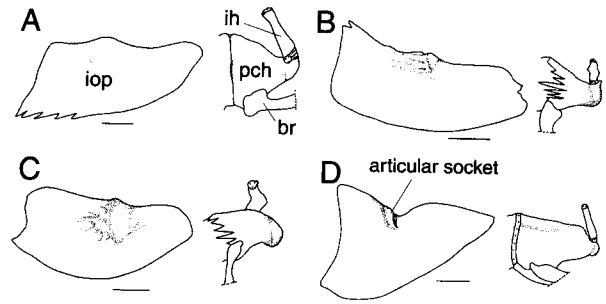

Fig. 85. Medial view of interopercle (left) and lateral view of posterior portion of hyoid arch (right). A, *Sacura margaritacea*, HUMZ 80748; B, *Leiognathus nuchalis*, HUMZ 48518; C, *Goniistius zebra*, HUMZ 36355; D, *Parupeneus heptacanthus*, BSKU 084326. Scales indicate 2 mm.

Character 6. Presence of interopercular medial socket (Fig. 85)

The interopercle of the mullids has a well-developed medial socket for articulating with the posterior tip of the posterior ceratohyal. Although there is no projection on the medial surface of the interopercle in most general percoids (Fig. 85A), a similar structure to that of the interopercle of mullids is found in *Leiognathus* and *Goniistius* among the percoids examined (Figs. 85B-C). However, the interopercle of those two genera are different from that of the mullids in shape. The mullids have a complete socket (Fig. 85D) rather than a simple elevated strut as in *Leiognathus* and *Goniistius*.

Character 7. Osteological differentiation of hyoid arch (Fig. 86)

The most notable character of the mullids is their pair of highly developed hyoid barbels under the chin.

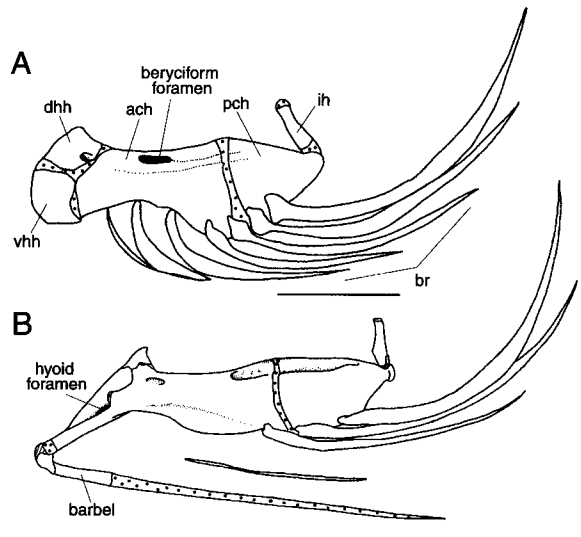

Fig. 86. Lateral view of hyoid arch, except basihyal and urohyal. A, *Parapristipoma trilineatum*, HUMZ 49224; B, *Upeneus japonicus*, HUMZ 105764. Scales indicate 5 mm.

Starks (1904) compared the hyoid arch and branchiostegal rays of mullids and the polymixiids, and suggested that the barbels of the mullids are structurally different from those of the polymixiids. Based on observation of the Atlantic species of *Mullus*, Lo Bianco (1907) reported that the branchiostegal rays show normal serial arrangement in the larval stage, and during growth, the anteriormost one moves forward to separate from the others. The formation of the barbel by a forward shift of the first branchiostegal ray was also observed in *Mullus auratus* (Caldwell, 1962) and in *Upeneus tragula* (McCormick, 1993). Gosline (1984) noted that sensory probes related to branchiostegal rays occur only in the family Mullidae and in the polymixiid genus *Polymixia*, and that these two hyoid barbels have evolved independently based on many structural differences between them.

The osteological differentiation of the hyoid arch of the Mullidae are summarized as follows.

Character 7-1. Modification of first branchiostegal ray into barbel

The hyoid barbel is a unique feature of the mullids among the percoids, and its forward movement is apparently accompanied by the forward projection of the lower portion of the anterior ceratohyal (Gosline, 1984; McCormick, 1993; pers. obs.).

Character 7-2. Diminishment of branchiostegal rays

There are five branchiostegal rays, including the barbel, while the common number of branchiostegal rays in percoids is seven (Fig. 86A), although five branchiostegal rays are also observed in Plesiopidae and Pseudoplesiopidae (McAllister, 1968) and *Leiognathus*. In the mullids the first branchiostegal ray is modified into a barbel, the second is a thread-like bone detached from the anterior ceratohyal, and the third to fifth are attached to the lateral surfaces of the anterior ceratohyal.

Character 7-3. Forward projection of anterior ceratohyal

The anterior ceratohyal of the mullids is projected forward. It results in the formation of a hyoid foramen, providing a passage for the extensor tentaculi, between the ventral hypohyal and the anterior ceratohyal, and a horizontal arrangement of the ventral and dorsal hypohyals. An anterior projection of the anterior ceratohyal, as in the mullids, was not found in any of the percoids examined, and the dorsal and ventral hypohyals are also arranged vertically in percoids.

Character 7-4. Lateral convexity of ceratohyals

The anterior and posterior ceratohyals of the mullids are convex laterally, serving as an attachment site for the retractor tentaculi, whereas the same bones are flat in all the percoids examined.

Character 8. Medial expansion of accessory subpelvic keel (Fig. 87)

The accessory subpelvic keel of the mullids is well-developed and expanded medially nearly to meet its antimere on the midline. The accessory subpelvic keel, (the additional ridge of Johnson, 1980, and the ventral wing of Stiassny and Moore, 1992), was first introduced by Katayama (1957) based on some Japanese serranids. Johnson (1980) reported its appearance in the etelines and apsilines within the Lutjanidae as well as in Nemipteridae among the sparoids. He also considered it as a primitive character because of its occurrence in beryciforms, lower percoids (*Symphysanodon*) and some percichthyids. Stiassny and Moore (1992) suggested that it has some potential significance in phylogenetic analysis, although it is sparsely distributed and its occurrence is restricted to perciform taxa.

In the present study, the accessory subpelvic keel was also observed in *Stereolepis, Chelidoperca, Sacura, Banjos, Lepomis, Priacanthus, Pristipomoides, Parapristipoma, Dentex, Scolopsis, Larimichthys, Pempheris, Pentaceros, Oplegnathus, Goniistius* and all genera of the mullids among the percoids examined. However, the expanded accessory subpelvic keel is found not only in *Priacanthus* (Fig. 87C) but also in the mullids (Fig. 87D). The structure in mullids is more expanded medially in *Priacanthus*, nearly meeting its antimere along its entire length and located between the abductor superficialis pelvicus and the abductor profundus pelvicus, separating these pelvic muscles. In *Priacanthus*, no separation between these pelvic muscles was found.

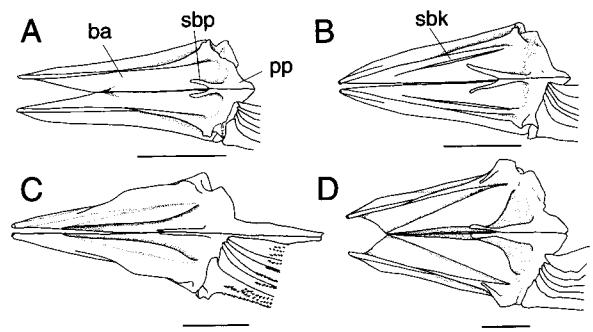

Fig. 87. Ventral view of pelvic girdle. A, *Acanthopagrus schlegeli*, HUMZ 103537; B, *Sacura margaritacea*, HUMZ 87048; C, *Priacanthus macracanthus*, HUMZ 97044; D, *Upeneus vittatus*, HUMZ 46769. Right pelvic fin rays removed. Scales indicate 5 mm.

Character 9. Presence of additional process on basipterygium (Fig. 88)

In the mullids there is an additional process which is projected medially on the subpelvic keel. A similar process is observed in *Apogon* among the percoid examined (Fig. 88A), but there are differences in the location and shape of the process between them. *Apogon* has a simple process which is projected medially to the opposite side of the pelvic lateral process, while that of the mullids is shoehorn-like and is projected antero-medially from the anterior portion where the pelvic lateral process is located (Fig. 88B).

Character 10. Rigid attachment of nasal with neurocranium (Fig. 89)

The nasal bone of the mullids is expanded into a leaf-like form and firmly attached to the mesethmoid medially, and the frontal and lateral ethmoid posteriorly. In contrast, the nasal bone of percoids is usually tubular and connected with the skull by connective tissue (Figs. 89A B). Gosline (1984) pointed out that the nasal in the mullids is rigidly attached to the skull. This rigidity of the anterior part of the skull is associated with the habit of ploughing up the bottom with its snout in some mullids, especially *Mullus* and *Upeneichthys* (Gosline, 1984; Ben-Tuvia, 1986).

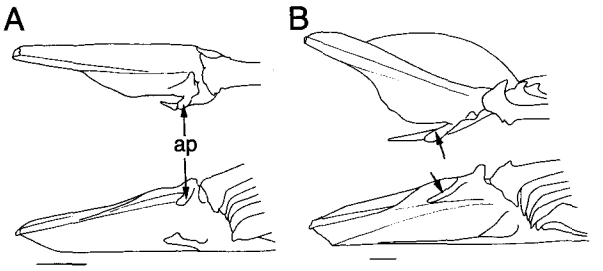

Fig. 88. Lateral (above) and ventral (below) views of left pelvic girdle. A, *Apogon semilineatus*, HUMZ 107056; B, *Parupeneus pleurostigma*, HUMZ 48219. Arrows show additional process. Scales indicate 2 mm.

Character 11. Myological differentiation of hyoid muscles

Character 11-1. Presence of four muscles related to barbel (Fig. 64)

The musculature related to the hyoid barbel of the mullids was first described by Gosline (1984). He indicated that each hyoid barbel has its own musculature to control movement of the barbel. He also depicted barbel mechanics in a diagram, showing the two muscle pairs that extend and retract the barbel are inserted onto the base of barbel by a ligament.

In the present study the four muscles related to each barbel are recognized in all genera of the mullids. These are composed of the extensor tentaculi, the retractor tentaculi and two sections of the rotator tentaculi. The extensor tentaculi and retractor tentaculi, corresponding to those of Gosline (1984), seem to be related to the anterior-posterior movement of the barbel. The posterior two seem to be related to the right-left movement of the barbel. As pointed out by Gosline (1984) they seem to be modified from the hyohyoideus system (Winterbottom, 1974), especially the hyohyoidei abductores and hyohyoidei adductores.

Character 11-2. Separation of protractor hyoidei of both sides (Fig. 63)

The protractor hyoidei of the mullids lies between the medial surface of the dentary and postero-lateral surface of the anterior ceratohyal, and the muscles of both sides are not connected on the midline. It is considered that the separation of both protractor hyoidei in the mullids resulted from the anterior elongation of the anterior ceratohyal to differentiate the hyoid barbel. Usually the protractor hyoidei connects the hyoid arch to the lower jaw, and its fibers arising from the left and right sides of the hyoid arch are fused on the midline anterior to the arch and are inserted onto the lower jaw as a

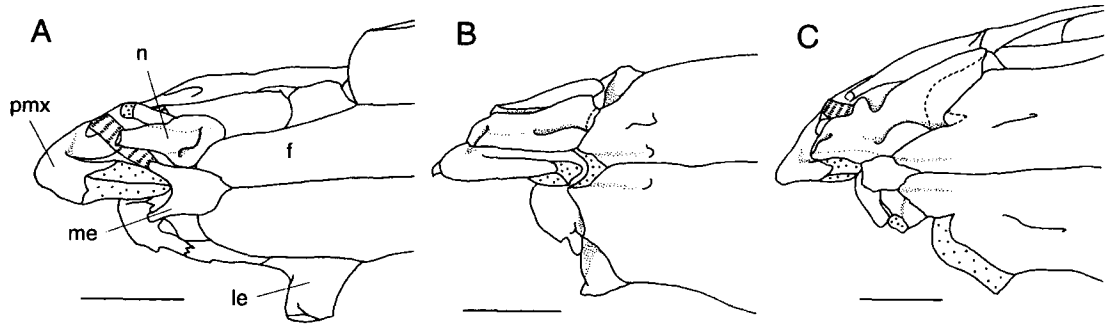

Fig. 89. Dorsal view of anterior portion of neurocranium, upper jaw and suspensorium. A, *Lates japonica*, HUMZ 138066; B, *Acanthopagrus schlegeli*, HUMZ 103537; C, *Upeneus pori*, HUJ 13549. Left elements except neurocranium are removed. Scales indicate 3 mm.

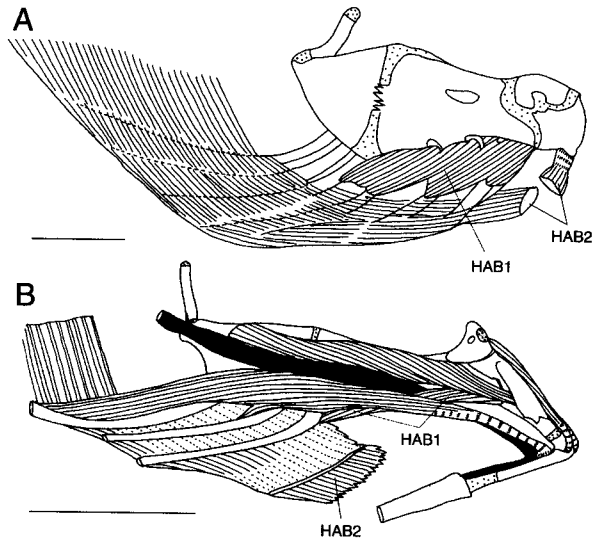

Fig. 90. Medial view of hyoid muscles. A, *Pentaceros japonicus*, HUMZ 90278; B, *Upeneus japonicus*, HUMZ 141203. Scales indicate 5 mm.

single unit in many fish groups (Winterbottom, 1974; Yabe, 1985; Shinohara, 1996; Imamura, 1996; Takahashi, 1999).

Character 11-3. Diminished insertion of hyohyoidei abductores section 1 (Fig. 90B)

The hyohyoidei abductores section 1 in the mullids originates from the medial surface of the anterior ceratohyal and inserts only onto the medial surface of the third branchiostegal ray. In the percoids the hyohyoidei abductores section 1 usually originates from the anteroventral region of the anterior ceratohyal or from the base of the preceding branchiostegal ray, and is inserted onto the proximal portions of each branchiostegal ray (Winterbottom, 1974; Yabe, 1985; Shinohara, 1994; Imamura, 1996; Takahashi, 1999), although the insertion on branchiostegal rays differs somewhat according to authors.

A similar insertion of the hyohyoidei abductores section 1 was observed in all percoids examined in the present study, while in all genera of mullids the insertion of the muscles is confined to the third branchiostegal ray. It seems that differentiation of some muscles related to movement of the barbel results in this diminishment of the hyohyoidei abductores section 1.

Character 11-4. Insertion of hyohyoidei abductores section 2 onto urohyal (Fig. 63)

The hyohyoidei abductores section 2 of the mullids connect the thread-like second branchiostegal ray with the ventral surface of the urohyal. Usually the hyohyoidei abductores insert onto the anteriormost branchiostegal ray, and its origin includes the hyoid arch of the same or the opposite side, or even from both (Winterbottom, 1974). Yabe (1985) reported two distributional patterns of this muscle in some scorpaeniforms, i.e., one originates from the hypohyal of opposite sides and crosses over its antimere, the other fuses with its antimere with a median raphe on the ventral midline. The former pattern of this muscle is also reported in platycephalids by Imamura (1996), and the latter is reported in hexagrammids by Shinohara (1994).

In the present study, most of the percoids examined show the first pattern of Yabe (1985), but in *Acanthopagrus, Dentex, Lethrinus* and *Goniistius* each muscle is fused along the ventral midline and is also connected with the ventral hypohyal and basihyal by connective tissue. That of *Microcanthus* is also fused with each element on the midline, but there is no connective tissue entering the ventral hypohyal. In addition, the fusion of this muscle along the ventral midline is also observed in *Leiognathus* and *Branchiostegus*. However, in the former the muscle originates from the ventral hypohyal via muscle fibers, in the latter it also originates from the ventral hypohyal via connective tissue, but the anterior portion is not fused along the midline. The hyohyoidei abductores section 2 of all mullid genera differs from those patterns mentioned above and appears to be a unique feature to the mullids among the percoids. This muscle of the mullids originates from the second branchiostegal ray and is inserted onto the ventral surface of the urohyal.

Character 12. Insertion of transversus dorsalis anterior onto interarcual cartilage (Figs. 68A-B)

The transversus dorsalis anterior of the mullids is located along the ventral surface of the parasphenoid, the basioccipital and the dorsal elements of the branchial arch. The composition of this muscle is various in the percoids. For example, in sciaenids it comprises only one element, the musculus transversus epibranchialis 2 (Anker, 1978), which originate from the dorsal surface of the second epibranchial and is fused with its antimere on the dorsal midline, while the another element, the musculus cranio-pharyngobranchialis 2 (Anker, 1978), which lies on the musculus transversus epibranchialis 2 and is connected with the anterior portion of the second pharyngobranchial, is present in the percichthyid *Acropoma* (Sasaki, 1989). Sasaki (1989) also considered the presence of the above two elements of the transversus dorsalis as a primitive character in the perciforms.

In the present study the above two elements of the muscle are found in *Stereolepis, Niphon, Sacura, Banjos,*

Apogon, Branchiostegus, Trachurus, Leiognathus, Lutjanus, Pristipomoides, Girella, Parapristipoma, Acanthopagrus, Dentex, Lethrinus, Scolopsis, Pempheris, Pentaceros, Rhyncopelates, Kuhlia, Oplegnathus and all genera of the mullids. Usually the musculus craniopharyngobranchialis 2 is inserted onto the antero-dorsal surface of the second pharyngobranchial. However, the insertion of the muscle in the mullids also includes the dorsal surface of the interarcual cartilage.

Character 13. Forward extension of supracarinalis medius and supracarinalis posterior (Fig. 76)

The supracarinalis medius of the mullids is located between both dorsal fins and connects the dorso-lateral surface of the last proximal pterygiophore of the first dorsal fin to the dorso-lateral surface of the first proximal pterygiophore of the second dorsal fin. It is also connected to the supracarinalis posterior, being continued from and passing anteriorly to insert onto the lateral wing of the second proximal pterygiophore of the first dorsal fin. The supracarinalis posterior connects the stay of the second dorsal fin to the anteriormost procurrent ray of the caudal fin. It also lies below the second dorsal fin and connects to the supracarinalis medius. Mooi and Gill (1995 : 131, fig. 11) also reported that the supracarinalis medius of the mullids is continuous with the supracarinalis posterior in their work about the epaxial muscles and acanthomorph relationships.

Character 14. Origin of adductor profundus from basipterygium (Fig. 70)

The origin of the adductor profundus of the pectoral girdle includes the basipterygium as well as the cleithrum and coracoid in the mullids. Usually the muscle in teleosts originates from the medial surfaces of the coracoid and cleithrum (Winterbottom, 1974).

In the present study, the origin of the muscle in most percoids examined is also from the medial surfaces of the coracoid and cleithrum. However, the expansion of the origin of the muscle to the basipterygium is found in *Chelidoperca, Banjos, Etelis, Lutjanus, Pristipomoides, Lethrinus* and all genera of mullids (except *Upeneus parvus*), i.e., the adductor profundus originates from the antero-dorsal portion of the basipterygium.

Character 15. Presence of additional scapular foramina (Fig. 91)

Starks (1930) described the scapula of the pectoral girdle having only one foramen, which is a major nerve passage in most teleosts. He also noted that the mullids are peculiar in having an increased number of scapular

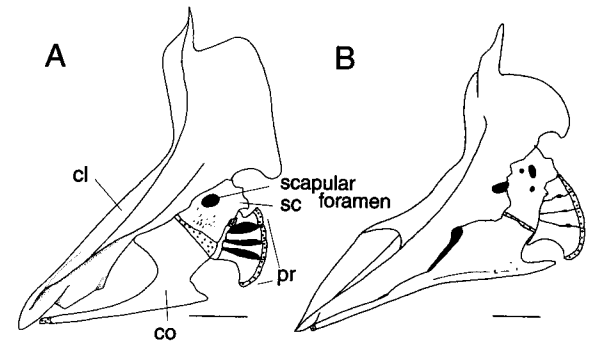

Fig. 91. Lateral view of pectoral girdle, except several elements. A, *Acanthopagrus schlegeli*, HUMZ 103537; B, *Parupeneus barberinus*, UW 010542. Scales indicate 5 mm.

foramina, that is, two or three foramina are contained in the scapula. Out those foramina, the anteriormost one corresponds to that of other fishes (Gosline, 1984). Shimokawa (1990) recorded two scapular foramina in three genera of cirrhitids, *Cirrhitus, Isocirrhitus* and *Amblycirrhitus*, and Starks (1930) recorded two in *Cirrhitus, Paracirrhites* and *Cheilodactylus*.

In the present study all percoids examined have only one scapular foramen, but additional scapular foramina are observed in all genera of the mullids. Although its number in the mullids varies from two to seven, and even differs somewhat on opposite sides of the same specimens, there is always at least two, as mentioned by Starks (1930).

Character 16. Diminishment of branched caudal fin rays (Fig. 92)

The mullids have seven and six branched rays in the upper and lower caudal lobes, respectively, and the principal caudal fin rays number 15 (8+7). According to Johnson (1984), the most common and primitive number of principal caudal fin rays is 17 (9+8) and the branched rays are eight and seven in the upper and lower lobes, respectively. He also suggested that the reduction of branched caudal rays is found in the Cheilodactylidae, Chironemidae, Cirrhitidae, Latrididae and Mullidae.

In the present study, most of the percoids examined have 8+7 branched caudal rays, and all genera of the mullids show a decreased number of branched caudal rays. Among percoids examined, seven branched rays in the upper caudal lobe were found in *Sacura, Priacanthus, Rhyncopelates, Oplegnathus* and *Goniistius*, and six branched rays in the lower caudal lobe were found in *Sacura, Hapalogenys, Parapristipoma* and *Plectorhinchus*. Among these genera, the same number of branched caudal rays in both lobes as mullids is observed only in *Sacura*.

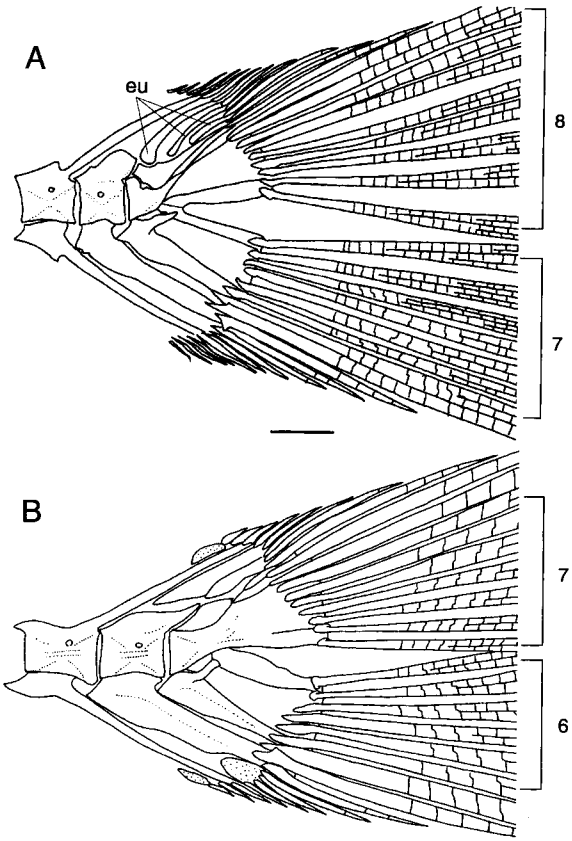

Fig. 92. Lateral view of caudal skeleton. A, *Kuhlia taeniura*, HUMZ 48520; B, *Parupeneus forsskali*, HUJ 9977. Numbers refer to branched rays. Scales indicate 2 mm.

Character 17. Diminishment of epural bone (Fig. 92)

The number of epural bones in the mullids is two, and their shape is relatively expanded and plate-like and attached to each other. Generally the epural bone of the caudal skeleton is three in many percoids, while it is two in the mullids (Fujita, 1990). Among the percoids observed in the present study, only *Lates* and *Trachurus* have two epurals; the rest have three. During osteological development in *Upeneus japonicus*, the epurals are three in the early developmental stage, but later the two lower epurals fuse with each other to form one (pers. obs.).

Character 18. Diminishment of anal spine (Fig. 93)

Character 18-1. Segment of second fin ray on anteriormost anal pterygiophore

Character 18-2. Branch of fin ray on second anal pterygiophore

Mullids have one anal spine, and it is too small to be observed by the naked eye. Johnson (1984) tabulated the number of supernumerary spines or soft rays in the anal fin of 91 groups of percoids, and suggested that the primitive percoid condition is to have two supernumerary spines on the first pterygiophores in the anal fin; this suggestion is also supported by Patterson (1992). The first two anal spines are supported by the first anal pterygiophore in supernumerary association, and the third one is supported by the second anal pterygiophore in serial association.

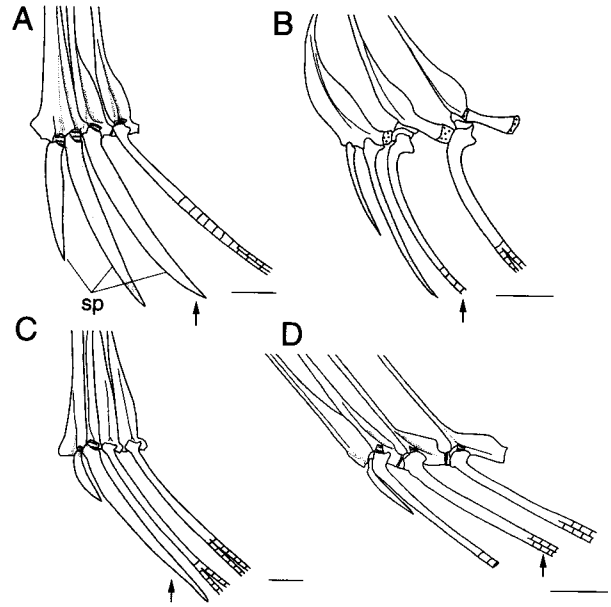

Fig. 93. Anterior three or four pterygiophores of anal fin and their related fin rays. A, *Kuhlia taeniura*, HUMZ 48520; B, *Branchiostegus japonicus*, HUMZ 65566; C, *Apogon semilineatus*, HUMZ 107056; D, *Parupeneus multifasciatus*, HUMZ 62786. Arrows show the third anal fin ray. Scales indicate 2 mm.

In the present study all percoids examined, except *Apogon* and all genera of mullids, have three spines in the anal fin in the above-mentioned arrangement of spines. As suggested by Fraser (1972) and Johnson (1984), *Apogon* has two spines, but only the first spine is serially associated with the first anal pterygiophore, suggesting that one spine was lost, and the second one is associated with the second pterygiophore. In mullids there is only one spine and one segmented unbranched ray, both supernumerarily associated with the first anal pterygiophore, suggesting that the second ray was not modified into a spine. In bathyclupeids, Johnson (1984) reported only one spine in the anal fin and it was serially associated with the first anal pterygiophore, suggesting that two anal spines were lost. Hence, the anal spine of mullids and bathyclupeids are not homologous. In addition, the third anal fin ray is usually a spine or segmented unbranched ray, for example, in *Branchiostegus* and *Larimichthys* in the percoids examined, while that of mullids is segmented and branched. This means that the third anal fin ray is not modified into a spine of a segmented ray in the mullids.

Character 19. Fusion of urostyle and fused third and fourth hypurals (Figs. 47-48)

In the mullids, the urostyle is fused with the third and fourth hypural bones to form a urostyle-hypural complex. But fusion of these caudal elements in most percoid fishes was not found (Fujita, 1990; Gosline, 1961; Johnson, 1984)

Character 20. Origin of dilatator operculi from frontal (Fig. 61)

The dilatator operculi, situated between the skull and the opercle, usually originates from the frontal, sphenotic, pterotic, and hyomandibula, and is inserted onto the antero-dorsal surface of the opercle (Winterbottom, 1974). The muscle in mullids is extended anteriorly over the postero-dorsal roof of the orbit via the gap between the postero-lateral region of the frontal and the dorsal portion of the sphenotic; it is inserted onto both the antero-dorsal surface and the dorso-lateral surface of the opercle. A similar expansion on the opercle of the dilatator operculi is found in *Branchiostegus* and *Lethrinus*. In the former, the dilatator operculi, comprising two components and one part, is connected between the pterotic and the dorso-lateral surface of the opercle, and the other part is connected between the pterotic and the dorso-medial surface of the opercle. The expanded muscle on the opercle seems to be a part of the levator operculi. However, in the latter case the dilatator operculi originates from the pterotic and is inserted onto the dorso-lateral surface of the opercle. Because two parts of this dilatator were able to divide into two distinct sections, it seems to be an expansion of the dilatator operculi, as in mullids.

Character 21. Absence of crescent expansion on endopterygoid

For detailed explanation see Chapter VIII.

Character 22. Anterior expansion of adductor arcus palatini

For detailed explanation see Chapter VIII.

Character 23. Fan-like expansion of supramaxilla (Fig. 20)

The supramaxilla of the mullids is a leaf-like bone located on the postero-dorsal portion of the maxilla. The supramaxilla is expanded posteriorly like a fan in all genera of mullids except *Upeneichthys* (see TS 13). Although the supramaxilla is also found in lower percoids, the posterior portion of the bone is not expanded like a fan.

Character 24. Presence of weak opercular medial strut (Fig. 32)

The opercular medial strut is a shelf-like structure located on the dorso-medial surface of the opercle. This strut is extended backwards to the posterior edge of the opercle, resulting in a reinforcement of the opercular spine in some species of *Upeneus, Mulloidichthys, Parupeneus* and *Pseudupeneus*. It is weak and reduced in *Mullus* and *Upeneichthys* (see TS 25).

Character 25. Fusion of third and fourth hypurals (Figs. 47-48)

The third and fourth hypural bones of the mullids are fused completely in *Upeneus, Mulloidichthys* and most of species of *Upeneichthys*, while they are fused incompletely in *Mullus, Pseudupeneus* and most of species of *Parupeneus* (see TS 30). In most percoid fishes, these caudal elements are not fused but separated from each other (Fujita, 1990).

Character 26. Anterior expansion of epaxialis on frontal (Fig. 77)

The epaxial muscles in the mullids are of two types depending on their anterior limits. First, the anterior limit of the muscle is to the mid-portion of the frontal near the opening of the epiphyseal branch of supraorbital sensory canal system, as observed in *Mullus* and several species of *Upeneus*. Second, the anterior limit of the muscle is to anterior portion of the frontal near the nasal and mesethmoid, and this condition is found in most of mullid genera except the several species above mentioned (see TS 40). Although the anterior limit of the epaxialis in the percoids varies, the muscle does not reach the mid-portion of the frontal in most of the percoid genera examined, for example, *Chelidoperca, Lepomis, Lutjanus, Pristipomoides, Hapalogenys, Acanthopagrus*, and *Larimichthys*. However, in several percoid genera, for example, *Priacanthus, Trachurus, Leiognathus, Pterocaesio, Girella* and *Parapristipoma*, the muscle is expanded to the anterior portion of the frontal or near the nasal.

As mentioned above, the family Mullidae is a monophyletic fish group supported by the above 26 synapomorphies, and the osteological and myological differentiations occurring in the hyoid arches are unique to the family Mullidae among perciform fishes. These autapomorphies strongly support the monophyly of the family Mullidae.

2. Phylogenetic relationships within the family Mullidae

2-1. Cladistic analysis

The cladistic analysis using the data matrix shown in Table 2 produced seven equally most parsimonious trees with a length of 72 steps and a consistency index of 0.74 (Figs. 94-95).

Among these seven trees, the cladistic relationships of five genera (except *Upeneus*) at the genus level is consis-

Table 2. Matrix of characters in 41 transformation series for examination of the interrelationships of mullid genera

Taxon	Transformation Series								
	1-5	6-10	11-15	16-20	21-25	26-30	31-35	36-40	41
OUTGROUP	00000	00000	00000	00000	00000	00000	00000	00000	0
U. taeniopterus	00000	11000	00100	00001	10000	10012	00000	11212	1
U. asymmetricus	00000	11000	00100	00001	10000	10112	10000	11212	1
U. crosnieri	00000	11000	00100	00001	10000	10112	10000	11212	1
U. japonicus	00000	11000	00100	00001	10000	10112	10000	11112	1
U. luzonius	00000	11000	00100	00001	10000	10112	00000	11212	1
U. moluccensis	00000	01000	00100	00001	10001	00102	00000	21211	1
U. parvus	00000	11000	00100	00001	10001	00002	00000	11211	1
U. pori	00000	11000	00100	00001	10000	10112	10000	11212	1
U. quadrilineatus	00000	01000	00100	00001	10001	00102	00000	21211	1
U. sulphureus	00000	01000	00100	00001	10001	00102	00000	21211	1
U. tragula	00000	11000	00100	00001	10000	10112	00000	11212	1
U. vittatus	00000	01000	00100	00001	10101	00102	00000	21211	1
M. argentinae	00001	00000	00101	10012	10001	11111	00000	12111	0
M. barbatus	00002	00000	00101	10012	10001	11111	00000	12111	0
M. surmuletus	00001	00000	00101	10012	10001	11111	00000	12111	0
Up. lineatus	00020	01000	00001	00012	10001	10021	00010	11102	0
Up. porosus	00020	01000	00001	00012	10001	10022	00010	11102	0
Up. stotti	00020	01000	00001	00012	10001	10022	00010	11102	0
Up. vlamingii	00020	01000	00001	00012	10001	10022	00010	11102	0
Mu. flavolineatus	10100	01100	10111	00012	10110	10112	00011	11102	0
Mu. martinicus	10100	01100	10111	00012	10110	10112	00011	11102	0
Mu. vanicolensis	10100	01100	10111	00012	10110	10112	00011	11102	0
Ps. grandisquamis	01100	01101	11202	01112	20010	10111	01110	11102	0
Ps. prayensis	01100	01101	11202	01112	20010	10111	01110	11102	0
P. barberinoides	01110	01111	11202	00112	21010	10111	01110	11102	0
P. barberinus	01110	01111	11202	00112	21010	10111	01110	11102	0
P. chrysonemus	01110	01101	11202	00112	21010	10111	01110	11102	0
P. chrysopleuron	01110	01101	11202	00112	21010	10111	01110	11102	0
P. ciliatus	01110	01101	11202	00112	21010	10112	01110	11102	0
P. cyclostomus	01110	01101	11202	00112	21010	10111	01110	11102	0
P. forsskali	01110	01111	11202	00112	21010	10111	01110	11102	0
P. heptacanthus	01110	01101	11202	00112	21010	10112	01110	11102	0
P. indicus	01110	01111	11202	00112	21010	10111	01110	11102	0
P. macronemus	01110	01101	11202	00112	21010	10111	01110	11102	0
P. margaritatus	01110	01111	11202	00112	21010	10111	01110	11102	0
P. multifasciatus	01110	01101	11202	00112	21010	10111	01110	11102	0
P. pleurostigma	01110	01101	11202	00112	21010	10111	01110	11102	0
P. prophyreus	01110	01101	11202	00112	21010	10111	01110	11102	0
P. procerigena	01120	01001	11202	00112	21010	10112	01110	11102	0
P. signatus	01110	01101	11202	00112	21010	10111	01110	11102	0
P. spilurus	01110	01101	11202	00112	21010	10111	01110	11102	0

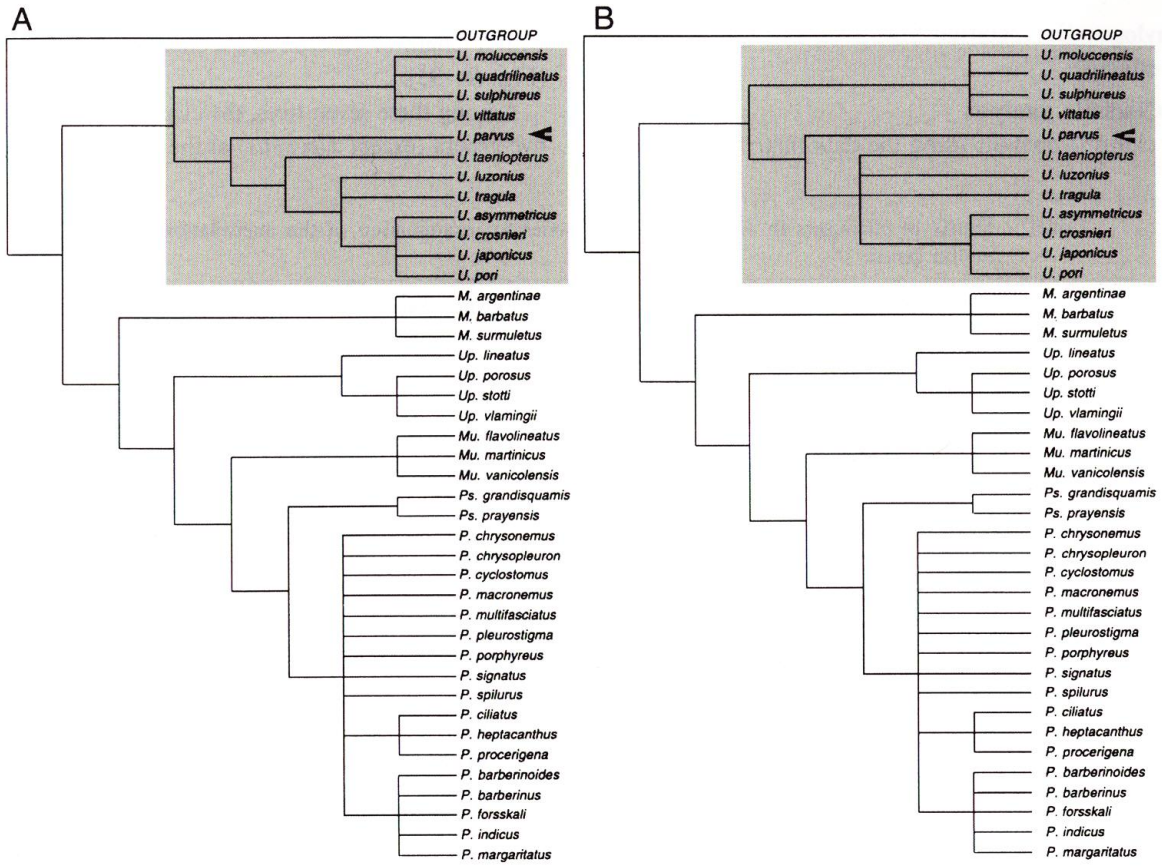

Fig. 94. First two cladograms among seven equally most parsimonious tree showing the phylogenetic relationships within the family Mullidae. Dotted areas mean the genus *Upeneus* forming a clade, and arrows indicate the position of *U. parvus* as a member of the clade.

tent with one another, except that there are different interspecific relationships within a genus, as in *Upeneichthys* and *Parupeneus* (Figs. 94–95). The major difference among them is the position of *Upeneus parvus* in each cladogram. In the first two cladograms (Fig. 94) the species is included within the monophyletic genus *Upeneus*, and in the another five cladograms (Fig. 95) it is first divided from the root as a sister group for the remaining clades.

To determine the phylogenetic relationships within the family Mullidae among seven equally most parsimonious trees, I employed the character evolution of preorbital scales as a criterion of selection. Preorbital scales are those covering the lacrimal region of the head (Fig. 96B), and they are found in six species of the genus *Upeneus*, comprising *U. asymmetricus, U. crosnieri, U. japonicus, U. luzonius* and *U. tragula*, while in the rest of the species of *Upeneus* they are lacking (Fig. 96A). This character was not used in the present analysis owing to the difficulty of deciding whether it is plesiomorphic or apomorphic in the genera of *Parupeneus* and *Pseudupeneus*.

The reconstruction of the character evolution of preorbital scales was traced onto the two selected trees inferring states of ancestors (Fig. 97). The assumption that preorbital scales are gained once by a common ancestor of *Upeneus asymmetricus, U. crosnieri, U. japonicus, U. pori, U. luzonius* and *U. tragula* (Fig. 97A) is more explicable than to gain parallelly the character in a common ancestor of *U. luzonius*, of *U. tragula*, and of the rest four species (Fig. 97B). Accordingly, I took the cladogram depicted in Figure 94A as representing the phylogenetic relationships within the family Mullidae.

There is a difference of character optimization in TS 7, 28, 38, and 39 between ACCTRAN and DELTRAN. According to DELTRAN, character 7–1 is obtained independently in clades A1 and B2, character 28–1 is obtained independently in B1, C2, F1 and H2, character 38–1 is obtained independently in A2 and *U. japonicus*, and character 39 is gained independently in both A1 and B1 (Fig. 98). According to ACCTRAN, characters 7–1, 28–1, 38–1 and 39–1 were obtained as synapomorphies of clade A and reversed in clades B1, F2, C1 and B2, respectively (Fig. 99). The DELTRAN optimization of characters is employed in the present study

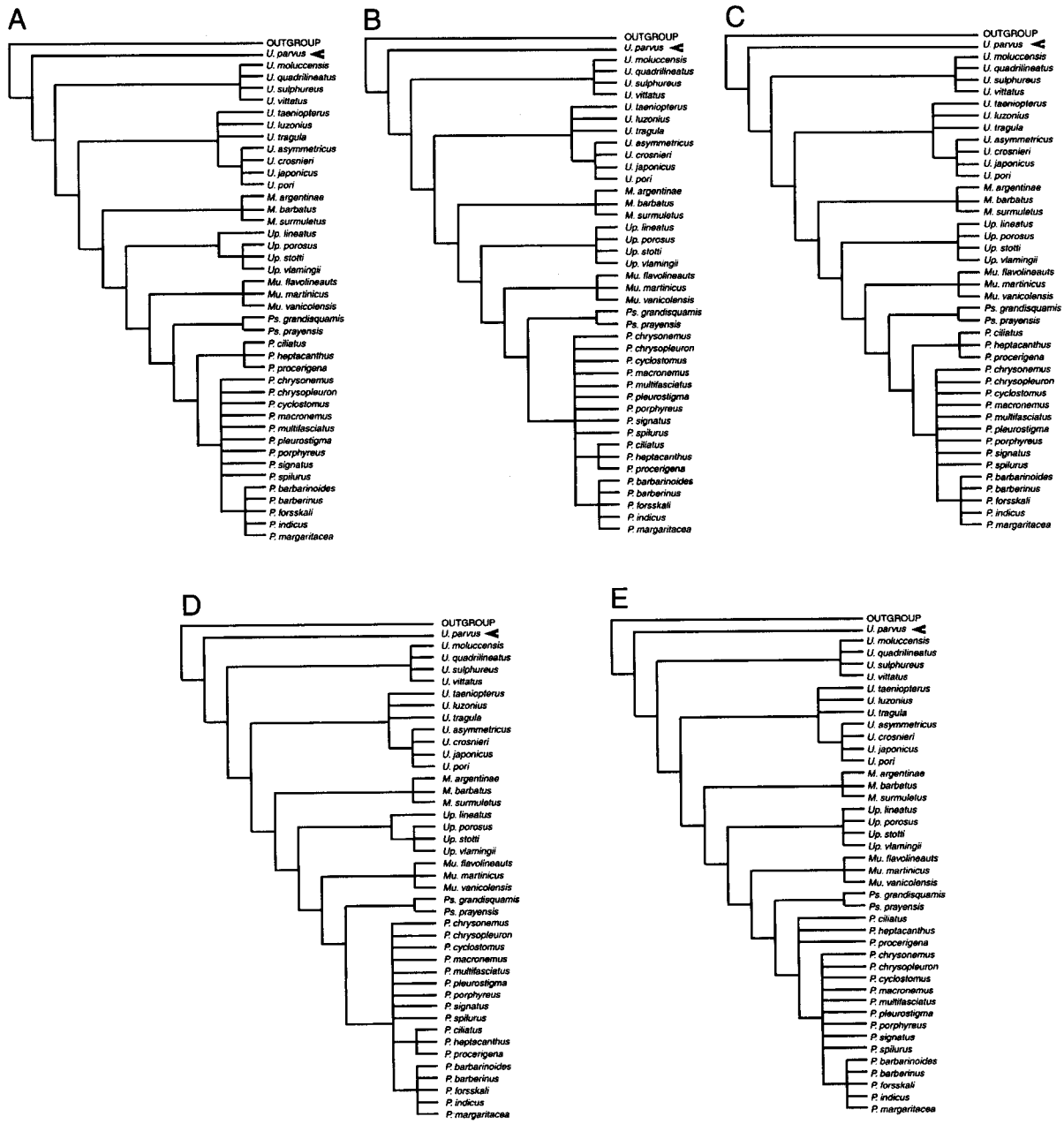

Fig. 95. Remaining five cladograms among seven equally most parsimonious trees. Arrows show the position of *Upeneus parvus* as a sister group for the other clades.

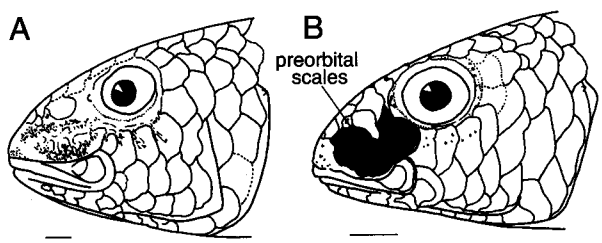

Fig. 96. Lateral view of head region of two species of *Upeneus* showing preorbital scales (dotted area in B). A, *U. taeniopterus*, BPBM 5590; B, *U. pori*, HUJ 135172. Scales indicate 5 mm.

2-2. Interrelationships of mullid genera

The interrelationships of 41 mullid species were reconstructed based on the most parsimonious tree (Fig. 94A). All included genera were recognized as monophyletic groups. After analysis, four characters (13-1, 25-1, 30-1 and 40-1) were recognized as synapomorphies for the family. The monophyly of the family Mullidae is supported by 26 apomorphies (see section 1 of Chapter VI). Clade A is divided into clades A1 and A2.

Clade A1 includes the species of *Upeneus*, and is supported by five apomorphies: each epiphyseal branch of supraorbital sensory canal on frontal is connected (7-

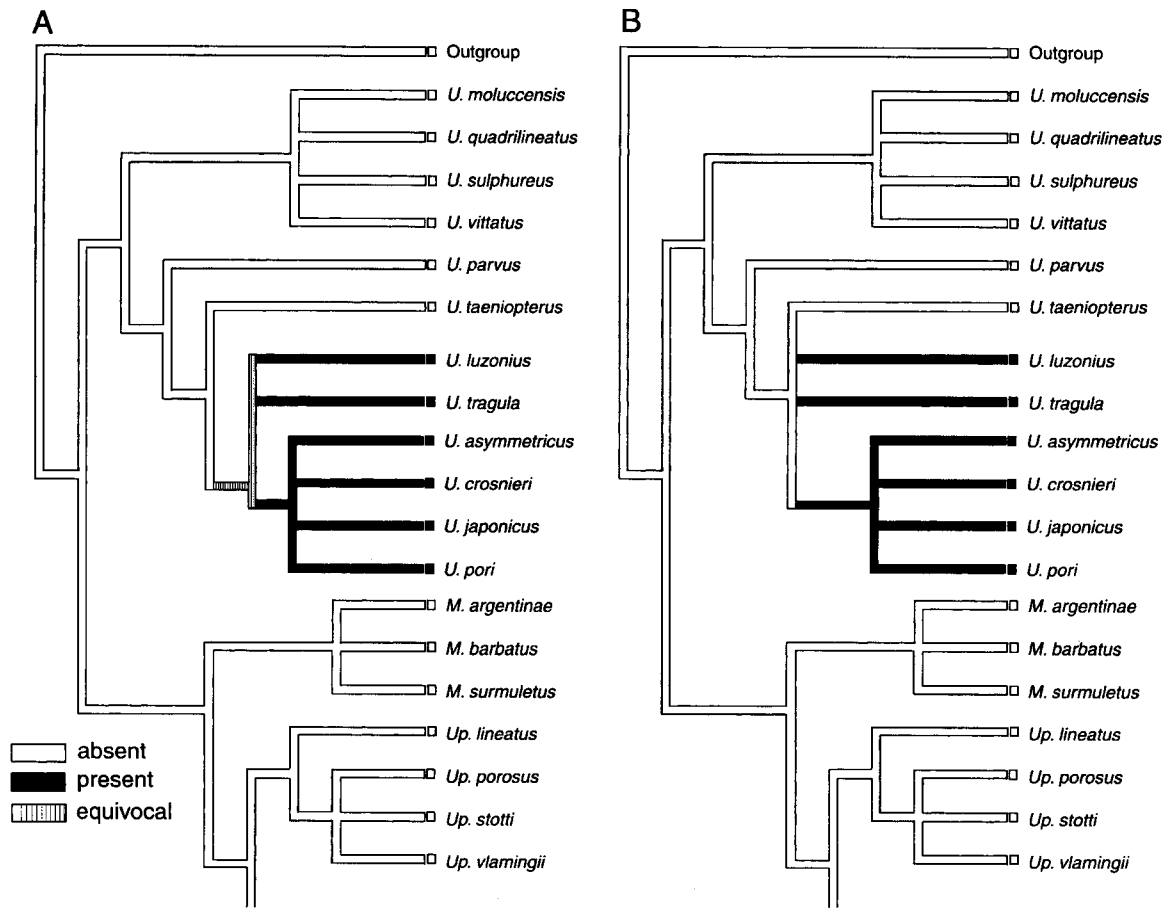

Fig. 97. Reconstruction of the character evolution of preorbital scales on some clades. Lower portion of cladogram is omitted.

1), third and fourth hypurals fused completely (30-2), rotator tentaculi subsection 2a not originating from anterior ceratohyal (38-2), adductor radialis originating from scapula, coracoid and pectoral fin radialis (39-1) and scales on second dorsal and anal fins present (41-1). The clade is divided into clades F1 and F2. Clade F1, including *U. moluccensis, U. quadrilineatus, U. sulphureus* and *U. vittatus*, is supported by two apomorphies of unossified first pharyngobranchial (28-1) and rotator tentaculi section 1 branched (36-2). Clade F2, including the remaining species of *Upeneus* except the above four species, is supported by one apomorphy of a prominent ventral crest on the vomer (6-1). The clade is divided into clades G1 and G2. The clade G1 includes *U. parvus* without apomorphy. The clade G2 includes four synapomorphies of a well-developed opercular medial strut (25-0r), a partly ossified barbel (26-1), a pointed postpelvic process (29-1) and an anterior expansion of epaxialis to anterior portion of frontal (40-2). The clade G2 is divided into clades H1, which includes *U. taeniopterus*, and H2, which includes three clades I1 to I3. Clade H2 is supported by a synapomorphy of an unossified first pharyngobranchial (28-1). Clades I1 and I2 include *U. luzonius* and *U. tragula*, respectively. Clade I3, supported by an absence of the first minute dorsal spine on the first dorsal pterygiophore (31-1), includes *U. asymmetricus, U. crosnieri, U. japonicus* and *U. pori*.

Clade A2 includes all the mullids (except *Upeneus*) having conical teeth on both jaws (15-1), no teeth on the palatine (19-1), a complete articulation between the palatine and endopterygoid (20-2), a partial ossification of the first branchiostegal ray (26-1), a pointed postpelvic process (29-1), and an origin of the adductor radialis from the pectoral fin radials, scapula and coracoid (38-1). The clade is divided into clades B1 and B2.

Clade B1 includes the species of *Mullus* and is supported by the following six apomorphies: an expansion of tooth plate on vomer (5-1), absence of teeth on upper jaw in adults (16-1), expansion of dorsal hypohyal (27-1), no ossification of first pharyngobranchial (28-1), rotator tentaculi section 2 not originating from dorsal hypohyal (37-2), and origin of adductor radialis involv-

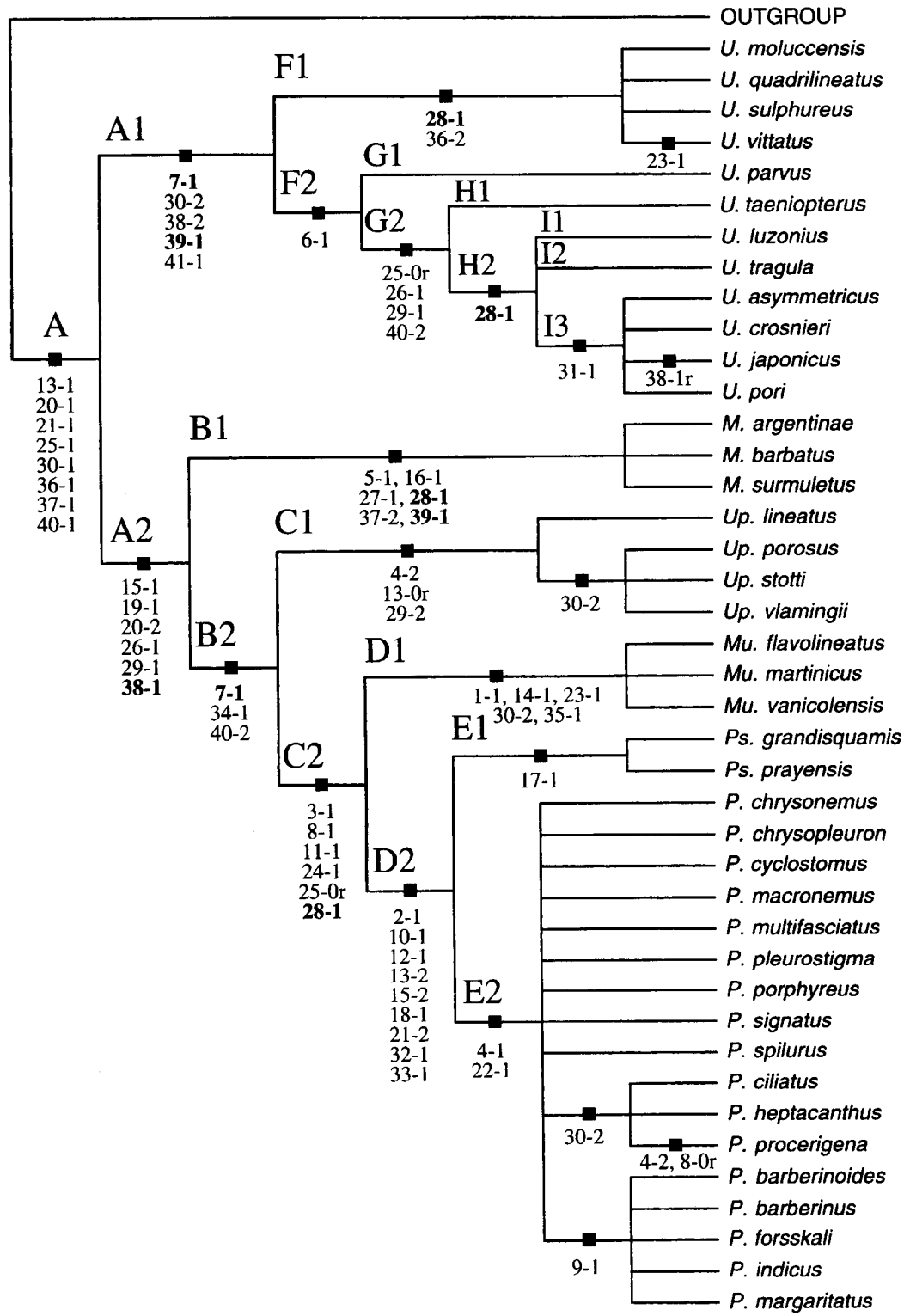

Fig. 98. Character optimization employing DELTRAN. Numbers correspond to those in the text and Table 2. Bold character numbers indicate parallelisms.

ing pectoral fin radials, scapula and coracoid (39-1).

Members of clade B2, including *Upeneichthys, Mulloidichthys, Pseudupeneus* and *Parupeneus*, share the following three synapomorphies: each epiphyseal branch of supraorbital sensory canal on frontal connected (7-1), levator arcus palatini extends ventrally onto preopercle (34-1), and epaxialis on dorsal region of skull extends to anterior region of frontal (40-2). The clade is divided into clades C1 and C2.

Clade C1 includes four species of *Upeneichthys* and is

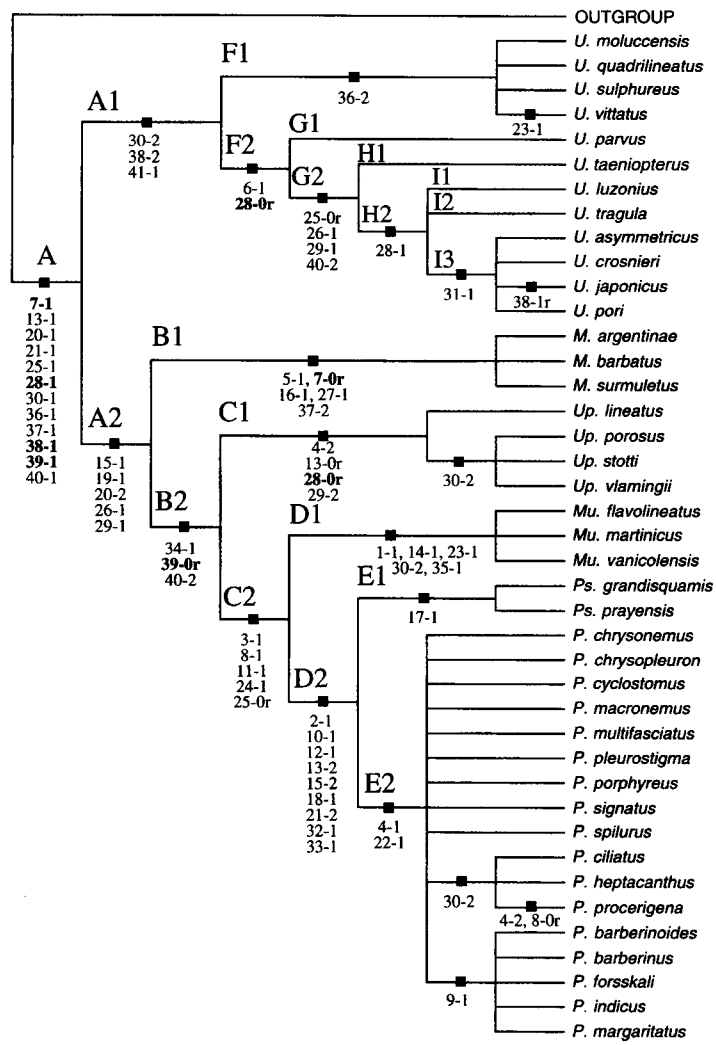

Fig. 99. Character optimization employing ACCTRAN. Numbers correspond to those in the text and Table 2. Bold character numbers indicate reversals.

supported by the following two apomorphies: connection of frontal crest with supraoccipital crest (4–2) and presence of an elongated postpelvic process (29–2).

Clade C2, including *Mulloidichthys, Pseudupeneus* and *Parupeneus*, shares the following five synapomorphies: nasal canal branched (3–1), supraorbital sensory canal on postero-lateral region of frontal branched (8–1), infraorbital sensory canal on lacrimal branched (11–1), preopercular sensory canal branched (24–1), and first pharyngobranchial not ossified (28–1). The clade C2 is divided into clades D1 and D2.

Clade D1 includes three species of *Mulloidichthys* and is supported by the following five synapomorphies: palatine articulated with lateral ethmoid (1–1), alveolar process of premaxilla shortened (14–1), metapterygoid lamina absent (23–1), third and fourth hypural bones fused completely (30–2), and levator operculi inserted onto dorso-medial and dorso-lateral surfaces of opercle (35–1).

Clade D2, including *Pseudupeneus* and *Parupeneus*, is supported by following nine synapomorphies: articular head to receive palatine of lateral ethmoid fused to its body (2–1), lacrimal elongated and elliptical (10–1), first infraorbital expanded (12–1), supramaxilla expanded posteriorly and as large as half size of maxilla (13–2), teeth on both jaws large, conical (15–2), maxillo-supramaxillary ligament present (18–1), endopterygoid strongly attached to lateral ethmoid (21–2), adductor mandibulae section 1 (A1) originates from infraorbitals (32–1), and additional small muscle mass of A1 present (33–1). The clade is divided into clades E1 and E2.

Clade E1 includes the species of *Pseudupeneus* and is supported by only one autapomorphic character, presence of enlarged conical teeth on upper jaw (17–1).

Clade E2 includes the species of *Parupeneus* and is supported by two synapomorphies, presence of frontal crest (4–1) and presence of ectopterygoid projection (22–1).

VI. Classification

The classification should be minimally redundant, minimally novel, and maximally informative (Wiley, 1981). In the present study, the phyletic sequencing convention (Nelson, 1972) was used to produce an exact reflection of the tree and to retain the traditional rank of each genus, that is, the genus level is assigned to each node of A1, B1, C1, D1, E1 and E2 (Fig. 100).

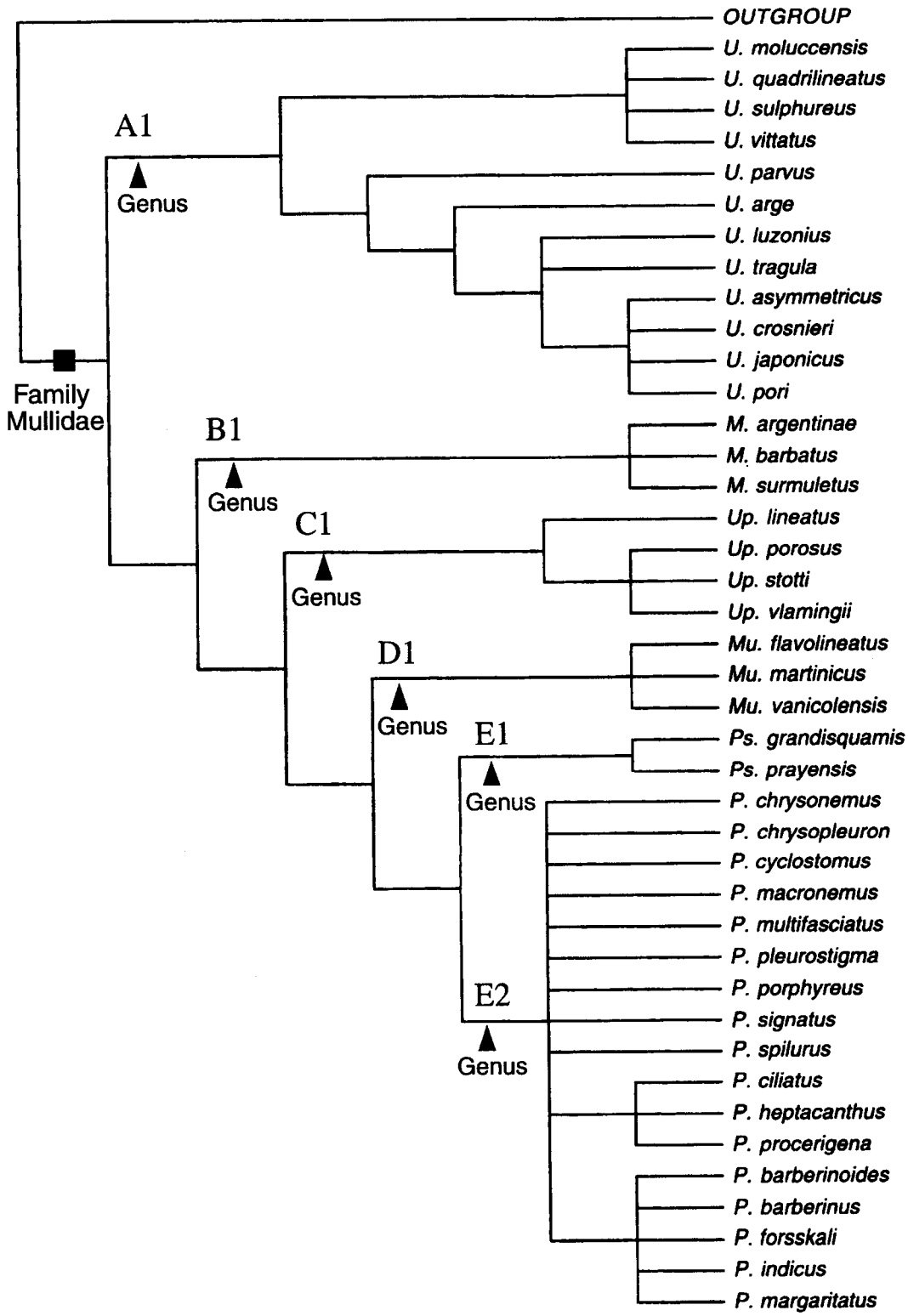

Fig. 100. Phylogenetic relationships within the Mullidae and ranking of genus level.

1. Family Mullidae

Diagnosis. First infraorbital articulated with lateral ethmoid; expanded subocular shelf on first infraorbital; endopterygoid articulated with lateral ethmoid; palatine with well-developed cartilaginous margin articulated with endopterygoid; symplectic interdigitated with metapterygoid on both sides; first branchiostegal ray modified into a barbel, five branchiostegal rays, anterior ceratohyal projected anteriorly, hypohyals arranged horizontally, hyoid foramen present, ceratohyals convex laterally, medial articular socket of interopercular present; accessory subpelvic keel expanded medially; nasal expanded posteriorly, firmly attached to skull; additional process present on basipterygium; four muscles related to barbel present; each protractor hyoidei separated; hyohyoidei abductores section 1 inserted onto third branchiostegal ray only, hyohyoidei abductores section inserted 2 onto the ventral surface of urohyal; transversus dorsalis anterior inserted onto interarcual cartilage; adductor profundus originating from dorsal surface of basipterygium; supracarinalis medius inserted onto second dorsal pterygiophore; additional scapular foramen present; seven and six branched rays in upper and lower caudal lobes, respectively; two epurals; second fin ray on first anal pterygiophore segmented, fin ray on second anal pterygiophore unbranched; crescent expansion on endopterygoid absent; adductor arcus palatini attached on medial surface of palatine and on ventral surface of vomer; dilatator operculi originating from the frontal; urostyle and hypurals 3-4 fused; supramaxilla expanded like a fan; a weak opercular medial strut present; third and fourth hypurals fused; epaxialis reaching frontal

2. Genera in the family Mullidae

In the present study, the six existing genera below listed are recognized as a natural group in the Mullidae.

Family Mullidae
- Genus *Mullus* Linnaeus, 1758
- Genus *Upeneus* Cuvier, 1829
- Genus *Mulloidichthys* Whitley, 1929
- Genus *Upeneichthys* Bleeker, 1855
- Genus *Pseudupeneus* Bleeker, 1862
- Genus *Parupeneus* Bleeker, 1863

3. Key to the genera of the family Mullidae

1a. Scales present on 2nd dorsal and anal fins, teeth on palatines present ..... *Upeneus*
1b. Scales absent from 2nd dorsal and anal fins, teeth on palatines absent 2
2a. Tooth plate of vomer expanded posteriorly ..... *Mullus*
2b. Tooth plate of vomer not expanded 3
3a. Teeth on vomer present ..... *Upeneichthys*
3b. Teeth on vomer absent 4
4a. Teeth on both jaws small, conical, arranged in more than two or more rows ..... *Mulloidichthys*
4b. Teeth on both jaws large conical arranged in one or two rows 5
5a. Two irregular rows of teeth on both jaws, with enlarged teeth on upper jaw ..... *Pseudupeneus*
5b. One row of teeth on both jaws, without enlarged teeth ..... *Parupeneus*

3-1. Genus *Upeneus* Cuvier, 1829

Upeneus Cuvier, 1829: 157 (type species: *Upeneus vittatus* Cuvier, designated by Bleeker, 1876: 333).
Hypeneus Agassiz, 1846: 190 (type species: *Mullus vittatus* Forsskål).
Upeneoides Bleeker, 1849: 62, 63 (type species: *Mullus vittatus* Forsskål, designated by Jordan, 1919: 240).
? *Megalepis* Bianconi, 1857: 270 (type species: *Megalepis alessandrini* Bianconi, 1857, monotypic).
Pennon Whitley, 1941: 32 (type species: *Upeneoides filifer* Ogilby, 1910, monotypic).

Diagnosis. Dentition complete, comprising small villiform teeth on both jaws, small conical or villiform teeth on vomer and palatines, sometimes vomerine teeth absent; scales present on second dorsal and anal fins.

Species. The genus *Upeneus* includes about 18 species: *U. vittatus* (Forsskål, 1775) (Fig. 101), *U. japonicus* (Houttuyn, 1782), *U. sulphureus* Cuvier, 1829, *U. taeniopterus* Cuvier, 1829, *U. subvittatus* Temminck & Schlegel, 1843, *U. tragula* Richardson, 1846, *U. parvus* Poey, 1852, *U. moluccensis* (Bleeker, 1855), *U. sundaicus* (Bleeker, 1855), *U. doriae* Günther, 1869, *U. luzonius* Jordan & Seale, 1907, *U. filifer* (Whitley, 1941), *U. asymmetricus* Lachner, 1954, *U. quadrilineatus* Cheng & Wang, 1963, *U. crosnieri* Fourmanoir & Guézé, 1967, *U. mascareinsis* Fourmanoir & Guézé, 1967, *U. pori* Ben-Tuvia & Golani, 1989 and *U. francisi* Randall & Guézé, 1992.

Distribution. Indo-Pacific Ocean, Mediterranean Sea (Ben-Tuvia and Kissil, 1988) and Western Atlantic Ocean (only *U. parvus*).

Remarks. The genus *Pennon* was established by Whitley (1941), and diagnosed as having a long dorsal spine and no teeth on the vomer and palatines. It was based on two of 12 specimens trawled from the Cape Gloucester, Queensland, Australia. Because intraspecific variation of vomerine teeth is found in some

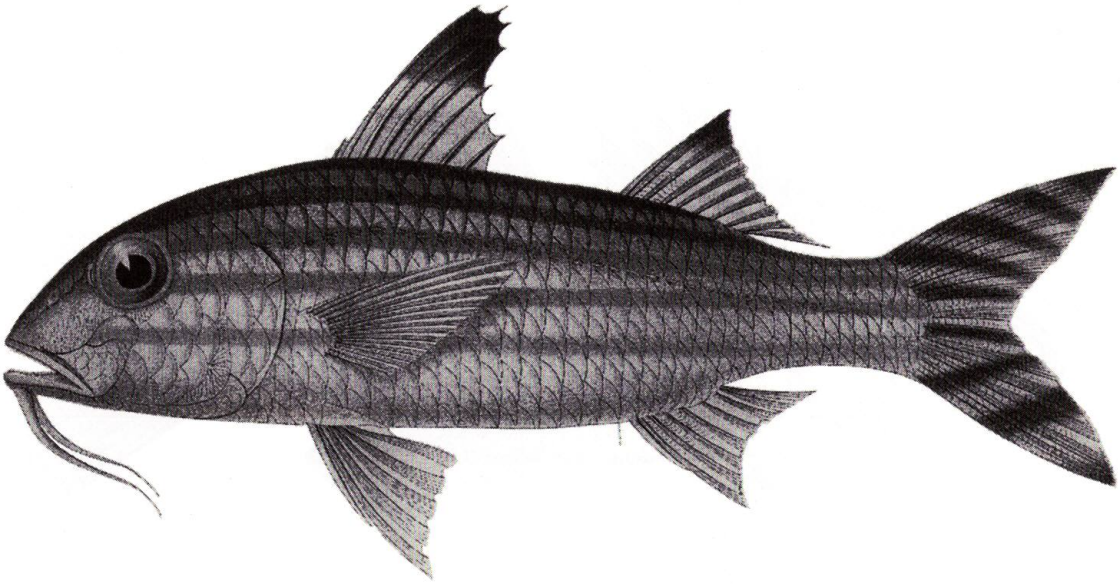

Fig. 101. Lateral view of *Upeneus vittatus*, type species of the genus (after Bleeker, 1877).

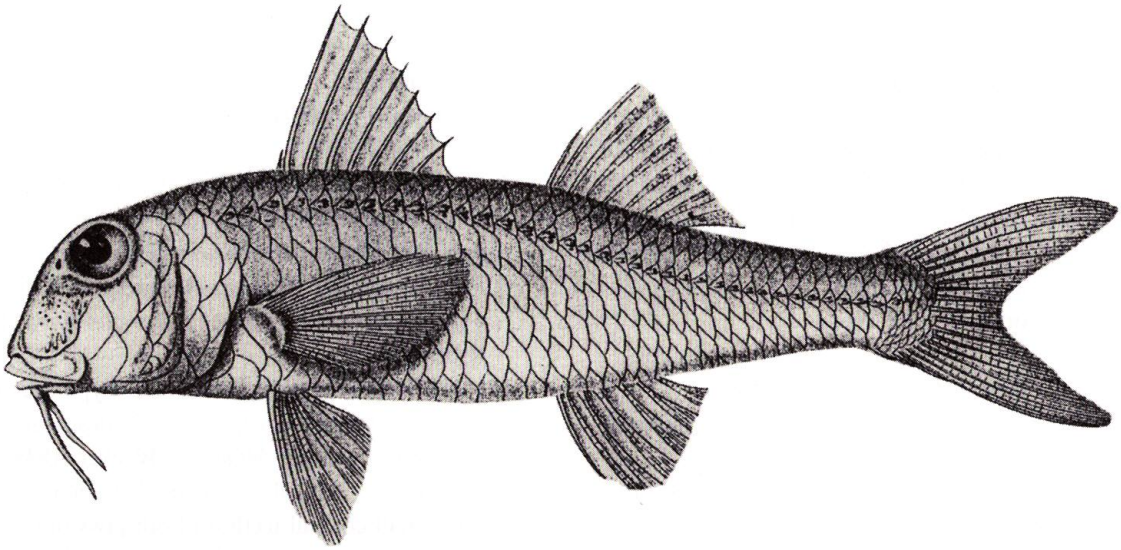

Fig. 102. Lateral view of *Mullus barbatus*, type species of the genus (after Cuvier and Valenciennes, 1829).

species of *Upeneus*, and because the presence of scales on the second dorsal and anal fins is also figured originally (Whitley, 1941 : 33, fig. 22), the diagnostic characters of *Pennon* are included in those of *Upeneus*. Accordingly, the genus *Pennon* is treated as a junior synonym of *Upeneus* in the present study.

Material examined. See Appendix 2.

3-2. Genus *Mullus* Linnaeus, 1758

Mullus Linnaeus, 1758 : 299 (type species : *Mullus barbatus* Linnaeus, 1758)

Diagnosis. No teeth on upper jaw in adults, lower jaw with moderate-sized conical teeth in one or two irregular rows ; tooth plate on vomer expanded posteriorly with pebble-like teeth ; opercular strut shortened with a flat weak projection ; numerous sensory pores on snout.

Species. The genus *Mullus* consists of six species : *M. barbatus* Linnaeus, 1758 (Fig. 102), *M. surmuletus* Linnaeus, 1758, *M. auratus* Jordan & Gilbert, 1882, *M. phillipsi* (Fowler, 1918), *M. barbatus ponticus* Essipov, 1927 and *M. argentinae* Hubbs & Marini, 1933.

Distribution. North-eastern Atlantic Ocean including the Mediterranean Sea and Black Sea (for *Mullus surmuletus, M. barbatus* and *M. barbatus ponticus* ; Ben-Tuvia, 1981 ; Fowler, 1936 ; Hureau, 1973, 1986 ; Wheeler, 1969), and western Atlantic Ocean (for *M. auratus, M. phillipsi* and *M. argentinae* ; Jordan and

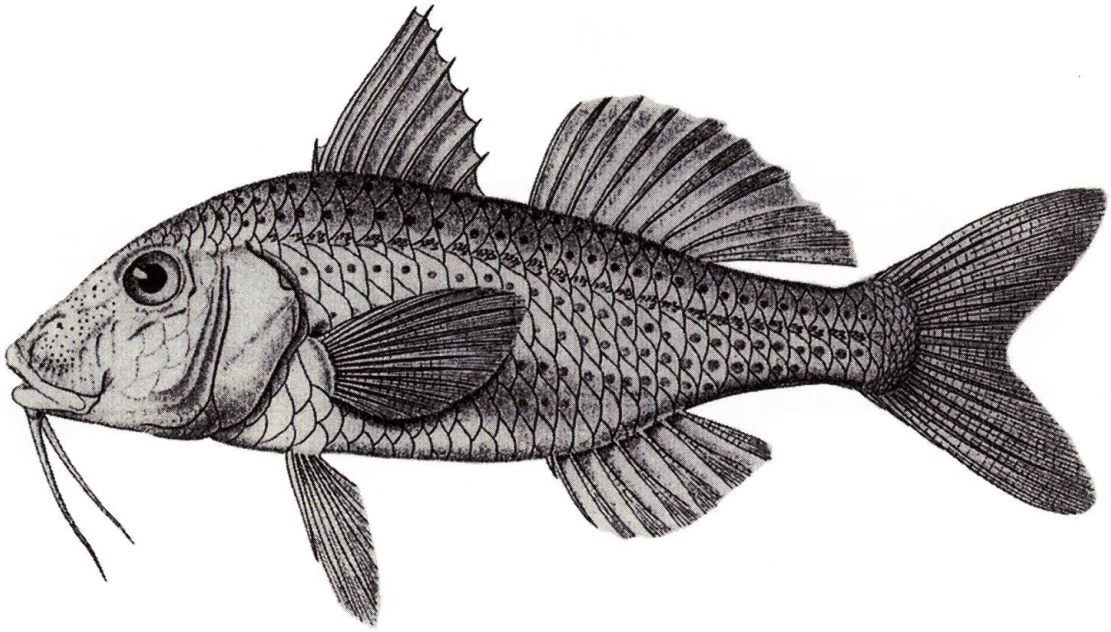

Fig. 103. Lateral view of *Upeneichthys porosus*, type species of the genus (after Cuvier and Valenciennes, 1829).

Evermann, 1896 ; Leim and Scott, 1966).

Remarks. Fowler (1936 : 871–872) and Hureau (1986 : 878–879) described *Mullus barbatus* and *M. surmuletus* as having teeth on both vomer and palatines, but members of the genus lack teeth on the palatines. It seems that they considered the expanded tooth plate of the vomer as that of the palatines.

Material examined. See Appendix 2.

3–3. Genus *Upeneichthys* Bleeker, 1855

Upeneichthys Bleeker, 1855 : 7 (type species : *Upeneus porosus* Cuvier, 1829).

? *Atahua* Phillipps, 1941 : 243 (type species : *A. clarki* Phillipps, 1941).

Diagnosis. Small conical teeth on both jaws in one or two irregular rows, and vomerine teeth present but palatines without teeth.

Species. The genus *Upeneichthys* comprises four species : *Up. lineatus* (Bloch & Schneider, 1801), *Up. porosus* (Cuvier, 1829), *Up. vlamingii* (Cuvier, 1829) (Fig. 103) and *Up. stotti* Hutchins, 1990.

Distribution. South and east Australia, and New Zealand (Ben-Tuvia, 1986 ; Hutchins, 1990).

Remarks. Ben-Tuvia (1986), who reviewed the genus *Upeneichthys*, recognized only one species, *Upeneichthys lineatus*. However, Hutchins and Swainston (1986) distinguished two species, *Up. lineatus* and *Up. vlamingii*. Later, Hutchins (1990) described *Up. stotti* from southwestern Australia and suggested that *Up. lineatus* is represented by three distinct subspecies, *Up. lineatus lineatus, Up. lineatus vlamingii* and *Up. lineatus porosus*.

Material examined. See Appendix 2.

3–4. Genus *Mulloidichthys* Whitley, 1929

Mulloides (not Richardson, 1843) Bleeker, 1849 : 6 (type species : *Mullus flavolineatus* Lacepède, 1802).

? *Pseudomulloides* Miranda-Ribeiro, 1915 : Mullidae p. 4 (type species : *Pseudomulloides carmineus* Miranda-Ribeiro, 1915).

Mulloidichthys Whitley, 1929 : 122 (type species : *Mullus flavolineatus* Lacepède 1802, designated by Jordan, 1919, through *Mulloides* Bleeker, 1849).

Diagnosis. Alveolar process of premaxilla shortened ; small conical teeth on both jaws in two or more irregular rows ; vomer and palatines without teeth.

Species. The genus *Mulloidichthys* includes at least six species : *Mu. flavolineatus* (Lacepède, 1801) (Fig. 104), *Mu. martinicus* (Cuvier, 1829), *Mu. vanicolensis* (Valenciennes, 1831), *Mu. dentatus* (Gill, 1862), *Mu. pfluegeri* (Steindachner, 1900) and *Mu. mimicus* Randall & Guézé, 1980.

Distribution. Mainly Indo-Pacific Ocean (Fowler, 1933), eastern Pacific Ocean (for *Mu. dentatus* ; Eschmeyer and Herald, 1983) and western Atlantic Ocean (for *Mu. martinicus* ; Böhlke and Chaplin, 1968 ; Briggs, 1958 ; Stepien et al. 1994).

Material examined. See Appendix 2.

3–5. Genus *Pseudupeneus* Bleeker, 1862

Pseudupeneus Bleeker, 1862 : 134 (type species : *Pseudupeneus prayensis* Cuvier, 1829).

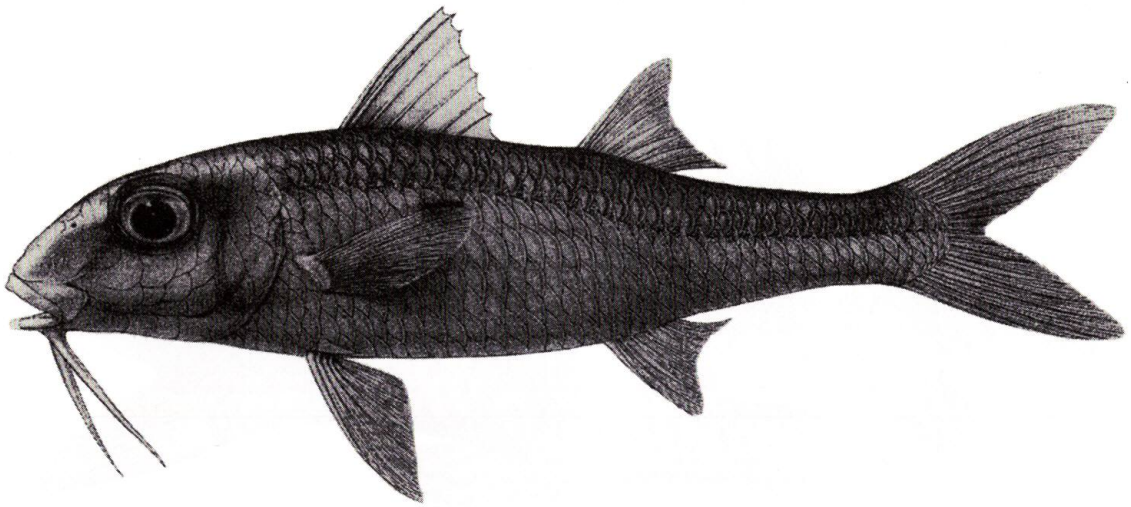

Fig. 104. Lateral view of *Mulloidichthys flavolineatus*, type species of the genus (from Günther, 1873-76).

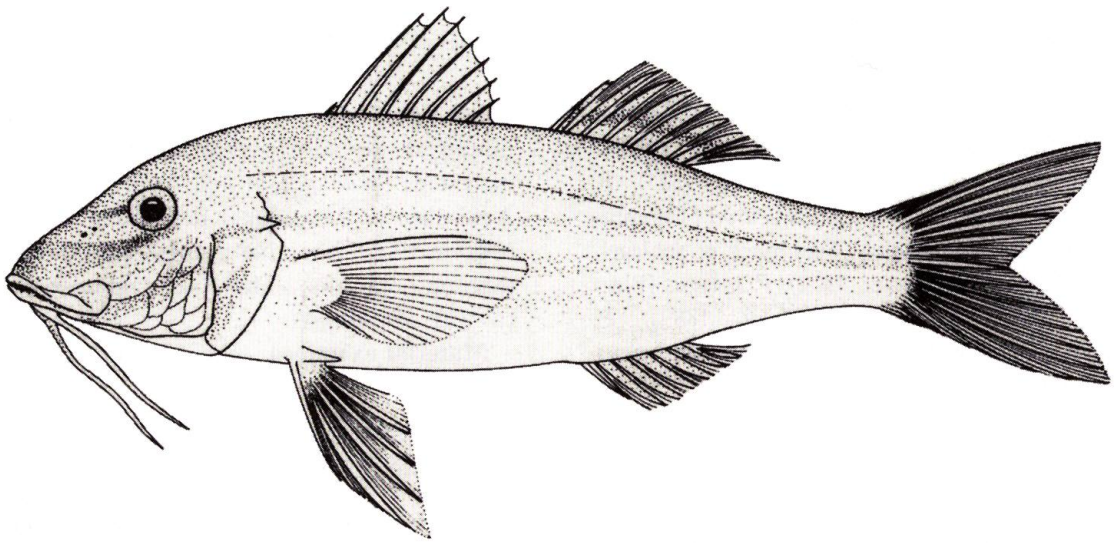

Fig. 105. Lateral view of *Pseudupeneus prayensis*, type species of the genus (after Ben-Tuvia, 1981).

Mullhypeneus Poey, 1868 : 307 (type species : *Mullus maculatus* Bloch, 1793).

Brachymullus Bleeker, 1876 : 333 (type species : *Upeneus tetraspilus* Günther, 1864 [junior synonym of *Pseudupeneus grandisquamis*]).

Diagnosis. Teeth on both jaws conical in irregular biserial rows ; an additional row of enlarged teeth present on upper jaw.

Species. The genus *Pseudupeneus* includes three species : *Ps. maculatus* (Bloch, 1793), *Ps. prayensis* (Cuvier, 1829) (Fig. 105) and *Ps. grandisquamis* (Gill, 1863).

Distribution. Eastern Pacific Ocean (for *Ps. grandisquamis*), western Atlantic Ocean (for *Ps. maculatus*) and eastern Atlantic Ocean (for *Ps. prayensis*).

Material examined. See Appendix 2.

3-6. Genus *Parupeneus* Bleeker, 1863

Parupeneus Bleeker, 1863 : 234 (type species : *Upeneus bifasciatus* Lacepède, 1802).

Hogbinia Whitley, 1929 : 92 (type species : *Upeneus filamentosus* Macleay, 1883).

Barbupeneus Whitley, 1931 : 317 (type species : *Upeneus signatus* Günther, 1867).

Caprupeneus Whitley, 1931 : 317 (type species : *Pseudupeneus jeffi* Ogilby, 1908).

Diagnosis. Teeth on both jaws large conical uniserial ; frontal crest present ; ectopterygoid projection present.

Species. The genus *Parupeneus* includes at least 22 species : *P. barberinus* (Lacepède, 1801), *P. bifasciatus* (Lacepède, 1801) (Fig. 106), *P. cyclostomus* (Lacepède, 1801), *P. heptacanthus* (Lacepède, 1802), *P. ma-*

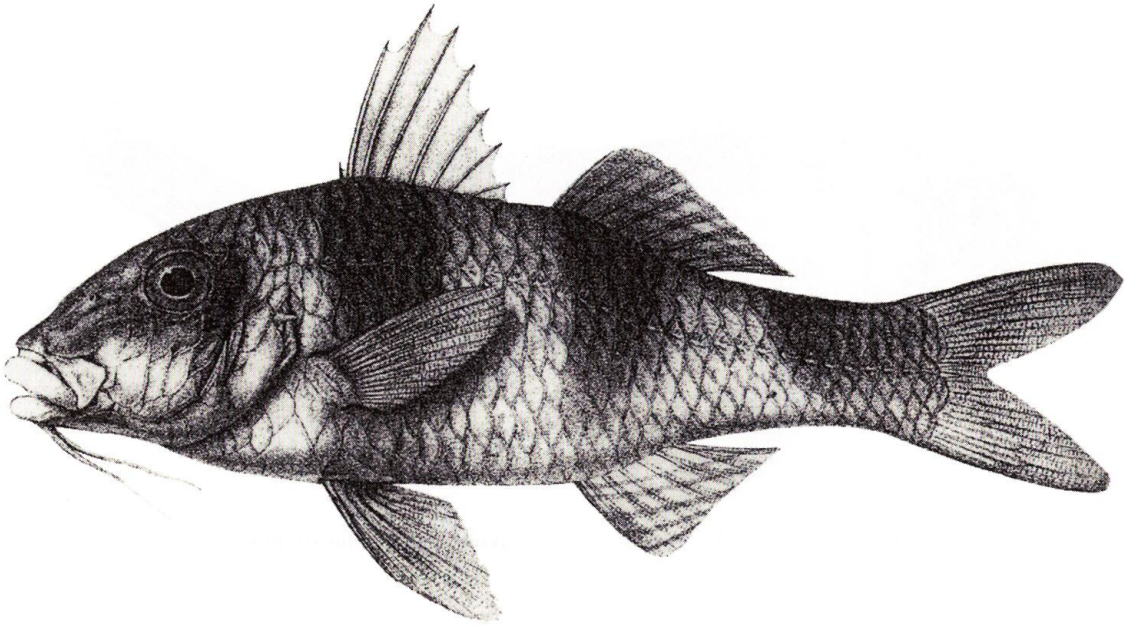

Fig. 106. Lateral view of *Parupeneus bifasciatus*, type species of the genus (from Günther, 1873–76).

cronemus (Lacepède, 1801), *P. rubescens* (Lacepède, 1801), *P. ciliatus* (Lacepède, 1802), *P. indicus* (Shaw, 1803), *P. multifasciatus* (Quoy & Gaimard, 1825), *P. pleurostigma* (Bennett, 1831), *P. chrysopleuron* (Temminck & Schlegel, 1943), *P. dubius* (Temminck & Schlegel, 1943), *P. barberinoides* (Bleeker, 1852), *P. spilurus* (Bleeker, 1854), *P. filamentosus* (Macleay, 1883), *P. chrysonemus* (Jordan & Evermann, 1903), *P. porphyreus* (Jenkins, 1903), *P. forsskali* (Foumanoir & Guézé, 1976), *P. posteli* (Foumanoir & Guézé, 1976), *P. margaritatus* Randall & Guézé, 1984, *P. moffitti* Randall & Myers, 1993 and *P. procerigena* Kim & Amaoka, 2001.

Distribution. Indian and Pacific Oceans (Weber and Beaufort, 1931 ; Lachner, 1960 ; Thomas, 1969).

Remarks. Whitley (1929) erected a new subgenus *Hogbinia* in the genus *Pseudupeneus*, designating *Upeneus filamentosus* Macleay as the type species and defining it as having a single row of spaced, stout teeth in each jaw, vomer and palatines without teeth, and third and fourth dorsal spines elongate. However, because the first three characters defined by him agree with those of the genus *Parupeneus*, and the length of the dorsal spines varies at the species level, *Hogbinia* is regarded as a junior synonym of *Parupeneus*. Whitley (1931) also established *Barbupeneus*, designating *Upeneus signatus* Günther as the type species, and distinguished it from *Hogbinia*, suggesting that *Barbupeneus* has a less elongated head and a shorter snout. The genus *Barbupeneus* is defined by its having a single row of teeth on the jaws and lacking teeth on the vomer and palatines. Because these characters are those of the genus *Parupeneus, Barbupeneus* is also regarded as a junior synonym of *Parupeneus*. The genus *Caprupeneus* was also erected by Whitley (1931), who designated *Pseudupeneus jeffi* Ogilby as the type species. According to the original description of that species (Ogilby, 1908 : 20), it has a single series of stout conical teeth on both jaws. Therefore, *Caprupeneus* is identical with *Parupeneus*.

Material examined. See Appendix 2.

VII. Inference of sister group for the family Mullidae

The suborder Percoidei, containing 71 families, 528 genera, and about the 2860 species, is the largest group among the perciforms (Nelson, 1994). It has been recognized as a non-monophyletic group by several workers (for example, Johnson, 1984 ; Johnson, 1993 ; Mooi, 1993 ; Nelson, 1994). Little attention has been given to the phylogenetic position of the Mullidae within the suborder Percoidei. There were only two suggestions concerning relationships of the Mullidae based on pre-cladistic methodology. Boulenger (1904) suggested a close relationships with the Sparidae, and Gosline (1984) a relationship with the Sparoidea (*sensu* Johnson, 1980). Boulenger (1904) considered the Mullidae closely related to the Sparidae because the two groups agree in the structure of the vertebral column and the presence of a subocular shelf. Gosline (1984) listed eight common characters possessed by mullids and sparoids : (1) a well developed scaly process in the axil of the pelvic fin, (2) 24 vertebrae, (3) two widely separated nostrils on each side of the head, (4) lacrimal bone

broadly overlapping the maxilla, (5) ethmoid-maxillary ligament functionally replaced by a ligament from the nasal bone to the maxilla, (6) maxillary blade of about equal width for most of its length and overlapped anteriorly by a palatine prong, (7) a gap between the sphenotic projection and the frontal border of the orbit, and (8) distally expanded symplectic. He did not, however, reach any firm conclusion to indicate their closer relationships, because of the absence of more reliable characters. He also considered that mullids and sparoid fishes are independently derived from two different bottom-feeding percoid groups.

An attempt was made to find a reliable indicator of sister-group relationships for the Mullidae using osteological and myological viewpoints in the present study. Among the synapomorphies of the mullid fishes, two morphological candidates that seem to be useful to infer sister groups of the Mullidae were selected and discussed below.

1. Absence of crescent medial expansion on endopterygoid (Fig. 107)

Generally the endopterygoid of most percoid fishes has a round crescent expansion which is projected medially and arranged nearly horizontally. Some percoids, including *Hapalogenys, Acanthopagrus, Dentex, Lethrinus, Scolopsis* and all genera of the mullids, do not have this crescent expansion. Furthermore, the endopterygoid of the mullids differs from those of the other percoid genera mentioned above in having an anterodorsal projection articulating with the lateral ethmoid and a strong strut supporting their articulation. It is reasonable to consider that such a unique structure of the endopterygoid in the mullids could have been derived from an initial condition found in the above percoids.

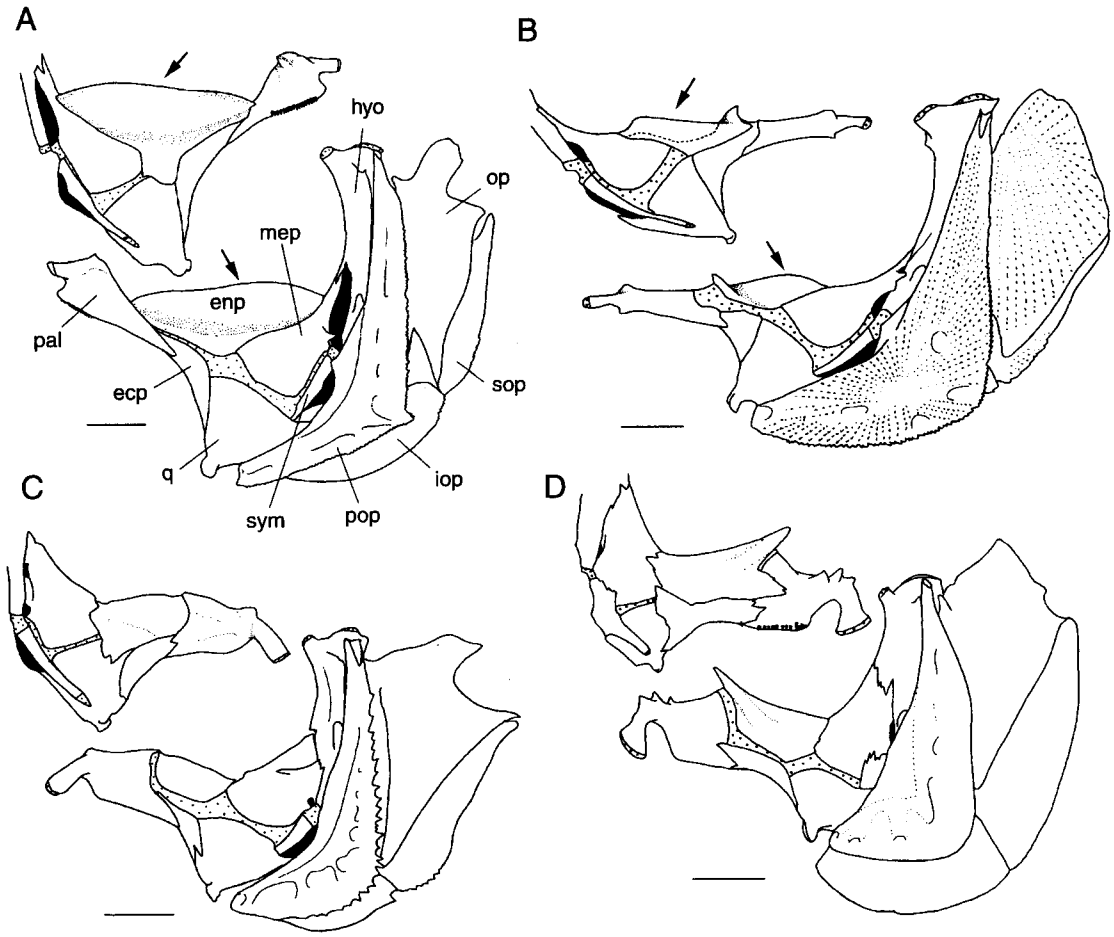

Fig. 107. Medial (above) and lateral (below) views of suspensorium. A, *Priacanthus macracanthus*, HUMZ 97044; B, *Pentaceros japonicus*, HUMZ 90278; C, *Hapalogenys mucronatus*, HUMZ 143107; D, *Upeneus vittatus*, HUMZ 46773. Arrows show crescent expansion of endopterygoid. Scales indicate 5 mm.

2. Anterior expansion of adductor arcus palatini (Figs. 108-109)

The adductor arcus palatini lies between the skull and the hyomandibula at the rear of the orbit in the primitive condition and expands anteriorly in the advanced form, forming the floor of the orbit between the skull and the palatal arch (Winterbottom, 1974). In the present study, it was found that the muscle in most percoids lies between the hyomandibula, metapterygoid, endopterygoid and palatine of the suspensorium, and the parasphenoid and vomer of the skull. In fishes having a crescent medial expansion on the endopterygoid (Figs. 108A-C) the muscle is attached to the lateral surface of the endopterygoid. In the mullids, as well as in *Hapalogenys, Acanthopagrus, Dentex, Lethrinus* and

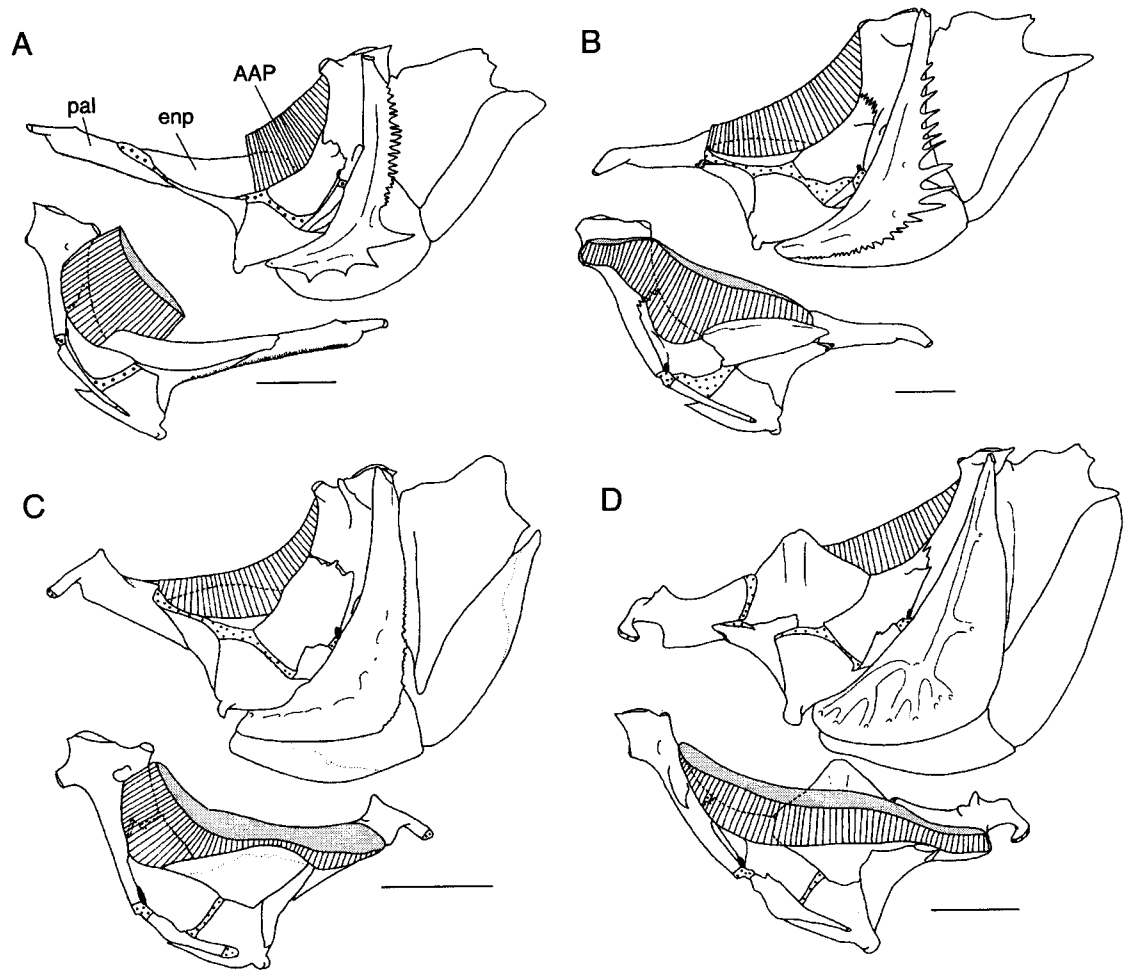

Fig. 108. Lateral (above) and medial (below) views of suspensorium and adductor arcus palatini. A, *Rhyncopelates oxyrhynchus*, HUMZ 39480; B, *Lates microlepis*, HUMZ 138066; C, *Nemipterus virgatus*, HUMZ 107573; D, *Parupeneus multifasciatus*, HUMZ 62786. Scales indicate 5 mm.

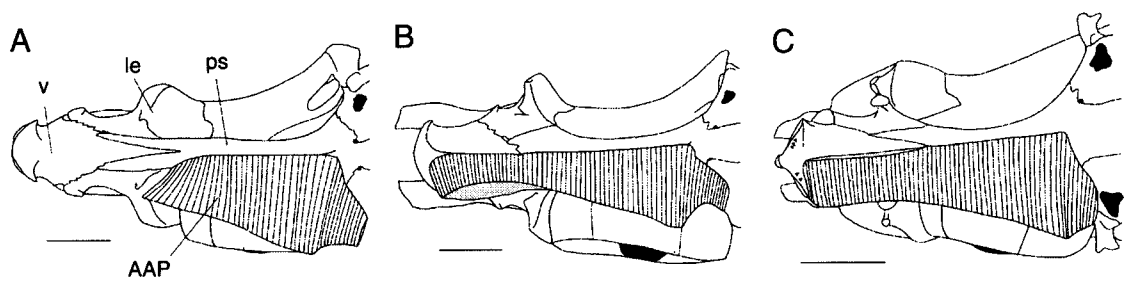

Fig. 109. Ventral view of neurocranium and adductor arcus palatini. A, *Rhyncopelates oxyrhynchus*, HUMZ 39480; B, *Lethrinus xanthochilus*, HUMZ 41408; C, *Upeneus vittatus*, HUMZ 46773. Right portion of the muscle removed. Scales indicate 5 mm.

Scolopsis, however, the muscle is attached to the medial surface of the endopterygoid (Fig. 108D). The endopterygoid of those fishes has no crescent medial expansion. In addition, the anterior expansion of the muscle to the palatine is found in only *Priacanthus, Hapalogenys, Lethrinus, Scolopsis, Nemipterus* and all mullid fishes among the percoids examined. Although the anterior limit of attachment of the adductor arcus palatini to the palatine is the same, the degree of expansion of the muscle on the palatine is various. The adductor arcus palatini of *Priacanthus* and *Hapalogenys* is attached to the postero-dorsal portion of the palatine, while it is expanded to the antero-ventral margin of the bone in medial aspect in *Lethrinus, Scolopsis, Nemipterus* (Fig. 108C) and all mullid fishes (Fig. 108D). Furthermore, the adductor arcus palatini does not reach to the ventral surface of the vomer in general percoids examined (Fig. 109A), whereas it is expanded anteriorly to cover almost the entire ventral surface of the vomer in *Lethrinus* (Fig. 109B), *Scolopsis* and *Nemipterus* and all mullid fishes (Fig. 109C). In *Priacanthus*, the vomer also serves as an attachment site for the adductor arcus palatini, but it is restricted to the posterior portion of the vomer. Therefore, the mullid fishes share a unique condition of the adductor arcus palatini, and its presumed ancestral condition is limited to only some percoids mentioned above.

Although it is impossible to specify the sister groups of the family Mullidae in the present study, two morphological characters were proposed as a valid relationship indicator to infer the sister groups for the family. According to the distribution of these characters among percoid fishes in the present study, haemuloid (*Hapalogenys*) and sparoid fishes (*Lethrinus, Scolopsis*, and *Nemipterus*) are suggested as sister groups of the family Mullidae.

VIII. Summary

The present study was executed to describe the comparative anatomy of the Mullidae, to verify their monophyly, to resolve their phylogenetic relationships and to propose a natural classification of the family. Six genera and 41 species of the family were treated and analyzed on the basis of cladistic methodology, employing outgroup criterion, and using general percoids as outgroups.

1) The skeletal and muscular systems of the family Mullidae were described in detail, and morphological features of the family were clarified. One of the outstanding features of the group is the osteological and myological differentiations related to the hyoid barbels.

2) The family Mullidae is a monophyletic group supported by 26 synapomorphies. Thirteen characters are autapomorphies unique to the family Mullidae and strongly support the monophyly of the group. For example, the hyoid arch is differentiated osteologically and myologically (modification of first branchiostegal ray into barbel, diminishment of branchiostegal rays, forward projection of anterior ceratohyal, lateral convexity of ceratohyals, presence of four muscles related to barbel, separation of right and left protractor hyoidei, diminished insertion of hyohyoidei abductores section 1, and insertion of hyohyoidei abductores section 2 on urohyal).

3) Seven equally most parsimonious trees were produced by cladistic analysis using 41 transformation series. Based on reconstruction of character evolution of preorbital scales, one tree among them was accepted as a cladistic hypothesis showing phylogenetic relationships within the family Mullidae. According to the tree accepted in the present study, the family Mullidae is made up of six clades, each corresponding to currently recognized genus. Based on DELTRAN optimization of characters, the corresponding clade of the genus *Upeneus* is supported by five apomorphies (for example, presence of scales on the second dorsal and anal fins, and rotator tentaculi subsection 2a not originating from anterior ceratohyal). The corresponding clade of the genus *Mullus* is supported by six apomorphies (for example, expansion of tooth-plate on vomer and absence of teeth on upper jaw in adult). The corresponding clade of the genus *Upeneichthys* is supported by two apomorphies (connection of frontal crest with supraoccipital crest and presence of elongated postpelvic process). The corresponding clade of *Mulloidichthys* is supported by five apomorphies (for example, palatine articulating with lateral ethmoid, and levator operculi originating from dorso-lateral face of opercle). The corresponding clade of *Pseudupeneus* is supported by one apomorphy (presence of an enlarged conical teeth on upper jaw), and that of *Parupeneus* is supported by two apomorphies (presence of frontal crest and ectopterygoid projection).

4) Although the sister group of the family Mullidae could not be determined in the present study, two characters (absence of crescent expansion on endopterygoid and anterior expansion of adductor arcus palatini) were considered as most probable indicators suggesting haemuloid or sparoid fishes (*sensu* Johnson, 1980) as a sister group for the family Mullidae.

5) The following six genera are recognized in the family Mullidae and are defined based on the present phylogenetic analysis.

Family Mullidae

Genus *Upeneus* Cuvier, 1829

Genus *Mullus* Linnaeus, 1758
Genus *Upeneichthys* Bleeker, 1855
Genus *Mulloidichthys* Whitley, 1929
Genus *Pseudupeneus* Bleeker, 1862
Genus *Parupeneus* Bleeker, 1863

IX. Acknowledgments

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XI. Appendices

Appendix 1. Anatomical abbreviations used in the text figures

Bones and cartilages

ach, anterior ceratohyal; acp, ascending process; alp, alveolar process; ang, anguloarticular; ap, additional pelvic process; arp, articular process; ba, basipterygium; bb, basibranchial; bh, basihyal; bo, basioccipital; br, branchiostegal ray; bsp, basisphenoid; cb, ceratobranchial; cl, cleithrum; cm, coronomeckelian; co, coracoid; den, dentary; dhh, dorsal hypohyal; dptg, distal pterygiophore; dpcl, dorsal postcleithrum; eb, epibranchial; ec, ethmoid cartilage; ecp, ectopterygoid; enp, endopterygoid; ep, epipleural; epo, epioccipital; es, extrascapula; eu, epural; exo, exoccipital; f, frontal; hb, hypobranchial; hp, hypurapophysis; hs, haemal spine; hy, hypural; hyo, hyomandibula; iac, interarcual cartilage; ic, intercalar; ih, interhyal; io, infraorbital; iop, interopercle; lac, lacrimal; le, lateral ethmoid; mc, Meckel's cartilage; me, mesethmoid; mep, metapterygoid; mx, maxilla; n, nasal; ns, neural spine; op, opercle; pa, parietal; pal, palatine; pb, pharyngobranchial; pch, posterior ceratohyal; phy, parhypural; pl, pleural rib; pmp, postmaxillary process; pmx, premaxilla; pop, preopercle; pp, postpelvic process; pptg, proximal pterygiophore; pr, pectoral fin radial; pro, prootic; ps, parasphenoid; pt, posttemporal; pte, pterotic; pts, pterosphenoid; pu, preural vertebra; q, quadrate; rc, rostral cartilage; ret, retroarticular; sbk, accessory subpelvic keel; sbp, subpelvic process; sc, scapula; scl, supracleithrum; smx, supramaxilla; sn, supraneural; soc, supraoccipital; sop, subopercle; sp, spine; sph, sphenotic; ss, subocular shelf; st, stay; sym, symplectic; tp, tooth-plate; un, uroneural; us, urostyle; uh, urohyal; v, vomer; vhh, ventral hypohyal; vpcl, ventral postcleithrum.

Muscles and ligaments

A1-3 and Aw, adductor mandibulae sections 1-3 and w; AAP, adductor arcus palatini; ABP, abductor profundus; ABPP, abductor profundus pelvicus; ABS, abductor superficialis; ABSP, abductor superficialis pelvicus; AD, adductor; ADP, adductor profundus; ADPP, adductor profundus pelvicus; ADS, adductor superficialis; ADSP, adductor superficialis pelvicus; ADO, adductor operculi; ADR, adductor radialis; ARD, arrector dorsalis; ARDP, arrector dorsalis pelvicus; ARV, arrector ventralis; ARVP, arrector ventralis pelvicus; BL, Baudelot's ligament; CR, coracoradialis; DA, depressores anales; DD, depressores dorsales; DO, dilatator operculi; EA, erectores anales; ED, erectores dorsales; EPAX, epaxialis; EXP, extensor proprius; EXT, extensor tentaculi; FD, flexor dorsalis; FDS, flexor dorsalis superior; FV, flexor ventralis; FVE, flexor ventralis externus; FVI, flexor ventralis inferior; HAB 1-2, hyohyoidei abductores sections 1-2; HAD, hyohyoidei adductores; HPAX, hypaxialis; HL, hypochordal longitudinalis; ICD, inclinatores dorsales; ICP, infracarinalis posterior; IM, intermandibularis; INT, interradialis; LAP, levator arcus palatini; LE, levator externus; LI, levator internus; LO, levator operculi; LP, ligamentum primordium; MPL, maxillopremaxillary ligament; NML, nasal-maxillary ligament; OBD, obliqui dorsales; OBP, obliquus posterior; OS, obliquus superioris; OV, obliqui ventrales; PCE, pharyngoclavicularis externus; PCI, pharyngoclavicularis internus; PPL, palato-premaxillary ligament; PRH, protractor hyoidei; PP, protractor pectoralis; RC, rectus communis; RD, retractor dorsalis; RET, retractor tentaculi; RIL, retroarticulointeropercular ligament; ROT 1-2, rotator tentaculi sections 1-2; RV, recti ventrales; SCA, supracarinalis anterior; SCM, supracarinalis medius; SCP, supracarinalis posterior; SO, sphincter oesophagi; SH, sternohyoideus; TDA, transversus dorsalis anterior; TDP, transversus dorsalis posterior; TVA, transversus ventralis anterior; TVP, transversus ventralis posterior.

Appendix 2. Materials examined in classification.

a. Genus *Upeneus*

Upeneus asymmetricus: USNM 154659 (holotype of *U. asymmetricus*), 74.9 mm SL. *Upeneus doriae*: BMNH 1869.3.4.36 (syntypes of *Upeneoides doriae*), 5 specimens, 76.7-93.8 mm SL, MSNG 13056 (syntypes of *U. doriae*), 11 specimens, 66.4-93.8 mm SL, ZMB 7056 (syntypes of *U. doriae*), 2 specimens, 70.6-83.5 mm SL.

Upeneus francisi: NSMT-P 34740 (paratype of *U. francisi*), 46.4 mm SL. *Upeneus japonicus*: NSMT-P 45177 (neotype of *Mullus japonicus*), 99.0 mm SL; RMNH 4683 (lectotype of *Mullus bensasi*), 119.3 mm SL, Japan; HUMZ 39635, 103.6 mm SL; HUMZ 44253, 70.3 mm SL; HUMZ 48056, 95.6 mm SL; HUMZ 48141, 97.6 mm SL; HUMZ 48175; HUMZ 48561, 83.6 mm SL; HUMZ 51857, 95.3 mm SL; HUMZ 60007, 81.0 mm SL; HUMZ 61959, 59.4 mm SL; HUMZ 70853, 86.8 mm SL; HUMZ 71801, 82.6 mm SL; HUMZ 71803, 84.3 mm SL; HUMZ 71804, 92.3 mm SL; HUMZ 79898, 122.1 mm SL; HUMZ 79899, 110.3 mm SL; HUMZ 90251, 70.6 mm SL; HUMZ 90293, 77.1 mm SL; HUMZ 90570, 99.7 mm SL; HUMZ 94251, 68.3 mm SL; HUMZ 95026, 99.1 mm SL; HUMZ 95027, 88.4 mm SL; HUMZ 95028, 87.8 mm SL; HUMZ 103107, 68.6 mm SL; HUMZ 103268, 76.5 mm SL; HUMZ 105764, 93.1 mm SL; HUMZ 105864, 127.9 mm SL; HUMZ 105890, 129.0 mm SL; HUMZ 106076, 81.8 mm SL; HUMZ 106202, 92.0 mm SL; HUMZ 107015, 100.1 mm SL; HUMZ 110429, 89.2 mm SL; HUMZ 110613, 64.6 mm SL; HUMZ 110808, 53.5 mm SL; HUMZ 110816, 54.1 mm SL; HUMZ 131441, 89.2 mm SL; HUMZ 131443, 82.0 mm SL; HUMZ 131446, 48.4 mm SL; HUMZ 131444, 72.1 mm SL; HUMZ 131447, 55.2 mm SL; HUMZ 131940, 119.1 mm SL; HUMZ 131941, 72.0 mm SL; HUMZ 131942, 83.2 mm SL; HUMZ 131943, 69.9 mm SL; HUMZ 139296, 70.9 mm SL; HUMZ 144253, 100.0 mm SL; HUMZ 144254, 92.7 mm SL; HUMZ 144255, 92.5 mm SL; HUMZ 144256, 90.2 mm SL. *Upeneus luzonius*: SU 9244 (paratype of *U. luzonius*), 94.3 mm SL; SU 20101, 2 specimens, 68.3-70.0 mm SL; MNHN 1977 174 (holotype of *Upeneus niebuhri*), 105.3 mm SL; ANSP 51904, 3 specimens, 86.0-108.7 mm SL; ANSP 51907, 34.8 mm SL; ANSP 52701, 6 specimens, 68.0-124.8 mm SL; ANSP 52708, 104.1 mm SL; ANSP 52696, 119.3 mm SL; ANSP 52697, 66.2 mm SL; ANSP 86365, 3 specimens, 75.3-101.1 mm SL; ANSP 91679, 3 specimens, 71.3-101.2 mm SL; ANSP 52707, 103.9 mm SL; NTM S.10954-001, 116.1 mm SL. *Upeneus mascareinsis*: MNHN 1965-72 (holotype of *U. mascareinsis*), 146.5 mm SL. *Upeneus moluccensis*: HUMZ 74102, 171.6 mm SL; HUMZ 82099, 169.2 mm SL; HUMZ 82100, 157.2 mm SL; HUMZ 82101, 159.2 mm SL; HUMZ 82102, 184.5 mm SL; HUMZ 82103, 156.9 mm SL; HUMZ 82105, 161.8 mm SL; HUMZ 82107, 153.2 mm SL; HUMZ 82108, 162.4 mm SL. *Upeneus parvus*: CU 43914, 4 specimens, 109.8-122.9 mm SL; HUMZ 31291, 128.3 mm SL; HUMZ 31292, 123.8 mm SL; HUMZ 31294, 104.8 mm SL; HUMZ 31301, 145.2 mm SL; HUMZ 31308, 113.3 mm SL; HUMZ 31309, 135.3 mm SL; HUMZ 31312, 114.6 mm SL; HUMZ 31313, 100.2 mm SL; HUMZ 31314, 105.3 mm SL; HUMZ 32730, 146.6 mm SL; HUMZ 32743, 144.2 mm SL; HUMZ 32755, 133.8 mm SL; HUMZ 32756, 114.9 mm SL; HUMZ 32757, 117.3 mm SL; HUMZ 32784, 140.8 mm SL; HUMZ 32785, 131.9 mm SL; HUMZ 32802, 133.4 mm SL; HUMZ 32812, 125.0 mm SL; HUMZ 32814, 123.0 mm SL; HUMZ 32815, 113.6 mm SL. *Upeneus pori*: HUJ 13517 (paratypes of *U. pori*), 2 specimens, 97.6-102.6 mm SL; HUJ 12358 (paratype of *U. pori*), 117.9 mm SL. *Upeneus quadrilineatus*: HUMZ 13969, 92.3 mm SL; HUMZ 37201, 95.1 mm SL; HUMZ 37650, 111.6 mm SL; HUMZ 46997, 150.9 mm SL; HUMZ 50149, 112.0 mm SL; HUMZ 73871, 97.6 mm SL; HUMZ 74103, 149.8 mm SL; HUMZ 74104, 197.2 mm SL; UMMZ 220286, 11 specimens, 74.0-82.4 mm SL. *Upeneus subvittatus*: RMNH 4700 (lectotype and paralectotype of *Mullus subvittatus*), 2 specimens, 106.5-109.5 mm SL. *Upeneus sulphureus*: HUMZ 43444, 84.5 mm SL; NTM S. 0398, 81.3 mm SL; NTM S. 0832, 118.0 mm SL; NTM S. 0833, 89.5 mm SL; NTM S. 0834, 80.5 mm SL; NTM S. 0835, 95.8 mm SL; NTM S. 0836, 86.7 mm SL; NTM S. 0837, 86.6 mm SL; NTM S. 0838, 82.6 mm SL; NTM S. 0859, 95.2 mm SL; NTM S. 0860, 94.8 mm SL; NTM S. 0861, 92.9 mm SL; NTM S. 0862, 115.2 mm SL; NTM S. 0963, 88.2 mm SL; NTM S. 0964, 86.5 mm SL; NTM S. 0968, 80.6 mm SL; NTM S. 1170, 80.9 mm SL; NTM S. 1171, 82.5 mm SL; NTM S. 1180. 93.7 mm SL, NTM S. 1181, 89.2 mm SL; NTM S. 10031 108, 8 specimens, 86.1-106.2 mm SL; NTM S. 10557-010, 94.6 mm SL; NTM S. 10132-001, 84.2 mm SL; NTM S. 11332-007, 137.7 mm SL; UMMZ 225612, 3 specimens, 87.8-105.1 mm SL; UMMZ 226398, 4 specimens, 89.2-112.0 mm SL; UMMZ 2199635, 5 specimens, 99.4-123.9 mm SL. *Upeneus sundaicus*: RMNH 5735 (syntypes including lectotype of *Upeneoides sundaicus*), 6 specimens, 89.8-124.7 mm SL. *Upeneus taeniopterus*: MNHN 9568 (holotype of *Upeneus taeniopterus*), 214.0 mm SL; BPBM 18863, 221.4 mm SL; USNM 267590, 5 specimens, 193.5-254.7 mm SL; USNM 50667 (holotype of *U. arge*), 164.3 mm SL; SU 7477 (paratype of *U. arge*), 249.3 mm SL; SU 23290 (paratype of *U. arge*), 4 specimens, 188.1-218.9 mm SL; BPBM 5590, 3 specimens, 133.7-181.7 mm SL; BPBM 10539, 3 specimens, 179.6-268.8 mm SL; RUSI 013915, 106.5 mm SL. *Upeneus tragula*: BMNH 1968.3.11.12 (syntype of *Upeneus tragula*), 154.0 mm SL; RMNH 5720 (lectotype of *Upeneoides variegatus*), 99.8 mm SL; RMNH 25498 (paralectotypes of *U. variegatus*), 49.9 94.2 mm SL; HUMZ 6465, 146.1 mm SL; HUMZ 13789, 138.3 mm SL; HUMZ 39659, 130.1 mm SL; HUMZ 58847, 130.1 mm SL; HUMZ 62157, 137.7 mm SL; HUMZ 119437,

107.9 mm SL ; HUMZ 131711, 120.1 mm SL ; HUMZ 131712, 120.6 mm SL ; HUMZ 163572, 40.1 mm SL ; NTM S. 0399, 127.8 mm SL ; NTM S. 11278-008, 69.8 mm SL ; NTM S. 10123-002, 2 specimens, 120.5-131.7 mm SL ; NTM S. 10031-107, 3 specimens, 128.0-149.4 mm SL ; NTM S. 10122-001, 71.2 mm SL ; RUSI 035638, 3 specimens, 125.6-137.7 mm SL. *Upeneus vittatus* : HUMZ 35789, 65.6 mm SL ; HUMZ 37203, 99.2 mm SL ; HUMZ 46772, 106.7 mm SL ; HUMZ 46774, 78.6 mm SL ; HUMZ 62518, 159.3 mm SL ; HUMZ 62523, 158.0 mm SL ; HUMZ 112067, 186.0 mm SL.

b. Genus *Mullus*

Mullus argentinae : BMNH 1982.5.13.1, 153.7 mm SL ; HUMZ 31269, 168.5 mm SL, HUMZ 31272, 166.0 mm SL ; MNHN 1975-204, 107.0 mm SL. *Mullus auratus* : TCWC 2040.02, 41.5 mm SL ; TCWC 2131.01, 115.2 mm SL ; TCWC 2242.02, 145.6 mm SL ; TCWC 2259.01, 141.9 mm SL ; TCWC 2333.01, 3 specimens, 124.8-132.8 mm SL ; TCWC 2341.01, 121.0 mm SL ; TCWC 2345.01, 122.3 mm SL ; TCWC 3530.03, 3 specimens, 138.4-155.4 mm SL ; TCWC 3949.02, 144.3 mm SL ; TCWC 1952.01, 123.4 mm SL ; TCWC 3955, 128.3 mm SL ; TCWC 4204.22, 4 specimens, 124.8-136.3 mm SL ; TCWC 4218.15, 2 specimens, 127.6-140.7 mm SL ; TCWC 4219.18, 2 specimens, 122.8-130.0 mm SL ; TCWC 7651.02, 4 specimens, 127.4-147.0 mm SL ; TCWC 7652.02, 4 specimens, 142.9-151.1 mm SL. *Mullus barbatus* : MNHN 1961-904, 103.4 mm SL ; HUMZ 149267, 125.1 mm SL ; HUMZ 154850, 104.4 mm SL ; HUMZ 154852, 98.7 mm SL ; HUMZ 154854, 92.3 mm SL ; HUMZ 154855, 81.3 mm SL ; HUMZ 154856, 93.8 mm SL ; HUMZ 154857, 87.9 mm SL ; HUMZ 154858, 85.0 mm SL ; HUMZ 154859, 93.6 mm SL ; HUMZ 154860, 104.3 mm SL ; HUMZ 154861, 97.7 mm SL ; HUMZ 154862, 93.5 mm SL ; HUMZ 154863, 83.0 mm SL ; HUMZ 154864, 81.6 mm SL ; HUMZ 154865, 68.6 mm SL ; HUMZ 154870, 97.9 mm SL ; HUMZ 154871, 94.5 mm SL. *Mullus barbatus ponticus* : BMNH 1960.9.23.31-34, 4 specimens, 51.9-120.0 mm SL. *Mullus phillipsi* : ANSP 130360, 5 specimens, 57.2-67.2 mm SL ; ANSP 130362, 8 specimens, 48.6-73.0 mm SL ; ANSP 130367, 2 specimens, 40.6-40.7 mm SL ; ANSP 130368, 69.8 mm SL ; ANSP 130370, 50.0 mm SL. *Mullus surmuletus* : MNHN 1977-410, 162.4 mm SL ; HUMZ 154851, 110.9 mm SL.

c. Genus *Upeneichthys*

Upeneichthys lineatus : CSIRO A696, 66.0 mm SL ; CSIRO C1927, 127.4 mm SL ; CSIRO B1535, 4 specimens, 48.7-61.5 mm SL ; CSIRO C2753, 118.9 mm SL ; CSIRO C3074, 140.9 mm SL ; CSIRO C4291, 189.4 mm SL. *Upeneichthys porosus* : CSIRO CA3447, 79.8 mm SL ; CSIRO A3448, 147.5 mm SL. *Upeneichthys* sp. : CSIRO H572-1, 3 specimens, 92.4-102.3 mm SL ; CSIRO H4262-01, 49.4 mm SL.

d. Genus *Mulloidichthys*

Mulloidichthys flavolineatus : MNHN A. 3512 (holotype of *Upeneus atherinoides*), 77.4 mm SL ; BMNH 1873.4.3.134 (syntype of *Mulloides samoensis*), 128.5 mm SL ; BMNH 1927.12.6.36 (type of *Upeneus queketti*), 176.3 mm SL ; MNHN B. 2352 (syntype of *Upeneus vanicolensis*), 86.5 mm SL ; HUMZ 3309, 108.5 mm SL ; HUMZ 53467, 289.2 mm SL ; HUMZ 3482, 234.4 mm SL, HUMZ 53515, 260.0 mm SL ; HUMZ 107326, 194.8 mm SL ; HUMZ 107327, 146.6 mm SL ; HUMZ 107328, 133.4 mm SL ; HUMZ 107329, 164.0 mm SL ; UW 009794, 148.6 mm SL ; UW 013326, 2 specimens, 142.6-145.2 mm SL ; UW 015145, 160.4 mm SL ; MCZ 11006, 2 specimens, 172.7-200.8 mm SL. *Mulloidichthys dentatus* : MCZ 29443, 8 specimens, 86.9-99.6 mm SL ; MCZ 30793, 9 specimens, 74.6-109.3 mm SL. *Mulloidichthys vanicolensis* : MNHN A.3520 (syntype of *Upeneus vanicolensis*), 103.2 mm SL ; MNHN A. 3521 (syntype of *U. vanicolensis*), 98.5 mm SL ; BMNH 1873.8.1.6, 209.3 mm SL ; HUMZ 53484, 243.2 mm SL, HUMZ 53514, 250.9 mm SL ; HUMZ 73360, 240.9 mm SL.

e. Genus *Pseudupeneus*

Pseudupeneus grandisquamis : BMNH 1864.1.26. 340-341 (syntypes of *Upeneus tetraspilus*), 2 specimens, 150.7-162.4 mm SL. *Pseudupeneus maculatus* : ANSP 121368, 10 specimens, 40.9-52.0 mm SL ; ANSP 133636, 98.9 mm SL ; ANSP 133637, 2 specimens, 142.5-154.3 mm SL ; ANSP 133851, 227.2 mm SL ; TCWC 650.02, 70.3 mm SL ; TCWC 1781.02, 66.7 mm SL ; TCWC 2437.06, 2 specimens, 46.6-63.4 mm SL ; TCWC 4471.20, 106 mm SL ; TCWC 5221.01, 108.3 mm SL. *Pseudupeneus prayensis* : RUSI 025636, 3 specimens, 101.0-182.2 mm SL ; RUSI 026531, 2 specimens, 105.3-114.3 mm SL ; RUSI 026567, 112.4 mm SL.

f. Genus *Parupeneus*

Parupeneus barberinoides : BMNH 1869.11.12.61 (syntype of *Upeneus atrocingulatus*), 55.6 mm SL ; HUMZ 39251, 156.3 mm SL ; HUMZ 39235, 101.1 mm SL. *Parupeneus barberinus* : ANSP 108845, 2 specimens, 89.8-91.2 mm SL ; ANSP 108846, 6 specimens, 35.0-76.9 mm SL. *Parupeneus chrysopleuron* : BSKU 09313, 119.0 mm SL ; BSKU 029102, 183.5 mm SL ; BSKU 084159, 63.7 mm SL ; BSKU 084311, 91.7 mm SL ; BSKU 084312, 81.6 mm SL ; BSKU 084313, 70.2 mm SL ; BSKU 085014, 212.9 mm SL ; BSKU 085320, 65.4 mm SL ; BSKU 085321, 77.5 mm SL ; CNUC 19763, 226.8 mm SL ; HUMZ 58816, 152.4 mm SL ; HUMZ 62154, 190.7 mm SL ; HUMZ 155971, 214.2 mm SL ; HUMZ 155972, 221.0 mm SL. *Parupeneus ciliatus* : MNHN A. 5700 (holotype of *Sciaena ciliata*),

300.0 mm SL ; HUMZ 49197, 184.8 mm SL ; HUMZ 62153, 190.1 mm SL, HUMZ 62173, 177.9 mm SL. *Parupeneus cyclostomus* : MNHN A. 5702 (neotype of *Mullus cyclostomus*), 328.0 mm SL ; HUMZ 48314, 159.9 mm SL ; UW 013330, 51.3 mm SL. *Parupeneus dispilurus* : BMNH 1867.3.9.82 (syntype of *Mullus dispilurus*), 130.1 mm SL. *Parupeneus dubius* : RMNH 4702 (holotype of *Mullus dubius*), 60.8 mm SL. *Parupeneus heptacanthus* : MNHN A. 5438 (holotype of *Sciaena heptacantha*), 155.0 mm SL ; MNHN A. 1696 (holotype of *Upeneus cinnabarinus*), 141.3 mm SL ; BMNH 1968.3.11.10-11 (syntypes of *Upeneus biaculeatus*), 2 specimens, 160.5-244.3 mm SL ; RMNH 5743 (syntype of *Upeneus pleurospilos*), 107.5 mm SL ; RMNH 25005 (syntype of *Upeneus pleurospilos*), 98.6 mm SL ; BSKU 084324, 123.0 mm SL ; BSKU 084325, 116.8 mm SL ; BSKU 084326, 95.7 mm SL (stained and dissected) ; BSKU uncatalog., 143.8 mm SL ; BSKU uncatalog., 147.2 mm SL ; HUMZ 6461, 156.3 mm SL ; HUMZ 6463, 156.2 mm SL ; HUMZ 6851, 131.2 mm SL ; HUMZ 13812, 173.9 mm SL ; HUMZ 33319, 133.2 mm SL ; HUMZ 38385, 147.1 mm SL ; HUMZ 38433, 174.5 mm SL ; HUMZ 38496, 212.5 mm SL ; HUMZ 38509, 210.1 mm ; HUMZ 38564, 207.5 mm SL ; HUMZ 38600, 198.4 mm SL ; HUMZ 46813, 153.7 mm SL ; HUMZ 46901, 191.2 mm SL ; HUMZ 46902, 158.1 mm SL ; HUMZ 46923, 158.4 mm SL ; HUMZ 46925, 161.7 mm SL ; HUMZ 75582, 132.0 mm SL ; HUMZ 75595, 142.9 mm SL ; HUMZ 82090, 257.9 mm SL ; HUMZ 82091, 250.4 mm SL ; HUMZ 82092, 227.0 mm SL. *Parupeneus indicus* : HUMZ 39671, 131.1 mm SL. *Parupeneus multifasciatus* : MNHN A. 3492 (holotype of *Mullus multifasciatus*), 144.0 mm SL ; HUMZ 62787, 142.3 mm SL. *Parupeneus pleurostigma* : HUMZ 53512, 205.9 mm SL. *Parupeneus posteli* : MNHN 1965-56 (holotype of *Parupeneus posteli*), 151.5 mm SL. *Parupeneus rubescens* : MNHN 1965-58 (neotype of *Mullus rubescens*), 242.0 mm SL ; USNM 306116, 210.5 mm SL ; USNM 330976, 237.6 mm SL. *Parupeneus signatus* : BMNH 1864.1.17.29-31 (syntypes of *Upeneus signatus*), 2 specimens, 109.0-142.7 mm SL. *Parupeneus spilurus* : HUMZ 48440, 153.0 mm SL ; HUMZ 62146, 173.5 mm SL ; HUMZ 62149, 163.6 mm SL ; HUMZ 62196, 154.8 mm SL.