The Stromateoid fishes: systematics and a classification

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THE STROMATEOID FISHES: SYSTEMATICS AND A CLASSIFICATION[1]

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HISTORICAL INTRODUCTION

The Stromateoidei are a small suborder of the perciform fishes, characterized primarily by toothed saccular outgrowths in the gullet immediately behind the last gill arch. The stromateoids are all marine, pelagic, and widely distributed in the temperate and tropical oceans of the world. Most species are rare and infrequently seen, but a few form the basis of fisheries. Adult stromateoids range from less than a foot to over four feet in length.

Certain stromateoids were recognized in classical times. *Stromateus* was the name applied by the Greeks of Egypt to a fish probably from the Red Sea. The name, derived from the word for a brightly colored rug, may have referred to the fish's shape and coloration. Later, however, Rondelet (1554) used the name for a similar Mediterranean fish known in the contemporary Roman vernacular as *fiatola*. Linnaeus (1758) described the same fish as *Stromateus fiatola*.

The oceanic fish *pompilus* was sacred to the Greeks. As *pompilus* accompanied ships, it brought a calm sea (Gesner, 1560). *Pompilus* has been equated with *Centrolophus* (Günther, 1860), and Gesner's figure (1560:113) certainly is of this fish. Thompson (1947), however, presents evidence that *pompilus* is the pilot fish *Naucrates*. Cuvier

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and Valenciennes (1833), citing Cetti's "Historia Naturale di Sardagni" (1777), suggested that *pompilus* might be a tuna. And while the subject of Ovid's heroic lines

> "Tuque comes ratium, tractique per aequora sulci
> Qui semper spumas sequeris, pompile, nitentes"

could well have been the centrolophid *Schedophilus ovalis*, it seems more likely that the poet is referring to *Coryphaena*, the dolphin. The classical name has been used in *Coryphaena pompilus* Linnaeus, 1758, an unrecognizable fish; in *Pompilus* Lowe, 1839, a synonym of *Centrolophus* Lacépède, 1803; and in *Pompilus* Minding, 1832, a synonym of *Naucrates* Rafinesque, 1810.

Identical figures of stromateoids were published by the Renaissance compilers Belon (1553), Rondelet (1554), Gesner (1560), and Aldrovandi (1613). Illustrations of clearly recognizable species appear in these works on the facing page with impossible monsters. Nonetheless, the information gathered by these men was to prove very useful to later authors, and was considered authoritative by many. Some of their work, for example, can be found almost word for word in Cuvier and Valenciennes (1833).

John Ray's studies (Willughby, 1686) are marked by their care and attention to detail. His anatomical work revealed for the first time the structure most characteristic of the stromateoid fishes, the peculiar pharyngeal sacs. Ray mistakenly believed that the sacs constituted a second stomach. Nonetheless, care that was not to reappear for several centuries is apparent in his description of the sacs of *Stromateus* (p. 156):

> "In palato duo oblonga ossicula aspera . . . Nam primo duos habet ventriculos; primum retro cor, prope ipsum os situm, quem echinum nun ab re dixeris: carnosus enim est, & apophysibus longis, asperis, crebris, pellis erinacei fere in modum intus consitur. (Appendices hae in sex radios divaricantur cylindriae supra centrum stellae erectae. D. Will.)"

During the first half of the nineteenth century a majority of the stromateoids were described and characterized reasonably well. The "Règne Animal" (Cuvier, 1817) and "Histoire Naturelle des Poissons" (Cuvier and Valenciennes, 1833) were especially valuable. Cuvier (1817) provided the basic arrangement which was expanded upon in the later "Histoire Naturelle."

Cuvier and Valenciennes (1833:381) added to Ray's description of the pharyngeal sacs of *Stromateus fiatola*:

> "A l'extérieur, cette partie présente la forme d'une bourse; les épines dont elle est armée sont de différent grosseur; les plus grandes sont un peu en forme fuseau; les petites garnissent les intervalles des grandes. Chacune de ces épines s'attache à la veloutée par sept ou huit ravines ou fibres disposées en étoile."

They continue later with their own observations on the sacs of *Stromateus candidus* (= *Pampus argenteus*) (p. 392):

> "Immédiatement après les os pharyngiens vient un oesophage en forme de sac ranflé et charnu, rond, un peu bilobé . . . garnies . . . de grosses épines osseuses . . ."

and of *Rhombus xanthurus* (= *Peprilus paru*) (p. 406):

> ". . . un oesophage charnu, armé intérieurement de dents osseuses coniques, les unes plus grandes, les autres plus petites . . ."

Cuvier and Valenciennes not only recognized this unique structure in "les Stromatées" but also described a similar structure in "les Centrolophes." Concerning *Centrolophus pompilus* (= *C. niger*) they wrote (p. 339):

> "Le pharynx du centrolophe présente une particularité remarquable, qui donne au commencement de leur oesophage un armure puissante. Entre les os pharyngiens . . . l'os supérieur du quatrième arceau porte plusiers appendices alongés et garnis de dents semblables . . . la partie latérale du pharynx a de profondes cannelures osseuses et dentées . . ."

They continue, observing that this seems to be:

> ". . . quelque analogie avec les épines dont le même cavité est armée dans les stromatées."

Here, for the first time, a relationship between the centrolophids and the stromateids was indicated.

Günther recognized a unifying character here and, in his Catalogue (1860:355), noted that in the Stromateina "tooth-like processes extend into the oesophagus." The "Catalogue" provided keys to the scombrid group Stromateina and to the two genera Günther included in it, *Stromateus* ("ventrals none in an adult state") and *Centrolophus* ("ventrals well developed"). The other groups in his family Scombridae were the Scombrina, Cyttina, Coryphaenina, and Nomeina, the last composed largely of stromateoids. The diagnostic pharyngeal sacs of the Nomeina remained to be discovered, for they were not mentioned in Günther's account.

Discussing the limits and arrangement of the scombroids, Gill (1862) corrected some of Günther's omissions. In doing so, however, he broke up the convenient group Nomeina, and added little to the classification. The Stromateina, though mentioned, were not defined.

"An Introduction to the Study of Fishes" (Günther, 1880) was essentially the same as the earlier "Catalogue" in its treatment of the stromateoids. Here, however, each group was given full family status as Stromateidae and Nomeidae. The close relationship of the two was still not indicated, and Günther continued to allocate a number of stromateoid genera to other families.

Although Günther's (1880) publication added almost nothing to the classification, it had an important incidental effect. Whether the cause was Günther's failure to have noticed Gill's earlier (1862) paper or whether it was his casual accounting cannot be said. At any rate, Günther's treatment of the stromateoids soon occasioned a vitriolic blast from Gill. In his "Notes on the Stromateidae," Gill (1884) united the forms scattered by Günther under the single family Stromateidae, still omitting *Nomeus* but including, albeit reservedly, *Psenes* and *Cubiceps*. The definition of the family noted "the gill-rakers of the upper segment of the last branchial arch enlarged and dentigerous or sacciform, and projecting backwards into the oesophagus" (p. 665). Gill furthermore recognized a basic dichotomy in the group by dividing the family into two subfamilies, the Stromateinae and the Centrolophinae:

> "These are distinguished by differences in the development of the vertebrae, the former [Stromateinae] having 14–15 abdominal and 17–21 caudal vertebrae, and the latter [Centrolophinae] 11 abdominal and 14 caudal vertebrae; these differences are supplemented by variations in the degree of complexity of the peculiar appendages representing and homologous with the gill-rakers of ordinary fishes, developed from the last branchial arch, and extending into the oesophagus (p. 654)."

He also observed that the Centrolophinae have normally persistent pelvic fins, while those of the Stromateinae are lost with growth. Gill considered the Centrolophinae to be the most generalized type; the Stromateinae he thought more specialized.

"Spolia Atlantica" of Lütken (1880) contained accounts of the genera *Psenes*, *Cubiceps*, *Stromateus*, and *Schedophilus*. The discussion of relationships was carefully done, and the listing of included species was especially good. Unfortunately, the work was in Danish, and has apparently been little used by subsequent investigators.

Fordice (1884) reviewed the American species of the Stromateidae. No mention was made of the pharyngeal sacs. Only two genera, *Stromateus* and *Leirus* (= *Schedophilus*) were mentioned, and, again, the division was based on the presence or absence of pelvic fins. Fordice provided keys and neat synonymies of most American stromateids. His paper was essentially an extension of the foundation laid down by Jordan and Gilbert's (1882) "Synopsis of the Fishes of North America," a work which erroneously reported (p. 448) for the Nomeidae, "No tooth-like processes in the oesophagus."

Relying heavily on the work of Gill, Jordan and Gilbert, and Fordice, Jordan and Evermann's (1896) "Fishes of North and Middle America" provided a synthesis of current thoughts on stromateoid classification. The Centrolophidae were considered a family apart from the Stromateidae, "differing in appearance and in the smaller number of vertebrae, although agreeing in the possession of teeth in the oesophagus" (p. 964). *Nomeus* and *Psenes*, in the family Nomeidae, remained distinct, and no mention of a relationship with the stromateids was made.

"Oceanic Ichthyology" (Goode and Bean, 1896) drew on Jordan and Gilbert, Gill, and Günther, for much of its information. An unexplained but correct innovation was the inclusion of *Icichthys* among the stromateoids. The treatment of the group was extremely casual; genera were shuffled into families more or less randomly without checking familial characters. The Nomeidae constituted almost the same unnatural group as set up by Günther (1860), with still no realization of its relationships. Goode and Bean's account confused, rather than improved, the stromateoid classification. Fortunately, it has been disregarded by most subsequent workers.

The first, and the only, world-wide revision of the stromateoids was that of Regan (1902). Regan gave the group its modern dimensions by adding the genera "*Nomeus*, *Cubiceps*, *Psenes*, *Bathyseriola*, and *Seriolella*, all of which have a toothed oesophagus exactly similar to that of a *Centrolophus*" (p. 117). His definition of the family was based largely on osteology, and made important contributions. His warnings of the pitfalls of allometry and of the unusual ubiquity of certain characters recognized a recurrent problem. Regan treated the group as one family, the Stromateidae, but disregarded the convenient subfamilial distinction made earlier by Gill (1884). Norman's much later "Draft Synopsis" (1957) differs from Regan only in this one respect, for Norman recognized two families based on the first couplet of Regan's key to genera, "ventral fins present" [Centrolophidae], or "ventral fins absent" [Stromateidae]. Citing correspondence with Boulenger, Regan suggested, for the first time, the affiliation of *Tetragonurus* to the stromateoids.

Boulenger was much impressed by one of Regan's diagnostic characters, the loose attachment of the pelvic bones to the pectoral arch in all stromateids. In his systematic account of the fishes for the "Cambridge Natural History" (1904), he removed the stromateids from the scombroids, where all previous workers had placed them, and ranked them among the Percesoces. Holt and Byrne (1903), using the same argument, also considered the stromateids to be allied with the Percesoces. Although in error with respect to the relationships of the group, their account of local British and Irish species was otherwise carefully done, and showed broad understanding.

Although the presence of teeth in saccular outgrowths in the gullet had long been used as a diagnostic character for the stromateoids, no one since John Ray had investigated the structure of this peculiar feature. Gilchrist (1922) examined teeth from the sacs of several South African stromateoids. He noted differences between species, but, although he recognized the value of the teeth in taxonomy, he did not indulge in systematic speculations. The sacs had previously been referred to as "oesophageal"; Gilchrist pointed out that they were "not strictly oesophageal, but . . . derived from . . . pharyngeal epithelium . . ." (p. 254). Later, in an incisive review, Barnard (1948) corrected some of Gilchrist's errors, and extended his work by examining more species and publishing more illustrations.

Bühler's (1930) monograph on the digestive system of the stromateoids pointed out, independently from Gilchrist, the pharyngeal origin of the toothed sacs. Bühler proposed the term "Rachensäche" [= pharyngeal sacs] to replace the misleading "oesophageal sacs" commonly in use. His work was done primarily with serial microscopic sections, allowing examination and description of great detail. It was a substantial contribution to understanding the origin, nature, and probable function of the teeth in the pharyngeal sacs. For details on any morphological aspect of the pharyngeal sacs, Bühler's work, or the recent detailed extension of this by Isokawa *et al.* (1965), should be consulted. Other parts of the digestive system were noted to change in rough correspondence with changes in the Rachensäche, and within Regan's (1902) framework Bühler proposed two subfamilies, the Lirinae, corresponding to Norman's (*vide supra*) Centrolophidae, and the Stromateinae, corresponding to Norman's Stromateidae.

The work of Gilchrist, Barnard, and Bühler offered sound characters for the stromateoid classification. But, because each study dealt with only a limited array of characters, the observations could not be properly or safely interpreted.

My work has dealt primarily with skeletal characters. I have looked at the soft anatomy only cursorily, and have found little of use except in a most general way. The study has involved only Recent fishes.

My conclusions are largely based on the presence or absence of pelvic fins, whether the dorsal fin is separated or continuous, the presence or absence of certain teeth, the number of vertebrae, the number of branchiostegal rays, and, in particular, the structure of the caudal region and the development of the papillae[1] in the pharyngeal sacs. The comparative morphology of these characters not only provides a reasonable separation of the suborder into five families, but also, because the characters change in a correlated fashion, it suggests the course of evolution in the stromateoids. In the trunk and caudal region the number of vertebrae increases, while the elements in the tail become fused and reduced, and the pelvic fins are lost. In the branchial region, the number of branchiostegals decreases, while the papillae of the pharyngeal sacs become increasingly more complex. The present geographical distributions of the different taxa support the conclusions based on anatomical evidence.

I propose for the stromateoids a hierarchy of five families and fourteen genera, as follows:

- Order Perciformes
- Suborder Stromateoidei
  - Family Centrolophidae
    - *Hyperoglyphe*
    - *Schedophilus*
    - *Centrolophus*
    - *Icichthys*
    - *Seriolella*
    - *Psenopsis*
  - Family Nomeidae
    - *Cubiceps*
    - *Nomeus*
    - *Psenes*
  - Family Ariommidae
    - *Ariomma*
  - Family Tetragonuridae
    - *Tetragonurus*
  - Family Stromateidae
    - *Stromateus*
    - *Peprilus*
    - *Pampus*

METHODS

Measurements were made point-to-point with a pair of fine-point dial calipers. A dissecting microscope with an eyepiece dial micrometer was used for a few very small specimens. Measurements routinely made were:

TOTAL LENGTH (TL), from the tip of the snout to the farthest tip of the caudal fin.

STANDARD LENGTH (SL), from the tip of the snout to the caudal fin base.

LENGTH OF HEAD, from the tip of the snout to the hindmost point on the opercular membrane, usually immediately above the pectoral fin.

LENGTH OF PECTORAL FIN, from the base of the uppermost ray to the farthest tip of the fin.

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[1] This term implies the unit composed of a bony base with teeth seated upon it. It is adopted here in conformance with past usage (Bühler, 1930; Barnard, 1948).

Length of pelvic fin, from the base of the most anterior ray to the farthest tip of the fin.

Longest D_1 spine, from the base of the spine to its extremity.

Predorsal distance, from the tip of the snout to the base of the first element of the dorsal fin.

Preanal distance, from the tip of the snout to the base of the first element of the anal fin.

Maximum depth, the greatest depth of the body, exclusive of fleshy or scaly fin bases.

Depth of peduncle, the least depth of the caudal peduncle.

Snout, from the tip of the snout to the anterior margin of the orbit.

Eye diameter, the greatest distance between the fleshy margins of the eye.

Length upper jaw, from the symphysis of the premaxillaries to the hindmost point, often covered by the lacrimal bone, on the maxillary.

Interorbital width, the least distance between the bony rims over the eyes.

The measurements used for showing allometry were length of head, length of pectoral fin, length of pelvic fin, predorsal distance, preanal distance, and maximum depth. These were expressed as a percentage of standard length. This percentage was plotted against standard length following the method advocated by Parr (1956). The measurements of snout, eye diameter, length of upper jaw, and interorbital width were expressed as a percentage of length of head.

Counts were made with a fine needle, usually under low magnification on a dissecting microscope. For extremely small specimens, median finray counts were made more easily using transmitted, polarized light. Counts routinely made were:

D, total dorsal fin elements, spines indicated by Roman numerals, rays by Arabic. In some cases it was impossible to distinguish between spines and rays; these counts are followed by the expression "total elements." The last, double ray of both dorsal and anal fins was counted as one element.

A, total anal fin elements.

P, total pectoral fin elements, one side, spine not distinguished from rays.

Gill rakers, the total number of rakers on the first arch, one side. Expressed as number on upper limb plus one, if at angle, plus number on lower limb (e.g. 8 + 1 + 17).

Lateral line scales, the number of scales along the position normally occupied by the lateral line, one side, terminating at the caudal fin base. In many stromateoids the tubed scales end on the peduncle, but the count was nonetheless continued to the caudal base. Often the deciduous scales are lost and scale pockets must be counted. Lateral line scales is a difficult count and cannot be made on most specimens.

Counts less routinely made were:

Branchiostegal rays (BR), left side.

Vertebrae, number of precaudal vertebrae plus the number of caudal vertebrae, including the hypural plate (= 1). Almost all vertebral counts were made from radiographs. Determination of the first caudal vertebra is hence somewhat subjective. Where skeletal material has been used, the count is followed by the expression "skel."

All measurements and counts conform with the standards of Hubbs and Lagler (1958).

The osteology was studied primarily with radiographs and cleared-and-stained preparations. With the use of soft X-rays, specimens as small as 20 mm SL could be successfully radiographed.

Small fishes, usually no longer than 65 mm TL, were cleared and stained. Gill arches and the associated pharyngeal sacs were dissected from larger fish, usually around 190 mm TL, and were also cleared and stained. To remove the arches and sacs, cuts were made between the hyal and opercular series, the tongue and dentaries, and the last gill arch and pectoral girdle. The unit so freed was carefully disconnected from the base of the neurocranium,

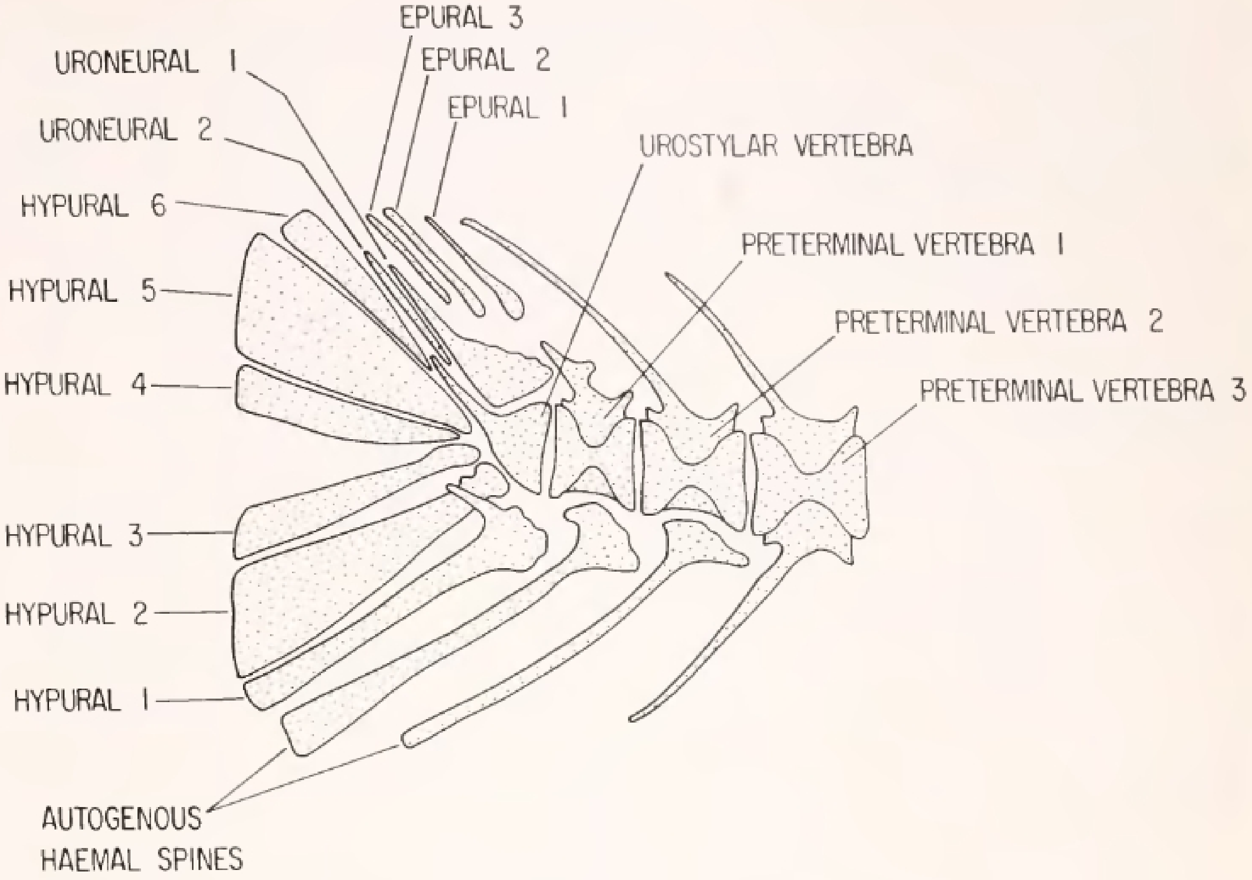

Figure 1. The bones of the caudal skeleton, schematic drawing of the basic centrolophid type.

and the pharyngeal sacs pulled forward from between the cleithra. The esophagus was cut behind the sacs, and the complete branchial apparatus removed. This was divided sagitally, and one half, usually the right, was cleared and stained. A more legible preparation was obtained if the gill filaments were stripped off prior to treatment. Teeth from the pharyngeal sacs were examined by macerating the sac in potassium hydroxide until the muscle was translucent, staining, and allowing the sac to disintegrate. Individual teeth could then be picked out and examined.

Excellent results were obtained following the clearing-and-staining method of Clothier (1950) modified from Hollister (1934). The entire clearing-and-staining procedure takes about two months.

A few complete skeletons were prepared, mostly from fresh specimens, by picking the meat carefully from the bones. Skulls were prepared by boiling the specimen until it fell apart. Only partial dissections were made in some cases. Whenever possible, skeletons in museum collections were examined. Scales were stained in alizarin, blotted dry, and mounted in balsam on slides.

Drawings of cleared-and-stained preparations were made through a Wild Dissecting Microscope with a camera lucida attachment. All caudal skeletons were drawn at 25 power, using transmitted light. Drawings of the branchial arches were made at 6 power, using transmitted light to draw the orientation of the bones, and reflected light to draw the arrangement and structure of the bases of the papillae. These drawings were redrafted on tracing paper and the final drawing was made with reference to the specimen through the 'scope without camera lucida. All anatomical drawings,

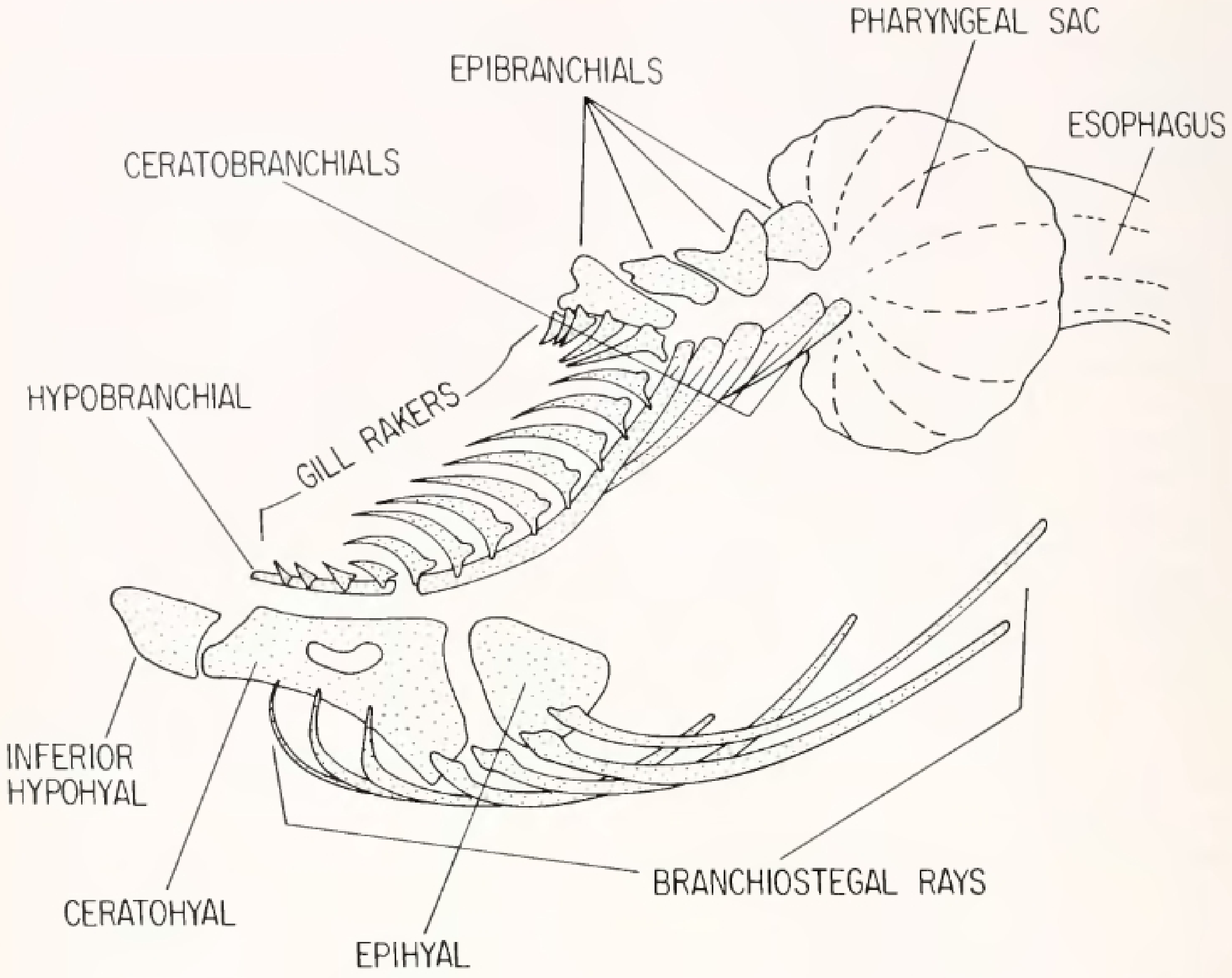

Figure 2. Elements of the branchial region, schematic drawing of the basic stromateoid type.

though made from specific preparations, are semi-diagrammatic.

The various elements in the drawings of the caudal skeleton are identified in Figure 1. Those of the branchial region are shown in Figure 2. Nomenclature of the caudal skeleton follows Gosline (1960, 1961); that of the head and branchial region follows Mead and Bradbury (1963).

MATERIAL

The specimens examined are arranged below under the classificatory scheme herein proposed. Museum and institutional names, in alphabetical order under each species, are abbreviated as follows:

ABE —Collection of Dr. T. Abe, Tokyo
AMS —Australian Museum, Sydney
ANSP —Academy of Natural Sciences of Philadelphia
BC —University of British Columbia, Vancouver
BCF —Bureau of Commercial Fisheries, Biological Laboratory, Washington, D. C.
BMNH —British Museum (Natural History), London
BOC —Bingham Oceanographic Collection, Yale University
CF —Danish Carlsberg Foundation, Charlottenlund Slot
CNHM —Chicago Natural History Museum
GTS —Guinean Trawling Survey
IIOE[1] —International Indian Ocean Expedition
MCZ —Museum of Comparative Zoology, Harvard University
MNHN —Muséum National d'Histoire Naturelle, Paris

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[1] These specimens will ultimately be catalogued in the MCZ.

NRF —Nankai Regional Fisheries Research Laboratory, Kochi
NTU —Department of Zoology, Faculty of Science, Tokyo University
SAM —South African Museum
SIO —Scripps Institution of Oceanography
SU —Natural History Museum, Stanford University
USNM —United States National Museum, Washington, D. C.
WHOI[1]—Woods Hole Oceanographic Institution
ZMC —Zoological Museum, Copenhagen

The number of specimens, the range of standard lengths, and the locality appear in that order within the parentheses. Types are marked with an asterisk (*), the species name following within the parentheses. Specimens radiographed are marked with a dagger (†); specimens that have been cleared and stained are marked CS.

Hyperoglyphe

H. antarctica (Carmichael): †AMS IB. 3825 (1, 170 mm, near Sydney, N.S.W.). *† BMNH 1855. 9. 19. 2 (1, 108 mm, coasts of Australia, *Diagramma porosa* Richardson). †SAM 23592 (1, 105 mm, Cape Point, South Africa).

H. bythites (Ginsburg): CNHM 46408 (1, 12 mm, Ocean Spring, Miss.). *†USNM 157776 (1, 197 mm, off Pensacola, Fla., *Palinurichthys bythites* Ginsburg); *†USNM 157778 (1, 187 mm, Mississippi Delta, paratype *Palinurichthys bythites* Ginsburg). WHOI (1, 204 mm, OREGON sta. 3762); WHOI (1, 203 mm, OREGON sta. 4011); WHOI (7, 188–213 mm, OREGON sta. 4030).

H. japonica (Döderlein): ABE 58-258, 60-107 to 111, 60-113 to 116, 60-139, 60-225, 60-370, 60-709, 60-744, 60-775, 61-452, 61-458, 61-461 to 464, 61-500 to 511, 62-302, 62-303, 62-336 to 368, 63-435, 63-476, 63-447, 63-480, 63-541 to 544, 63-547, 63-668, 63-708, 63-728, 63-872 (35, 35–233 mm, Manazuru, Japan); ABE 64-2201 and 2202 (2, 400, 415 mm, Tokyo market); ABE 2236 (1, 695 mm, Tokyo market); ABE plankton collection (1, 20 mm, East China Sea). CNHM 59428 (1, 420 mm, Tokyo).

H. perciforma (Mitchill): †MCZ 36624 (2, 159, 209 mm, Woods Hole, Mass.). WHOI (47, 101–198 mm, 40°10′N 69°30′W, gill arch CS); WHOI (1, 50 mm, 38°37′N 69°24′W, CS).

Schedophilus

S. griseolineatus (Norman): †BMNH 1936. 8. 26. 1068–9 (2, 258, 258 mm, South Atlantic); *†BMNH 1936. 8. 26. 1070–1 (2, 193, 196 mm, South Atlantic, *Palinurichthys griseolineatus* Norman).

S. maculatus Günther: *†BMNH 48. 3. 16. 150 (1, 37 mm, China Seas, *S. maculatus* Günther).

S. huttoni (Waite): †ZMC (1, *ca.* 40 mm, 34°24′S 94°45′W).

S. marmoratus Kner and Steindachner: *†Hamburg Museum H464 (1, 37 mm, Südsee, *S. marmoratus* Kner and Steindachner). †ZMC (2, 28 and 46 mm, GALATHEA sta. 176).

S. medusophagus Cocco: *BMNH 60. 3. 18. 3 (1, *ca.* 405 mm, stuffed, Cornwall, *Centrolophus britannicus* Günther). †CF (7, 59–188 mm, North Atlantic). †USNM 163880 (1, 333 mm, Kitty Hawk). WHOI (19, 5.5–435 mm, North Atlantic, one CS).

S. ovalis (Cuvier and Valenciennes): *†BMNH 1860. 7. 17. 2–3 (2, 171, 186 mm, Madeira, *Leirus bennettii* Lowe). *MNHN 264. 4. 1. 2 (1, 299 mm, Nice, *Centrolophus ovalis* Cuvier and Valenciennes); *MNHN 264. 5. 1. 2 (1, 144 mm, Canary Islands, *Crius berthelotti* Valenciennes).

S. pemarco (Poll): BCF 928 (1, 95 mm, 4°31′S 10°53′E). †GTS (11, 103–217 mm, Gulf of Guinea, gill arch CS).

Centrolophus

C. niger Lacépède: *†BMNH 1862. 6. 14. 16 (1, 290 mm, Madeira, *Schedophilus elongatus* Johnson); BMNH 50. 9. 7. 3 (1, 385 mm, no locality); BMNH 55. 9. 19. 1461 (1, 124 mm, Hasler Coll.); BMNH 80. 12. 11. 1 (1, 183 mm, Falmouth); BMNH 1934. 8. 8. 67 (1, 362 mm, SW Ireland); BMNH 1934. 8. 8. 68–9 (2, 498, 560 mm, SW Ireland). †CF (2, 147, 204 mm, DANA sta. 4205, gill arch CS). MCZ 34246 (1, 443 mm, 42°10′N 66°45′W); MCZ 37983 (1, 284 mm, Provincetown); MCZ 37984 (1, 490 mm, Sable Island Bank). *†MNHN 264. 2. 2. 1 (1, 287 mm, Fécamp, *Centrolophus niger* Lacépède); *MNHN 264. 2. 2. 2, 264. 2. 2. 3 (3, 169–207 mm, Nice, *Centrolophus morio* Cuvier and Valenciennes); MNHN 264. 2. 2. 9 (1, 180 mm, Naples); *MNHN 264. 4. 2. 1 (1, 121 mm, Marseille, *Centrolophus valenciennesi* Moreau). †USNM 44440 (1, 189 mm, Dennis, Mass.); USNM 48367 (1, 39 mm, Naples); †USNM 48906 (1, 265 mm, North Truro, Mass.); USNM 49335 (1, 220 mm, Genoa). WHOI (1, 1065 mm, 40°13′N 65°45′W).

Icichthys

I. lockingtoni Jordan and Gilbert: ABE 63-526, 63-527, 63-529, 63-530, 63-548, 63-549, 63-555 (12, 72–173 mm, Manazuru, gill arch CS). BC 53-99A (1, 164 mm, Vancouver

Island); BC 59-652 (1, 132 mm, Vancouver Island). *SU 7442 (1, 65 mm, Monterey Bay, *Schedophilus heathi* Gilbert); SU 17346 (1, 42 mm, Seal Beach); SU 22955 (1, 41 mm, Catalina Island); SU 22971 (1, 26 mm, Monterey Bay); SU 41028 (8, 15–78 mm, Monterey Bay, CS). *†USNM 27397 (1, 159 mm, Point Reyes, *Icichthys lockingtoni*); *†USNM 89398 (3, 28–65 mm, Monterey Bay, *Centrolophus californicus* Hobbs). WHOI (2, 17, 83 mm, Monterey Bay, received through Giles Mead).

Seriolella

S. *brama* Günther: †AMS IA. 10170 (1, 233 mm, Sydney Harbour, New South Wales); †AMS I. 10333 (1, 152 mm, 40 miles W Kingston, South Australia). *BMNH (1, 298 mm, New Zealand, stuffed, *Neptomenus brama* Günther).

S. *punctata* (Bloch and Schneider): †AMS I. 10840 (1, 192 mm, Oyster Bay, Tasmania); †AMS I. 14747 (1, 220 mm, Portobello). *†BMNH 1869. 2. 24. 42–44 (3, 234–243 mm, Tasmania, *Neptomenus dobula* Günther). USNM 176915 (2, 190, 195 mm, Queensland, gill arch CS); †USNM 176968 (1, 149 mm, New South Wales); †USNM 177109 (2, 197, 203 mm, New South Wales).

S. *porosa* Guichenot: †USNM 176478 (1, 218 mm, Tictoc Bay, Chile); †USNM 176535 (1, 198 mm, Puerto Auchemo, Chile); †USNM 176593 (3, 197–203 mm, Auellon, Chile).

S. *violacea* Guichenot: †MCZ 17239 (2, 430, 445 mm, Callao, Peru). *SU 9590 (1, 262 mm, Callao, Peru, paratype *Neptomenus crassus* Starks). *†USNM 53465 (1, 265 mm, Callao, Peru, *Neptomenus crassus* Starks); †USNM 77513 (1, 130 mm, Mellendo, Peru); †USNM 77593 (1, 150 mm, Mellendo, Peru, gill arch CS); †USNM 77611 (1, 173 mm, Callao, Peru); †USNM 77625 (1, 213 mm, Callao, Peru). †ZMC (1, 87 mm, 14°S 77°W).

Psenopsis

P. *anomala* (Temminck and Schlegel); ABE 60-1232, 63-752, 63-1141 (3, 93–119 mm, Manazuru market); ABE 62-656 (1, 40 mm, Japan, CS); ABE 61-590 (1, 160 mm, Tsubaki); ABE 64-1223 to 1225 (25, 43–84 mm, 32°09′N 123°15′E); ABE 64-1972 to 1959 (8, 17–52 mm, Kozu); ABE 64-2014 to 2017, 64-2142 to 2144, 64-2148 to 2150 (14, 7.5–93 mm, off Misaki); ABE 64-2037 to 2039 (3, 30–42 mm, Amakusa Island); ABE, plankton collection (9, 7–28 mm, East China Sea); ABE (1, 150 mm, Tokyo market, gill arch CS). BC 56-29 (1, 136 mm, Tokyo market); BC 59-555 (1, 138 mm, Aberdeen market). CNHM 57288 (3, 91–124 mm, Kobe). †MCZ 1186 (2, 122, 143 mm, Kanagawa); MCZ 31150 (1, 125 mm, Yenosima). †USNM 6424 (1, 149 mm, Hong Kong); †USNM 49465, 71131, 151829 (3, 146–156 mm, Tokyo market); †USNM 59618 (1, 141 mm, Matsushima Bay); †USNM 177426 (2, 132, 142 mm, Taipei market).

P. *cyanea* Alcock: *†BMNH 1890. 11. 28. 9 (1, 120 mm, Ganjam Coast, India, *Bathyseriola cyanea* Alcock); †BMNH 1937. 6. 28. 1–8 (9, 103–110 mm, off Cananore).

Psenopsis sp.: †USNM 98818 (1, 132 mm, Maré Island, Dutch East Indies).

Cubiceps

C. *athenae* Haedrich: *†MCZ 42974 (1, 68 mm, 38°36′N 71°24′W, *Cubiceps athenae* Haedrich). *†USNM 198058 (1, 81 mm, 28°54′N 88°18′W, paratype *Cubiceps athenae* Haedrich). WHOI (1, 33 mm, 24°21′N 81°15′W, CS).

C. *caeruleus* Regan: *†BMNH 1913. 12. 4. 28–29 (2, 86, 95 mm, Three King's Isl., New Zealand, *Cubiceps caeruleus* Regan); BMNH 1926. 6. 30. 50 (1, 282 mm, Lord Howe Isl., Tasman Sea).

C. *capensis* (Smith): *BMNH (1, 905 mm, South Africa, *Atimostoma capensis* Smith, stuffed); †BMNH 1925. 10. 14. 1–4 (3, all *ca.* 160 mm, 70 mi. WNW Saldanha Bay, South Africa).

C. *carinatus* Nichols and Murphy: CNHM 61958 (5, 93–99 mm, 83°15′W 5°15′N); †CNHM 61939 (2, both 110 mm, 125 mi. SW Cape Mala, Panama). SIO 63-538 (1, 101 mm, 21°35′N 107°00′W); SIO 63-882, 63-888, 63-892 (4, 65–101 mm, Golfo de Tehuantepec); SIO 63-1027 (1, 91 mm, 13°33′N 95°59′W); SIO H 49–77 (1, 87 mm, off El Salvador); SIO H 52-351 (2, 90, 94 mm, 13°45′N 99°22′W). ZMC (1, 57 mm, 11°52′N 97°19′W); ZMC (2, 64, 71 mm, 12°14′N 97°46′W); ZMC (1, 70 mm, 12°38′N 98°14′W); ZMC (1, 72 mm, 13°00′N 98°41′W); ZMC (1, 71 mm, 13°41′N 97°34′W).

C. *gracilis* Lowe: †BMNH 63. 12. 12. 7–8 (2, 143, 150 mm, Madeira); BMNH 1960. 12. 19. 8 (1, 165 mm, 51°51′N 13°43′W). CF (5, 40–57 mm, DANA sta. 855); CF (2, 50, 59 mm, DANA sta. 856); CF (26, 5–35 mm, DANA sta. 939, one CS); CF (1, 69 mm, DANA sta. 1372); CF (1, *ca.* 70 mm, DANA sta. 1378); CF (1, 77 mm, DANA sta. 1380); CF (1, 43 mm, DANA sta. 4017, CS); CF (4, 43–76 mm, DANA sta. 4185); CF (18, 16–80 mm, DANA sta. 4192); CF (37, 11–61 mm, DANA sta. 4195);

CF (50, 10–58 mm, DANA sta. 4197). *MNHN 42-29 (1, 195 mm, Sète, *Trachelocirrhus mediterraneus* Doumet). WHOI (8, 20–51 mm, DELAWARE 63–4 sta. 3); WHOI 12, 25–51 mm, 39°27′N 27°35′W); †WHOI (1, 92 mm, DELAWARE 63–4 sta. 13); †WHOI (2, 75, 81 mm, DELAWARE 63–4 sta. 16).

C. longimanus Fowler: *ANSP 55058 (1, 42 mm, Durban, Natal, *Cubiceps longimanus* Fowler). HOE (1, 29 mm, ANTON BRUUN 6 sta. 338).

C. pauciradiatus Günther: ABE 57-347 (1, 120 mm, Manazuru, Japan); ABE 10832 (1, 80 mm, Kōchi, Japan). *ANSP 68380 (1, 124 mm, 40 mi. S Christmas Isl., Line Islands, *Cubiceps nesiotes* Fowler). *†BMNH 1870. 8. 31. 124 (1, 113 mm, Misol, Molucca Isl., *Cubiceps pauciradiatus* Günther). SIO 60-216 (1, 93 mm, 10°26′N 128°22′W).

C. squamiceps (Lloyd): ABE 57-348, 59-37, 61-843, 62-13, 62-106 (5, 84–154 mm, Manazuru, Japan); ABE 64-1348 (1, 264 mm, 6°15′N 164°10′W); ABE 10833 (1, 159 mm, Kōchi, Japan).

Nomeus

N. gronovii (Gmelin): ABE 64-1280 (1, 68 mm, Kushimoto, Japan); ABE plankton collections (5, 8–38 mm, Japan). BCF 1002 (1, 61 mm, 3°41′N 0°05′E); BCF 1003 (1, 40 mm, GERONIMO 4-155). BOC 602 (6, 17–101 mm, Key West Harbor); BOC 3361 (21, 10–118 mm, Atlantic Ocean); BOC 3515 (22, 13–149 mm, Gulf of Mexico); †BOC 3516 (8, 31–153 mm, Gulf of Mexico); BOC 3517 (14, 16–133 mm, 28°07′N 89°53′W); BOC 3518 (11, 13–114 mm, Atlantic Ocean). †CNHM (1, 225 mm, OREGON sta. 1178). HOE (4, 20–45 mm, 2°20′N 65°54′E); HOE (9, 12–41 mm, 8°00′S 65°00′E). †MCZ 35327 (2, 144, 154 mm, 39°27′N 70°38′W gill arch CS). *MNHN 264. 6. 2. 3 (3, largest *ca.* 42 mm, seas of Java, *Nomeus peronii* Cuvier and Valenciennes). SIO 60-263 (4, 22–40 mm, 5°18′N 160°05′W); SIO 61-84 (2, 20, 25 mm, 5°58′S 149°31′W); SIO 61-87 (1, 33 mm, 1°32′S 148°39′W); SIO 61-89 (3, 32–41 mm, 5°32′N 146°09′W). WHOI (2, 45, 66 mm, 17°00′N 65°05′W, CS).

Psenes

P. arafurensis Günther: ABE 60-101 (1, 72 mm, Manazuru, Japan); ABE 62-651 (1, 35 mm, Japan, CS); ABE 64-212 (1, 150 mm, Nagasaki); ABE 64-1767 (1, 92 mm, Komatsubara, Japan); ABE, plankton collection (2, 19, 37 mm, East China Seas). *†BMNH 1889. 7. 20. 55 (1, 30 mm, China Seas, *Psenes arafurensis* Günther). HOE (1, 25 mm, 2°20′S 64°54′E); HOE (1, 20 mm, 4°01′S 65°02′E). MCZ 41550 (5, 14–18 mm, 10°52′N 29°26′W). WHOI (1, 20 mm, 41°33′N 54°55′W).

P. benardi Rossignol and Blache: *MNHN 264. 9. 1. 1 (1, 63 mm, 3°38′S 9°22′E, *Psenes benardi* Rossignol and Blache); *MNHN 264. 9. 1. 2 (2, 63, 65 mm, 1°55′S 8°30′E, paratypes, *Psenes benardi* Rossignol and Blache).

P. cyanophrys Cuvier and Valenciennes: *†BMNH 1871. 7. 20. 156 (1, 111 mm, Manado, Philippines, *Cubiceps multiradiatus* Günther). CF (1, 28 mm, Dansk Vestindien sta. 132, CS). *†MNHN 264. 9. 2. 4 (1, 117 mm, New Ireland, Bismarck Archipelago, *Psenes cyanophrys* Cuvier and Valenciennes). CNHM 46409 (1, 80 mm, 25°N 89°W). WHOI (1, 38 mm, CRAWFORD 62, CS). †WHOI (2, 119, 128 mm, OREGON sta. 3715, gill arch CS).

P. maculatus Lütken: ABE 64-1226 (1, 20 mm, Japan): ABE plankton collection (1, 20 mm, East China Sea). CF (1, 48 mm, 15°31′N 18°05′W). †MCZ 41122 (1, 59 mm, 40°49′N 64°57′W). WHOI (1, 27 mm, 38°26′N 68°15′W); WHOI (1, 35 mm, 41°36′N 60°30′W). *†ZMC (2, 57 and 72 mm, 39°00′N 34°10′W, *P. maculatus* Lütken).

P. pellucidus Lütken: ABE 59-172, 60-102, 60-106, gill arch CS, 60-140 and 141, 61-21, 61-82 and 83, 61-459 (13, 72–147 mm, Manazuru, Japan); ABE 63-1064 (1, 89 mm, Tokyo market). †BCF 957 (1, 130 mm, 4°07′S 10°23′E). CF (1, 60 mm, 15°31′N 18°05′W); CF (1, 39 mm, ACENT PETERSEN sta. 769, CS). CNHM 5285 (1, 54 mm, Bermuda); †CNHM 49189 (1, 131 mm, Bermuda); *†CNHM 57097 (1, 193 mm, Okinawa, *Icticus ischanus* Jordan and Thompson). *†USNM 49745 (1, 67 mm, Newport, Rhode Island, *Psenes edwardsii* Eigenmann). SU 43310 (1, 93 mm, Bermuda). WHOI (1, 25 mm, 38°38′N 68°50′W). *†ZMC (1, 38 mm, Surabaya, *P. pellucidus* Lütken).

Ariomma

A. africana (Gilchrist and von Bonde): *†BMNH 1927. 12. 6. 45 (1, 166 mm, Agulhas Bank, South Africa, co-type, *Psenes africanus* Gilchrist and von Bonde).

A. bondi Fowler: *ANSP 52528 (1, 79 mm, Grenada, British West Indies, *Ariomma bondi* Fowler).

A. dollfusi (Chabanaud): *†BMNH 1931. 4. 16. 1 (1, 112 mm, Gulf of Suez, co-type, *Cubiceps dollfusi* Chabanaud).

A. evermanni Jordan and Snyder: *†USNM

57783 (1, 156 mm, Honolulu, Hawaii, *Ariomma evermanni* Jordan and Snyder).

A. *indica* (Day): BC 59-555 (1, 151 mm, Aberdeen market, Hong Kong). *†BMNH 1889. 2. 1. 3255–6 (2, 74, 90 mm, Madras, India, *Psenes indicus* Day). NTU 51941 to 51946 (6, 123–181 mm, near Hainan Island, gill arch CS).

A. *lurida* Jordan and Snyder: *SU 8441 (1, *ca.* 190 mm, Honolulu, Hawaii, paratype *Ariomma lurida* Jordan and Snyder). *†USNM 51400 (1, 166 mm, Honolulu, Hawaii, *Ariomma lurida* Jordan and Snyder); †USNM 109418 (1, 193 mm, Honolulu).

A. *melana* (Ginsburg): *†USNM 157779 (1, 154 mm, Mississippi Delta, *Cubiceps melanus* Ginsburg).

A. *multisquamis* (Marchal): *MNHN 264. 7. 2. 1 (type), 264. 7. 2. 2 (paratype) (2, 159, 147 mm, Ivory Coast, *Paracubiceps multisquamis* Marchal).

A. *nigriargenteus* (Ginsburg): *MCZ 37183 (1, 113 mm, Sandwich, Massachusetts, paratype *Cubiceps nigriargenteus* Ginsburg). *†USNM 151954 (1, 190 mm, off Cape Romain, South Carolina, *Cubiceps nigriargenteus* Ginsburg).

A. *regulus* (Poey): †USNM 197110 (2, 142, 150 mm, British Guiana). †WHOI (1, 136 mm, 29°59′N 87°06′W).

Ariomma sp. Western North Atlantic: MCZ 40259 (1, 116 mm, Provincetown, Massachusetts); MCZ 40498 (1, 115 mm, Provincetown, Massachusetts). SU 57297 (1, 86 mm, Bermuda). WHOI (3, 87–121 mm, OREGON sta. 3725); WHOI (2, 103, 109 mm, OREGON sta. 3733); WHOI (3, 122–134 mm, OREGON sta. 4014); WHOI (1, 143 mm, 9°03′N 81°22′W); WHOI (2, 141, 149 mm, 9°13′N 80°44′W); WHOI (3, 139–140 mm, 16°45′N 81°27′W); WHOI (3, 131–140 mm, 28°57′N 88°41′W); WHOI (2, 125, 133 mm, 29°07′N 88°34′W); WHOI (3, 130–140 mm, 28°54′N 88°51′W, gill arch CS); WHOI (1, 23 mm, CRAWFORD 62 sta. 29, CS); WHOI (1, 28 mm, 24°N 81°W, CS).

Ariomma sp. Japan: ABE 59-404, 59-408, 60-124, 60-144, 60-224, 60-478 and 479, 60-1611, 61-1188, 62-738, 62-955, 62-1387, 62-1628 (13, 99–226 mm, Manazuru, Japan). NRF 1441 (1, *ca.* 800 mm, Bonin Islands).

Tetragonurus

T. *atlanticus* Lowe: *†BMNH (1, 197 mm, Madeira, *Tetragonurus atlanticus* Lowe). MCZ 41726 (1, 21 mm, 39°47′N, 70°32′W, CS); MCZ 41791 (1, 66 mm, 39°41′N 69°54′W, CS). WHOI (2, 15, 20 mm, tropical Atlantic).

T. *cuvieri* Risso: CNHM 64218 (1, 340 mm, 46°51′N, 155°00′W, gill arch CS).

Stromateus

S. *brasiliensis* Fowler: *ANSP 11354 (1, 276 mm, Rio Grande do Sul, Brazil, *Stromateus brasiliensis* Fowler). †MCZ 4599 (3, 254–285 mm, Rio Grande do Sul, Brazil).

S. *fiatola* Linnaeus: †BMNH 87. 3. 2. 30 (1, 76 mm, Lower Congo). †GTS (6, 200–240 mm, 7°20′N 12°40′W). †MCZ 16729 (1, 257 mm, Mediterranean?). †SU 1537 (1, 44 mm, Palermo, Italy). †USNM (1, 177 mm, Fed. Fish. Serv. Nigeria, No. 4046).

S. *stellatus* Cuvier: †USNM Acc. No. 167496 (2, 230, 237 mm, 42°29′S 72°46′W). *MNHN 264. 11. 3. 1–2 (2, 144, 164 mm, Valparaiso, Chile, *Stromateus maculatus* Cuvier and Valenciennes). †USNM 176474 (3, 178–250 mm, Calbucco, Chile); †USNM 176494 (1, 193 mm, 41°52′S 73°53′W).

Peprilus

P. *alepidotus* (Linnaeus): †USNM 127352, 127353 (2, 122, 141 mm, Grand Terre, La.); †USNM 23215 (1, 130 mm, Bay Chaland, La.). WHOI (1, 39 mm, SILVER BAY sta. 4331, CS).

P. *palometa* (Jordan and Bollman): *†USNM 41136 (5, 53–61 mm, Perlas Isl; Panama, *Stromateus palometa* Jordan and Bollman; †USNM 50337 (2, 136, 169 mm, Panama).

P. *paru* (Linnaeus): †MCZ 4600 (1, 55 mm, Brazil); †MCZ 41064 (2, 48, 57 mm, Port-au-Prince, Haiti). *MNHN (1, 93 mm, Rio de Janeiro, *Seserinus xanthurus* Quoy and Gaimard).

P. *simillimus* (Ayres): †MCZ 26875 (1, 110 mm, San Diego, Calif.). †SU 48000 (1, 82 mm, Oceanside, California).

P. *snyderi* Gilbert and Starks: *†BMNH 1903. 5. 15. 190 (1, 217 mm, Panama, co-type *Peprilus snyderi* Gilbert and Starks). *†USNM 50448 (1, 189 mm, Panama, *Peprilus snyderi* Gilbert and Starks). †USNM 76796 (1, 178 mm, Panama City).

P. *triacanthus* (Peck): †ABE 64-1920, 1924, 1930 (3, 80–110 mm, Florida). †WHOI (7, 157–195 mm, SILVER BAY sta. 4104); †WHOI (4, 127–155 mm, 40°01′N 71°23′W); †WHOI (1, 120 mm, Woods Hole, gill arch CS); WHOI (1, 36 mm, BEAR 188 sta. 371, CS).

Pampus

P. *argenteus* (Euphrasen): †ABE 64-1231, 1233 (2, 105, 147 mm, Bangkok); †ABE 64-1929 (1, 133 mm, Hong Kong); †ABE 1936, 1937

(2, 48, 72 mm, off mouth of Shiota River, Ariake Sound, Kyushu, CS); †ABE 64-1964 (1, 156 mm, East China Sea); †ABE P 4347 (1, 92 mm, Sarawak, North Borneo). †HOE (6, 65–161 mm, Bombay). †USNM 44900 (1, 299 mm, Japan).

P. chinensis (Euphrasen): †ABE 64-1229 (1, 89 mm, Bangkok); †ABE P 2211, P 4319 (2, 77, 112 mm, Sarawak, North Borneo). †CNHM 15917 (1, 74 mm, Batavia, Java). †MCZ 16772 (1, 84 mm, Singapore).

P. echinogaster (Basilewsky): †ABE 64-902, 64-906, 64-909, 64-911, 64-926, 64-1192 (5, 165–207 mm, East China Sea); †ABE 64-1112 (1, 221 mm, Tokyo market); †ABE 1743 (1, *ca.* 180 mm, Tokyo market, gill arch CS); †ABE 64-1934 (1, 158 mm, south of Poi Toi Isl., Hong Kong). †CNHM 55810 (3, 81–106 mm, Chinnampo, Korea). †SU 22292 (3, 77–87, Chinnampo, Korea). †USNM 75941 (1, 236 mm, Japan?).

In addition to stromateoid fishes, the following non-stromateoids were examined:

- Apolectidae
  - *Apolectus* [= *Parastromateus*] *niger* MCZ 15912 (3, Singapore).
- Arripididae
  - *Arripis trutta* ZMC 74.P.475 (3, New Zealand).
- Atherinidae
  - *Menidia* sp. WHOI (2, Morehead City).
- Carangidae
  - *Caranx hippos* WHOI (1, Woods Hole). *Naucrates ductor* WHOI (1, ATLANTIS sta. 219). *Selar crumenopthalmus* WHOI (1, Woods Hole). *Trachinotus glaucus* WHOI (1, Trujillo, Honduras).
- Coryphaenidae
  - *Coryphaena equiselis* WHOI (1, OREGON sta. 1297).
- Ephippidae
  - *Platax ocellatus* MCZ 2748 (1, Manila).
- Icosteidae
  - *Icosteus aenigmaticus* BC 63-98 (1, Alaska); BC 64-12 (1, Spiller Channel). MCZ 34915 (1, California). SU 1171 (1, Pacific Grove); SU 25640 (1, Monterey Bay). *USNM 27398 (1, Point Reyes); USNM 75159 (1, Pacific Grove).
- Girellidae
  - *Boops vulgaris* MCZ 21706 (1, France). *Girella nigricans* MCZ 10775 (1, California).
- Kuhliidae
  - *Kuhlia malo* MCZ 29367 (1, Papeete).
- Kyphosidae
  - *Kyphosus sectatrix* WHOI (2, 32°08'N 67°10'W). *Pimelepterus boscii* MCZ 2610 (1, Florida).
- Monodactylidae
  - *Monodactylus argenteus* MCZ 34101 (1, Dar es Salaam).
- Nematistiidae
  - *Nematistius pectoralis* BC 60-15 (1, Acapulco market).
- Pomatomidae
  - *Pomatomus saltatrix* MCZ 16941 (5, New Jersey). WHOI (5, Woods Hole).
- Scomberesocidae
  - *Scomberesox saurus* WHOI (1, 40°12'N 62°54'W).
- Scombridae
  - *Auxis thazard* WHOI (1, 41°16'N 57°37'W). *Scomber scomber* WHOI (1, Quisset, Mass.).
- Scorpididae
  - *Scorpis californiensis* MCZ 4896 (2, California).
- Theraponidae
  - *Autisthes puta* WHOI (2, Australia, received through James Moulton). *Pelates* sp. WHOI (2, Australia, received through James Moulton). *Therapon jarbua* MCZ 24823 (2, Java).
- Zaproridae
  - *Zaprora silenus* BC 61-573 (1, Cross Sound, Alaska).

SYSTEMATIC SECTION

In the classification which follows, the suborder, the families, and the genera are characterized. Categories below the genus are not. In a number of cases, subgeneric division is certainly called for. This action is not taken here, but is reserved for critical treatment in a planned series of monographs. Likewise, the proper sorting of species is left for the future. As a preliminary step in clarifying the confusion which surrounds stromateoid classification, however, lists of nominal species are included under each genus. Species synonymies, whenever given, are to be considered tentative.

The synonymy of the suborder is fairly complete and is intended as a guide to most works, especially those of a faunistic nature, that include references to stromateoids. Distributional notes concerning single or very few species, however, have not been included. The synonymies of each family contain only major references. Family names have been used with such confusion in the past that complete synonymies would be essentially meaningless.

Included under each taxon are: synonymy, diagnosis or brief characterization, description, distribution (suborder, families), natural history (suborder, genera), relationships, and key to included taxa or list of nominal species. An asterisk (*) precedes the names of species of which I have seen the types.

Suborder STROMATEOIDEI

Stromatini. Rafinesque, 1810:39 (*Stromateus*, *Luvarus*).

Stromateini. Bonaparte, 1846:76 (*Stromateus*, *Peprilus*, *Luvarus*, *Kurtus*).

Stromatiniae. Swainson, 1839:177 (*Seserinus*, *Stromateus*, *Peprilus*, *Kurtus*, *Keris*).

Stromateina. Günther, 1860:397 (+ Nomeina p. 387, def., *Stromateus*, *Centrolophus*, *Gasterochisma*, *Nomeus*, *Cubiceps*, *Neptomenus*, *Platystethus*, *Ditrema*).

Stromateidae. Gill, 1884:665 (def., gen. synopsis, *Centrolophus*, *Schedophilus*, *Lirus*, *Stromateus*, *Stromateoides*, *Psenopsis*). Day, 1875:246 (+ Nomeidae, p. 237. descr.; India). Jordan and Gilbert, 1882:449 (key, descr.; North America). Fordice, 1884: 311 (key, synon.; America). Collett, 1896:26 (+ Nomeidae, p. 31. descr.; eastern Atlantic). Goode and Bean, 1896:213 (descr.; oceanic spp.). Regan, 1902: 117 (major revision, *Nomeus*, *Cubiceps*, *Psenes*, *Seriolella*, *Psenopsis*, *Centrolophus*, *Lirus*, *Stromateus*, *Peprilus*, *Stromateoides*). Holt and Byrne, 1903:71 (key, descr.; British Isles). Boulenger, 1904:643 (popular account). Smith, 1907:221 (key, descr.; North Carolina). Miranda-Ribeiro, 1915 (key, descr.; Brazil). Gilchrist, 1922:249 (papillae). Gilchrist and von Bonde, 1923:1 (descr.; South Africa). Meek and Hildebrand, 1925:407 (key, descr.; Panama). Bühler, 1930:62 (digestive system). Fowler, 1936:658 (key, descr.; West Africa). Fowler, 1941:152 (+ Nomeidae, list; Brazil). Fowler, 1944:78 (+ Centrolophidae, p. 79; Nomeidae, p. 80. descr.; Chile). Hildebrand, 1946:416 (descr.; Peru). Barnard, 1948:394 (descr., sacs and papillae; South Africa). Smith, 1949:302 (key, descr.; South Africa); 1949a:839 (revision; South Africa). Lozano y Rey, 1952:648 (descr.; Iberia). Mori, 1952:138 (+ Nomeidae, list; Korea). Bigelow and Schroeder, 1953:363 (+ Centrolophidae, p. 369, descr.; Gulf of Maine). Herre, 1953:258 (+ Nomeidae. list, synon.; Philippines). Tchang *et al.*, 1955:195 (descr.; Gulf of Pechili, Yellow Sea). Poll, 1959:125 (descr.; West Africa). Blache, 1962:70 (list; West Africa). Lowe, 1962:694 (list; British Guiana). Chu *et al.*, 1963:407 (descr.; East China Sea).

[Stromateidae.] Lütken, 1880:513, 521 (disc. gen., oceanic spp.). Günther 1889:10 (disc. gen., descr.; CHALLENGER). Nobre, 1935:332 (descr.; Portugal). Okada, Uchida, and Matsubara, 1935:123 (descr., ill.; Japan). Kamohara, 1940:173 (descr.; Japan).

Nomeiformes. Gregory, 1907:502 (relationships).

Stromateiformes. Jordan, 1923:182 (list, fam., gen.). Jordan, Evermann, and Clark, 1930: 226 (list, synon.; North America).

Centrolophidae. Fowler, 1928:138 (descr.; Pacific); 1931:325 (descr.; add. Pacific); 1934: 403 (descr.; add. Pacific); 1949:75 (descr.; add. Pacific). Norman, 1937:115 (+ Stromateidae, p. 118. descr.; Patagonia). Sanz-Echeverria, 1949:151 (otoliths). Tortonese, 1959:57 (revision; Gulf of Genoa).

Stromateoids. Gregory, 1933:306 (skull of *Rhombus* [= *Peprilus*]).

Stromateoidei. Berg, 1940:324 (def., fam. synopsis); 1955:247 (def., fam. synopsis). Bertin and Arambourg, 1958:2441 (fam., gen. synopsis). Munro, 1958: 117 (descr.; Australia). Duarte-Bello, 1959:119 (list; Cuba). Gosline and Brock, 1960:281 (descr.; Hawaii). Chu *et al.*, 1962:759 (descr.; South China Sea). Scott, 1962:142 (key, descr.; South Australia).

Stromateoidea. Blegvad and Løppenthin, 1944:178 (descr.; Iranian Gulf). Beaufort and Chapman, 1951:85 (descr.; Indo-Australian Archipelago). Norman, 1957:216 (fam., gen. synopsis, after Regan). Herald, 1961:243 (popular account). Marshall, 1964:398 (key, descr.; Eastern Australia).

Stromateoidae. Clemens and Wilby, 1961:230 (descr.; British Columbia).

Distinctive characters. There is no mistaking the "stromateoid look." Though the characters given in the diagnosis are the only ones that absolutely identify a member of the suborder, these fishes nonetheless have a physiognomy that nine times out of ten says "Stromateoid!" to an experienced ichthyologist. Once recognized, the stromateoid expression is not likely to be forgotten. It is a fat-nosed, wide-eyed, stuffed-up look, smug and at the same time apprehensive. Some stromateoids might even be accused of a certain prissiness.

The stromateoid look results from the expanded lacrimal bone all but covering the maxillary, the slightly underslung lower jaw shutting within the upper, the large centrally located eye rimmed with adipose tissue, and the protruding, inflated, naked, and pored snout and top of the head.

Diagnosis. Perciform fishes with toothed saccular outgrowths in the gullet immediately behind the last gill arch. Small teeth approximately uniserial in the jaws.

Description. Body slender to deep, compressed or rounded. Dorsal fin single or double; dorsal spines present, very weak in some species. One to three anal spines, never separated from the rays. Dorsal and anal fins coterminal. Pelvic fins present or absent. Rays in pectoral fin 16 to 25. Body scaled, snout and top of head naked. Scales usually thin, cycloid, deciduous, but very weakly ctenoid in some nomeids and *Schedophilus medusophagus*, and heavy, keeled, and adherent in *Tetragonurus*. Scales usually covering bases of median fins. Lateral line present, the scales with simple tubes, except no tubed scales in *Tetragonurus*. No bony scutes or keels associated with lateral line. Usually a well developed subdermal mucous canal system communicating to the surface through small pores liberally scattered over head and body. Eyes small to large, lateral, not entering into profile of head. Nostrils double, the anterior round, the posterior usually a vertical slit. Jaw teeth small, simple or minutely cusped, arranged more or less in a single series, close-set or spaced. Teeth on vomer, palatines, and basibranchials present or absent. No teeth on entopterygoid or metapterygoid. Small teeth usually present on inner edge of gill-rakers. Gills 4, a slit behind the fourth. Gill-rakers 10 to 20 on lower limb of first arch. Well developed pseudobranch usually present, but absent in *Pampus*; rudimentary gill-rakers under pseudobranch commonly present. Gill-membranes usually free from isthmus, but united in *Pampus*.

Skeleton never strongly ossified. Epiotic forked, orbitosphenoid absent, 15 principal branched rays in caudal fin. Pelvic fin, when present, with one spine, five rays. A bony bridge partially covering the anterior vertical canal of the ear. Opercular bones thin, denticulate or entire, never with strong spines, except moderate preopercular spines in *Schedophilus*. No bony stay for the preopercle. Five to seven branchiostegal rays. Lacrimal bone usually enlarged, often covering maxillary almost completely. Lacrimal absent in *Pampus*. Premaxillary scarcely if at all protractile. A slender supramaxillary present or absent. Pelvic bones not firmly attached to coracoid. Vertebrae 25, 26, or 29 to 60, including hypural. Caudal skeleton with two to six hypural elements, two or three epural elements, two autogenous haemal spines, except three in *Icichthys*, hypuropophysis present on first hypural. Sometimes two but usually three free interneurals ahead of dorsal fin, but six or more in *Icichthys*. Lower pharyngeal bones not united, partially supporting pharyngeal sacs. In the sacs, numerous simple teeth on irregularly-shaped or stellate bony bases [= papillae] seated in the muscular walls, arranged in longitudinal bands or not.

Distribution. All stromateoid fishes are marine. They are found in the three major oceans of the world on the high seas, over the continental shelves, and in large bays. Most species live in tropical and temperate waters, but a few occur in colder areas. No stromateoids have been reported from the Arctic Ocean, the Bering Sea, the Okhotsk Sea, the Baltic Sea, the Black Sea, and the Antarctic Ocean.

Natural history. The association between stromateoid fishes and medusae or siphonophores is widely known and well documented. Mansueti (1963) has reviewed the literature concerning this unusual association. His lists of all fish species involved is made up largely of stromateoids, and includes centrolophids, nomeids, tetragonurids, and stromateids. Only one ariommid has been reported from under a jellyfish, a 36-mm *Ariomma indica* taken in a 305-mm diameter ctenophore in Durban Bay, Natal (Fowler, 1934a).

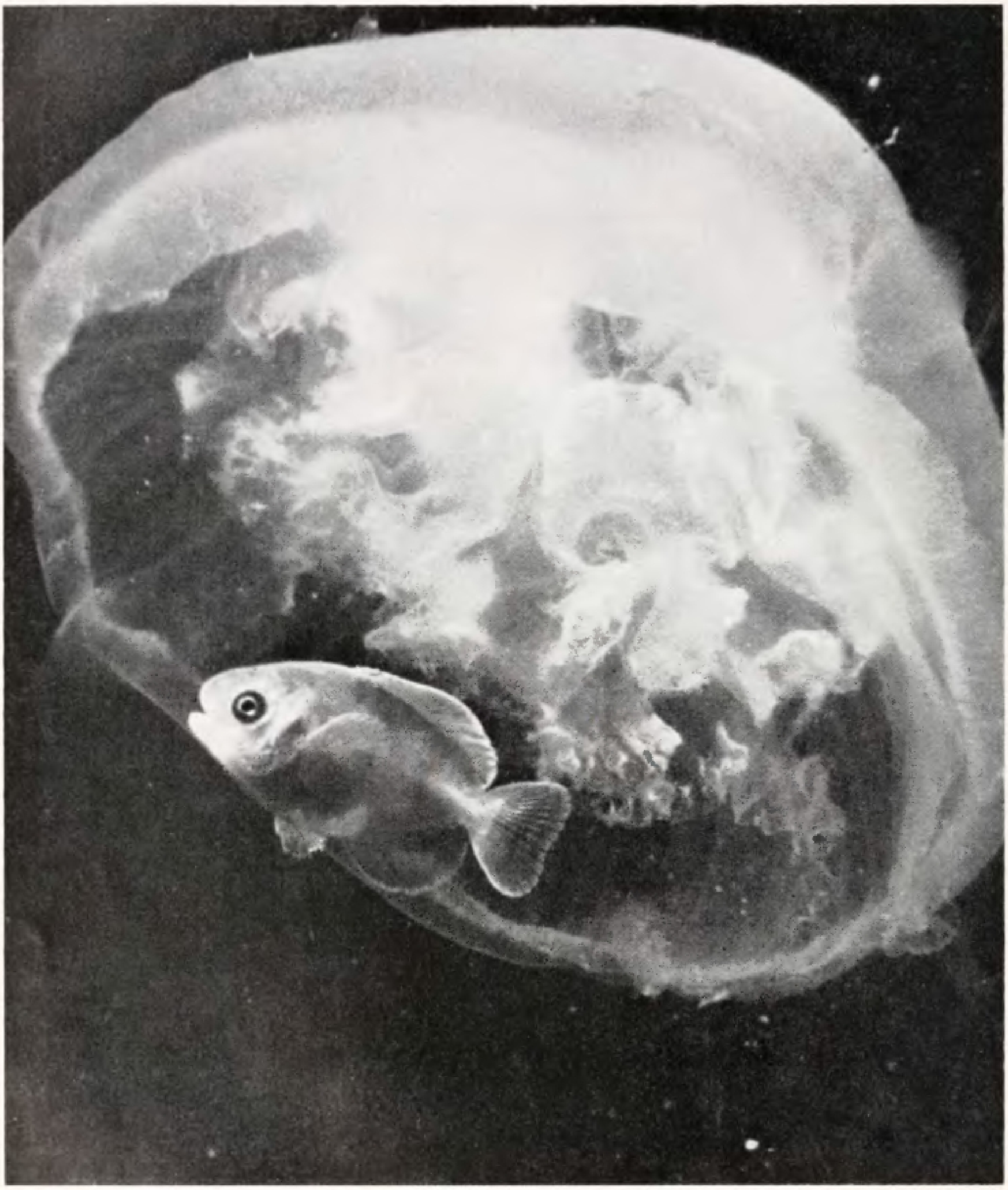

Plate 1. A young stromateoid, *Psenopsis anomala*, under a medusa. Iwago photo.

Young stromateoids are pelagic, and it is not surprising that it is the young stages that are found with jellyfishes. As they grow older, the fishes desert their surface-living host, and descend to deeper layers, the adult habitat. Stromateoids also hover beneath flotsam and *Sargassum* weed (Besednov, 1960). It is this characteristic

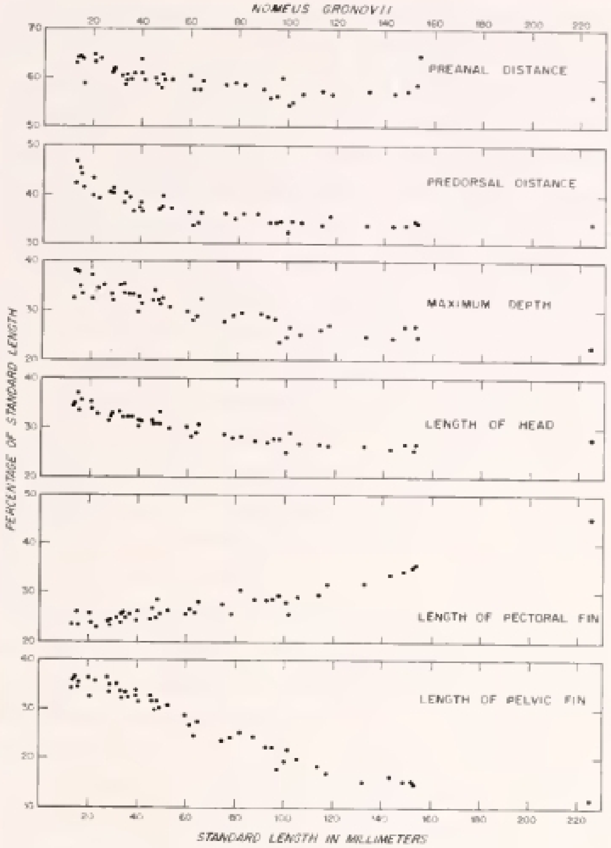

Figure 3. Scatter diagram of the allometric growth in the nomeid *Nomeus gronovii*.

habit which gives the barrelfish, *Hyperoglyphe,* its common name. Young stromateoids typically have a banded pattern, whereas adults tend to be plain. Undoubtedly, the banding is protective coloration for the fishes during that period of their lives when they live in the shifting shadows under a jellyfish.

Shelter is not all the jellyfish provide. Many stromateoids have been observed actively feeding on their hosts (*Schedophilus*, Maul, 1964; *Nomeus*, Kato, 1933; *Peprilus*, Mansueti, 1963, photo p. 63). The diagnostic pharyngeal sacs of stromateoids may have been perfected partially in response to this sort of diet. *Tetragonurus*, one of the most highly specialized stromateoids with great slicing teeth and a long pharyngeal sac, may feed almost entirely on soft-bodied medusae, ctenophores, and salps (Grey, 1955).

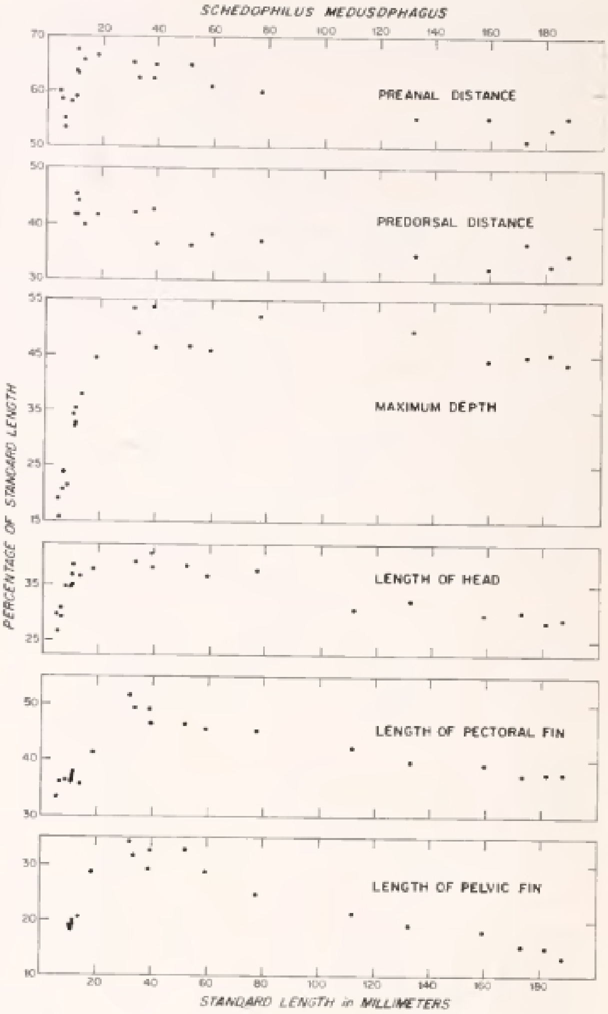

Figure 4. Scatter diagram of the early growth in the soft-spined centrolophid *Schedophilus medusophagus*, a fish which grows to 500 mm SL.

Stromateoids do show high resistance to the toxins of jellyfish (Lane, 1960; Maul, 1964) but they are by no means immune to it (Garman, 1896; Totton, 1960). Besides the relatively high resistance to the toxins, simple avoidance of the tentacles and the characteristic heavy coating of slime probably are important in allowing the fishes to swim with impunity under their hosts.

Because of the efficient shredding of food by the papillae, stomach contents of stromateoids are largely unidentifiable. Shredded transparent tissues, probably from jellyfish, ctenophores, and salps, predominated in stomachs examined. But I have also

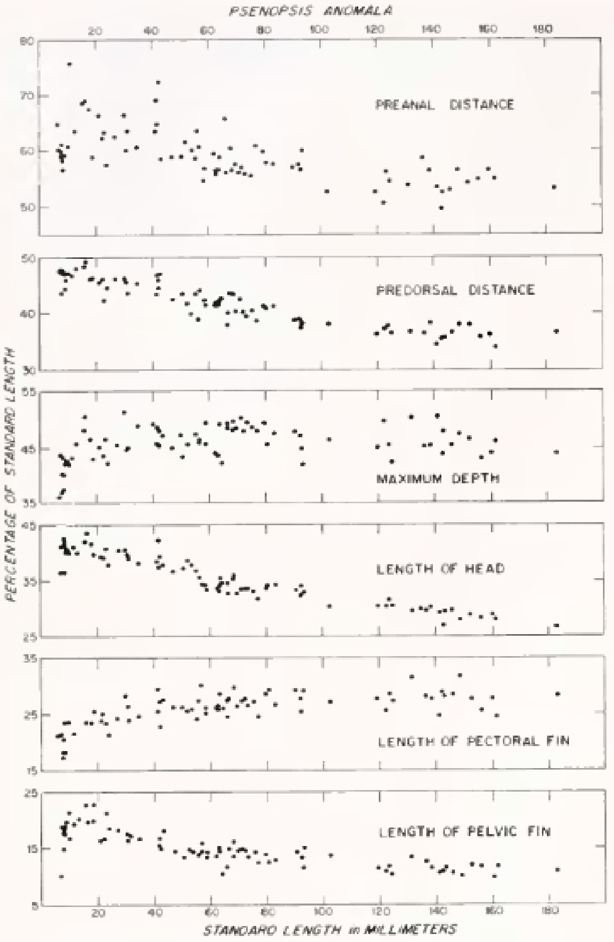

Figure 5. Scatter diagram of the growth in the hard-spined centrolophid *Psenopsis anomala*.

found remains of fishes, large crustaceans, and, rarely, squids.

With growth, marked changes occur. The fish are no longer in the immediate upper layers, but tend to live deeper in the water. The typically banded pattern of the young fish gives way to the plainer colors of the adult. The most pronounced changes are in relative proportions. Allometry is the rule among stromateoids. Generally, the relative length of the head, length of the pelvic fins, predorsal distance, and preanal distance increase rapidly, then decrease with growth. The relative length of the pectoral fin and the maximum depth may increase steadily, or increase and then decrease. Allometry is especially marked in nomeids (Fig. 3), most of which have a similar pattern of growth, and centrolophids (Figs. 4, 5). The growth curves given for *Tetragonurus* (Grey, 1955) are fairly regular, and rarely show a range of variation exceeding ten per cent. McKenney's (1961) curves for *Ariomma*, perhaps based on two species, likewise show regular and little variation. The pectoral fin of the stromateids may relatively lengthen or shorten with age and the fin lobes may be very long in the young, but the allometry is in general not remarkable in this family.

The largest stromateoids are the centrolophids, many of which reach three feet in length. A large *Centrolophus* or *Hyperoglyphe* will exceed four feet. A few nomeids attain two feet, but most are smaller. There is a diminutive species group in the family; its members rarely exceed six inches. Tetragonurids are said to reach two feet in length (Fitch, 1951). The largest reported ariommid was almost three feet long (Klunzinger, 1884), but most seem to be much smaller. A large stromateid barely exceeds 18 inches.

Stromateids, the subjects of substantial fisheries in the eastern United States, India, China, and Japan, and ariommids, with commercial potential but as yet unfished, are schooling fishes. The centrolophids *Psenopsis* and *Hyperoglyphe*, commercial fishes in Japan, and *Seriolella*, fished to a lesser extent in Peru, Chile, and Australia, are also found in shoals. Numerous young specimens of the more oceanic stromateoids are often taken by dipnet collecting, but data is too sparse, and large specimens too few, to know whether these fishes occur in schools or not.

Little is known of the breeding of stromateoids. The eggs are pelagic. Those of *Peprilus triacanthus* are described as buoyant, transparent, and containing a large oil globule (Bigelow and Schroeder, 1953). All species seem dioecious. There is some evidence that the sexes may be slightly dimorphic, with respect to color and/or relative proportions.

Relationships. The stromateoid fishes are a well-defined unit. Pharyngeal sacs are the diagnostic character. These are present in all species, and are readily apparent on dissection. A somewhat similar organ is found in *Dorosoma*, a clupeoid (Miller, 1964), and in *Trisotrophis*, a serranid (Katayama, 1959).

Within the group, there is a broad spectrum from primitive to highly advanced forms. Between existing families, there is evidence of phyletic relationships. The natural coherence of the group and the tendency toward direct internal lines from the generalized to the specialized condition, makes it unlikely that the stromateoids have given rise to other groups. *Tetragonurus*, a highly specialized form, is sometimes placed in a suborder of its own, in which case it would be considered a derived group. *Tetragonurus* is certainly far removed from the mainstream of stromateoid evolution, but its degree of divergence is probably not great enough to warrant subordinal recognition. It retains the characteristic sacs, and is here considered the sole genus of the stromateoid family Tetragonuridae.

Günther (1880) considered the stromateoids a subdivision of the scombroids. Little subsequent attention has been paid to the relationships of the suborder, with the exception of Boulenger (1904) and Holt and Byrne (1903) who found cause for including them in the Percesoces. General classifications have continued to place them near the Scombroidei. There is a close resemblance between some stromateoids and the carangids, a group standing near the base of the scombroid stem (Suzuki, 1962).

Freihofer's (1963) survey of patterns of the *ramus lateralis accessorius* (a facial nerve complex) in fishes indicated that the stromateoids might be related to entirely different groups. His pattern-10 teleosts are a novel assemblage, composed of stromateoids (centrolophids, nomeids, stromateids), pomatomids, kyphosids, scorpidids (excluding *Scorpis*), arripidids, girellids, theraponids, and kuhliids. The nematistiids have a reduced pattern 10.

The pattern of a nerve complex, because of its basically conservative nature, should be a strong taxonomic character in dealing with higher categories. The common pattern of the *ramus lateralis accessorius* in the above families is probably good cause for considering them a phylogenetic unit. But is there additional evidence for lumping these families together? The stromateoids, almost without exception, have a bony bridge across the inside of the anterior vertical canal of the ear. Because of its widespread occurrence in the diverse forms of the suborder, I consider this a conservative character, useful at higher categories. This bridge is also present, at least in some species and at some stage of growth, in pattern-10 families. The bridge is absent, however, in other perciform families examined (see Table 1 and Material examined, p. 43).

Many pattern-10 families have characteristics common to basal perciforms. Many have 25 vertebrae, seven branchiostegal rays, a suborbital shelf, and a caudal skeleton near to the basal perciform type with six hypurals and three epurals. In most, the shape of the body is of the most generalized type. The general impression is of an older group of fishes which have managed to remain successful without diverging too far from the basal stock.

The common *ramus lateralis accessorius* pattern and the bridge over the anterior vertical canal are strong evidence for considering that the relatively specialized stromateoids arose from somewhere in this relatively undifferentiated assemblage. Nonetheless, it is unlikely that the stromateoids are the descendents of any living pattern-10 family, all of which are specialized in some respect. With the present imperfect knowledge of the comparative osteology of these groups, the best that can be said is that all share a common heritage.

The fin spines of stromateoids are not remarkably developed, and the teeth are uniserial in the jaws. Pattern-10 families with moderate-to-weak fin spines and a major row of uniserial teeth (some have

TABLE 1. SELECTED CHARACTERS OF SOME TELEOSTEAN FAMILIES. + DENOTES PRESENCE; — ABSENCE.

	RLA PATTERN[1]	AVC BRIDGE	VERTEBRAE[2]	SUB-ORBITAL SHELF[3]	BRANCHI-OSTEGAL RAYS[4]
Centrolophidae	10	+	25–60	+	7
Stromateidae	10	+	30–48	—	5–6
Nomeidae	10	+	30–42	*	6
Ariommidae	*	+	30–33	*	6
Tetragonuridae	*	+	43–58	*	5–6
Pomatomidae	10	+	26	+	7
Kyphosidae	10	+	25	—	7
Arripididae	10	+	25	+	7
Scorpididae	10	+	25	+	7
Girellidae	10	—	27	+	7
Theraponidae	10	±	25	+	6
Kuhliidae	10	+	25	—	6
Nematistiidae	reduced 10	—	*	*	*
Apolectidae	9	+	24	*	7
Carangidae	9	—	24–27	±	7
Scombridae	none	—	31–66	—	7
Coryphaenidae	*	—	30–33	—	7
Atherinidae	6	—	31–60	±	5–6
Monodactylidae	reduced 9	—	24	+	6
Ephippidae	9	—	24	+	6

* not examined
[1] From Freihofer 1963
[2] Largely from Regan 1913, and Bertin and Arambourg 1958
[3] From Smith and Bailey 1962
[4] Largely from Günther 1859, 1860, 1861

very reduced rows behind the major row) are the pomatomids, kyphosids, and scorpidids. These could be the groups most closely associated with the line leading to the stromateoids. The arripidids, girellids, theraponids, and kuhliids have teeth in bands and heavy fin spines.

There is a strong resemblance between the kyphosids and the centrolophids, the primitive stromateoids. In both, the general rule is 10 + 15 vertebrae, a caudal skeleton with six hypural and three epural elements, a perforate ceratohyal, an expanded lacrimal, and scaled fin bases. Behind the major row of uniserial teeth in *Kyphosus*, there are rows of small villiform teeth (Moore, 1962); there is only one row of teeth in centrolophids. The kyphosids, however, lack the subocular shelf found in some centrolophids.

The kyphosids are today one of the most primitive perciform families. They retain the teeth on the ectopterygoid and endopterygoid and the two foramina in the facial wall of the *pars jugularis*, conditions associated with the beryciform level. Patterson (1964) offers evidence for the derivation of the kyphosids, scorpidids, and monodactylids from the Cretaceous polymixioid *Berycopsis*. If this is the case, and if the stromateoids arose from near the kyphosid stem, a direct line can be drawn from the berycoid level to *Pampus*, one of the most advanced perciforms.

The carangids were probably derived from the Cretaceous dinopterygoid *Aipichthys* (Patterson, 1964). Their development,

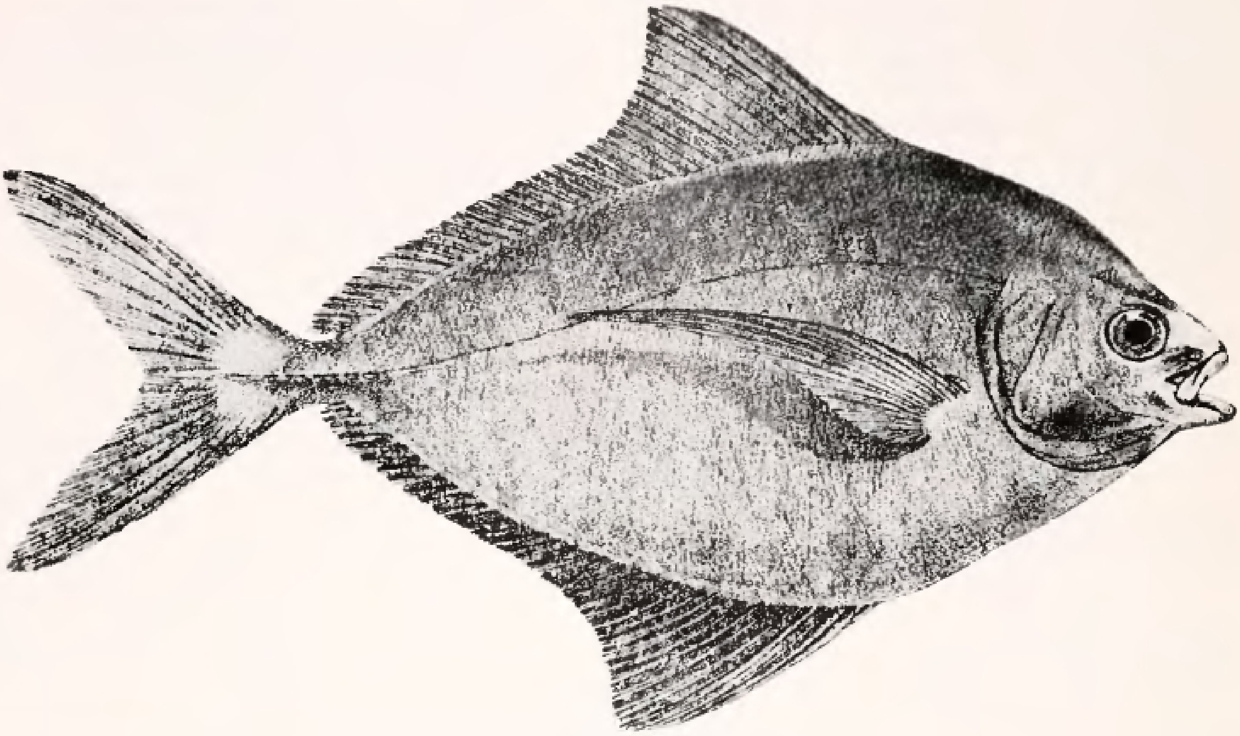

Figure 6. *Parastromateus niger*, drawing of a 15-inch specimen, from Day, 1875.

from beryciform to perciform level, has been independent of the line which produced the stromateoids. The resemblances between certain members of these two groups must therefore be considered an evolutionary convergence.

A problem remains in the genus *Parastromateus* (= *Apolectus*) (Fig. 6). Bloch (1795) described the sole representative of the genus as a species of *Stromateus*. The shape of the body and the small pelvics which are lost with age were good cause for this action. But *Parastromateus* lacks pharyngeal sacs and, because of this, Regan (1902) removed the genus from the stromateoids and placed it in the carangids. More extensive comparisons by Apsangikar (1953) supported the separation, but divergence from the carangids was noted and the new subfamily Parastromateinae of the Carangidae proposed. Suzuki (1962), in his great review of Japanese carangids, followed Jordan (1923) in considering *Parastromateus* the sole representative of a monotypic family.

Parastromateus is a pattern-9 teleost, as are the carangids (Freihofer, 1963), but has a bony bridge over the anterior vertical canal of the ear, as do the stromateoids. The only reason, other than the bony bridge, for relating *Parastromateus* to the stromateids is the similarity in body form. *Parastromateus*, however, has 10 + 14 vertebrae, while all stromateids have at least 13 + 17. Even if *Parastromateus* is related to the stromateids, the relationship is at most a very distant one.

Within the suborder Stromateoidei, there are three distinct groups, the primitive centrolophids, the intermediate nomeids with their specialized off-shoots the tetragonurids and the ariommids, and the advanced stromateids. The stromateids are an obvious derivative of the centrolophid line. The nomeids, an evolutionary grade above the centrolophids, have evolved parallel to the centrolophids, but from an earlier common ancestor. The probable relationships between the stromateoid families, discussed

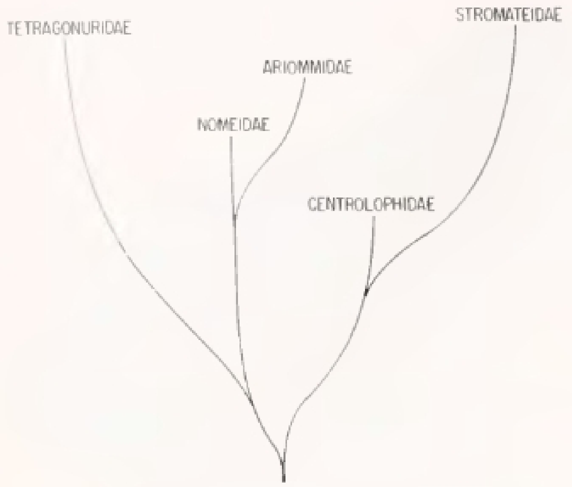

Figure 7. Dendrogram showing probable relationships of the five stromateoid families.

more fully in the family accounts, are expressed diagrammatically in Figure 7.

Fossils. The Cretaceous *Omosoma*, usually considered a stromateid (Arambourg, 1954) has been shown by Patterson (1964) to be a polymixioid, standing, interestingly enough, near *Berycopsis*. *Carangodes cephalus*, from the Monte Bolca beds of Austria, is well described and figured by Heckel (1856). Though it looks somewhat like some stromateoids and was considered a nomeid by Jordan (1923), the diagnostic characters are missing and it cannot be affiliated with this group with any certainty. *Aspidolepis* Geinitz 1868, based on a scale, was considered a stromateid by Jordan (1923). But the scales of the majority of stromateoids are in no way distinctive, and thus the possible relationships of this fossil genus cannot be determined. Two new fossil genera have been found by Bonde (1966) in the lower Eocene Mo-clay of Denmark.

Key to Stromateoid Families

1 (6). Two dorsal fins, distinctly, though scarcely, separated, the first usually with ten to twenty spines; if there are fewer than ten spines, the longest spine is about the same length as the longest dorsal finray. Pelvic fins always present. Vomer, palatines, and basibranchials toothed or not. 2

2 (5). The first dorsal fin with about ten long, slender spines, often folded into a groove, the longest spine nearly as long as, or longer than, the longest finray in the second dorsal. Anal finrays 14 to 30. Scales cycloid, thin, deciduous. Fleshy lateral keels on peduncle near caudal fin base absent or only slightly developed. Vertebrae 29 to 42. 3

3 (4). Vomer, palatines, and usually basibranchials with small, often almost indistinguishable, teeth. Caudal peduncle compressed, its least depth greater than 5 per cent of the standard length, without lateral keels. Usually more than fifteen rays in both the dorsal and anal fins. .... NOMEIDAE, p. 76

4 (3). Vomer, palatines, and basibranchials toothless. Caudal peduncle square in cross-section, its least depth less than 5 per cent of the standard length, with two low lateral keels on each side near caudal fin base. Fourteen or fifteen rays in both the dorsal and anal fins. .... ARIOMMIDAE, p. 88

5 (2). The first dorsal fin with ten to twenty short spines, the longest only half the length of the longest finray in the second dorsal. Anal finrays 10 to 16. Scales keeled, heavy, very adherent. Modified scales form two well developed lateral keels on each side of peduncle near caudal fin base. Vertebrae 43 to 58. .... TETRAGONURIDAE, p. 94

6 (1). A continuous dorsal fin, or two dorsal fins scarcely separated, the first with less than ten spines; if spines are present, the longest spine is less than half the length of the longest dorsal finray. Pelvic fins present or absent. Vomer, palatines, and basibranchials toothless. 7

7 (8). Pelvic fins always present. None or one to five weak spines, or five to nine stout spines precede dorsal finrays. Anal finrays 15 to 30. Median fins never falcate; their bases rarely the same length. Jaw teeth all conical, simple. Supramaxillary bone usually present, but hard to find in some. Seven branchiostegal rays. Vertebrae 25 to 30 or 50 to 60. .... CENTROLOPHIDAE, p. 53

8 (7). Pelvic fins never present in adults, rarely present in the young. No stout spines precede dorsal finrays, but, in some species, five to ten small blade-

like spines resembling the ends of free interneurals protrude ahead of the fin. Anal finrays 30 to 50. Median fins often falcate; their bases about equal in length. Jaw teeth laterally compressed, with three cusps. No supramaxillary bone. Five or six branchiostegal rays. Vertebrae 30 to 48. .... STROMATEIDAE, p. 98

Family CENTROLOPHIDAE

Type genus: *Centrolophus* Lacépède 1803

Centrolophes. Cuvier and Valenciennes, 1833:330 (descr.).

Centrolophinae. Gill, 1861:34 (list); 1862:127 (genera listed); 1884:666–667 (def., gen.). Jordan and Gilbert, 1882:450 (name, descr.).

Centrolophidae. Jordan and Evermann, 1896: 962 (descr.; North America). Jordan, 1923: 182 (in part, list). Norman, 1937:115 (descr., relationships; Chile). Tortonese, 1959:57 (in part, revision; Gulf of Genoa).

Lirinae. Bühler, 1930:62 (in part, morph., digestive system).

Nomeidae. Berg, 1940:323 (in part, dist.); 1955: 248 (part, dist.). Norman, 1957:503 (in part, def., genera listed).

Diagnosis. Stromateoid fishes with pelvic fins present in adults, continuous dorsal fin, toothless palate, seven branchiostegal rays, and six hypural bones in the tail. The papillae in the pharyngeal sacs with irregularly shaped bases, arranged in ten to twenty longitudinal bands.

Description. Body slender to deep, usually somewhat compressed. The rayed portion of the continuous dorsal fin preceded by six to eight short stout spines in *Hyperoglyphe*, *Seriolella*, and *Psenopsis*; none or one to five thin weak spines in *Centrolophus*, *Schedophilus*, and *Icichthys*. In the latter group and in *Psenopsis* the spines graduating to the rayed portion of the fin; in the others not. Three anal fin spines, not separated from the rays. Pelvic fins usually attached to the abdomen by a thin membrane and folding into a broad shallow groove. Head conspicuously naked, usually covered with small pores. Scales cycloid, but with minute cteni in *Schedophilus medusophagus*, and usually deciduous. Tubed scales of lateral line extending onto peduncle. Margin of preopercle usually moderately denticulate, but spinulose in most young stages and in *Schedophilus*. Opercle thin, with two flat, weak spines; the margin denticulate. Seven branchiostegal rays. Mouth large, maxillary extending at least to below eye. A nearly uniserial row of small conical teeth in the jaws; vomer, palatines, and basibranchials toothless. Supramaxillary bone present in most but absent in *Psenopsis*. Adipose tissue around eye usually not conspicuously developed. Vertebrae 25 or 26 in most species, except 50 to 60 in *Icichthys*. Caudal skeleton with six hypurals and usually three epurals, except two in *Icichthys*. Pharyngeal sacs with irregularly shaped papillae in ten to twenty longitudinal bands. Teeth seated directly on top of the bony base. Adults one to four feet in length, usually dark-colored and without conspicuous pattern.

Distribution. Centrolophids are pelagic, usually on the high seas and over the edge of the continental shelves, although *Psenopsis* and *Seriolella* occur in shallow water near the coast. Some are found in tropical waters, but the majority are fishes of temperate seas. The soft-spined centrolophids (*Centrolophus*, *Icichthys*, and *Schedophilus*) tend to be more oceanic than the hard-spined centrolophids (*Hyperoglyphe*, *Seriolella*, and *Psenopsis*). To some extent, the distributions of these two groups complement each other (Figs. 52, 53).

The distribution of the centrolophids is in part a relict distribution. *Centrolophus* is bipolar, found in the North Atlantic, South Africa, and Southern Australia and New Zealand. *Icichthys*, very similar in appearance to *Centrolophus*, is bipolar in the Pacific. In the waters from Australia to the coasts of Chile, the endemic genus *Seriolella* has evolved.

No centrolophids occur across the broad tropical Pacific or Indian Oceans.

Relationships. The Centrolophidae stand at the base of the line leading to the Stromateidae. Of all stromateoids, they are the least differentiated from the perciform ancestor. Most have 25 vertebrae, the well-known basic perciform number. Most have a supramaxillary bone. There are seven branchiostegal rays, and the caudal skeleton (Figs. 10, 12, 23) is of the basic perciform type (Gosline, 1961a). In this sense, the centrolophids can be considered the most primitive stromateoids.

The caudal skeleton of the nomeids, with hypurals 2 + 3 and 4 + 5 of the basic six fused, could easily have been derived from the centrolophids. The stellate papillae, also, and loss of one branchiostegal represent a grade above the centrolophid condition. But teeth are present on the vomer, palatines, and basibranchials of the nomeids, in general a primitive condition (Liem, 1963), and are absent in the centrolophids. This makes it unlikely that the former group has been derived from the latter. Rather, the two must represent approximately parallel lines, derived from an earlier form which had palatal dentition.

There is a fairly close and probably direct relationship between the advanced centrolophid genera *Seriolella* and *Psenopsis* and the stromateids *Stromateus* and *Peprilus*. Fishes in both these groups have well-ossified sclerotic bones, minute body pores, slender tapering branchiostegals, and extremely deciduous scales.

Key to Centrolophid Genera

1 (6). Spines of the dorsal fin weakly developed and all graduating to the dorsal rays. 2

2 (5). Weak denticulations on preopercular margin. Origin of dorsal fin usually well behind insertion of pectoral fins, but over pectoral insertion in very small specimens. Body elongate, maximum depth usually less than 30 per cent of the standard length. 3

3 (4). Total elements in anal fin 23 to 27. Scales small, very deciduous, preopercle and cheek naked. Scales in lateral line 160 to 230. Vertebrae 25. *Centrolophus*, p. 62. Fig. 13

4 (3). Total elements in anal fin 27 to 31. Scales moderate in size, not especially deciduous, present on preopercle and cheek. Scales in lateral line 100 to 130. Vertebrae 50 to 60. *Icichthys*, p. 65. Fig. 15

5 (2). Nine to fifteen small spines on preopercular margin. Origin of dorsal fin usually before insertion of pectoral fins, but over pectoral insertion in very large specimens. Body deep, maximum depth usually greater than 35 per cent of the standard length. *Schedophilus*, p. 58. Fig. 11

6 (1). Five to nine stout dorsal spines, shorter than and not graduating (graduating slightly in *Psenopsis*) to the dorsal rays. 7

7 (8). Dorsal finrays 19 to 25; anal finrays 14 to 21. Preopercular margin spinulose. Scales not especially deciduous. Lateral line arched anteriorly, straightening out over the anal fin. Adipose tissue around eye not well developed. Sclerotic bones not well ossified; golden iris appears as a complete ring. *Hyperoglyphe*, p. 54. Fig. 8

8 (7). Dorsal finrays 25 to 40; anal finrays 18 to 30. Preopercular margin entire or finely denticulate. Scales very deciduous. Lateral line follows dorsal profile. Adipose tissue around eye well developed. Sclerotic bones usually well ossified; golden iris appears divided by a vertical bar. 9

9 (10). Insertion of pelvic fins behind insertion of pectorals. Supramaxillary bone present. At least seven more dorsal finrays than anal finrays. Usually eight dorsal spines, the third, fourth, and fifth the longest. *Seriolella*, p. 69. Figs. 18, 19

10 (9). Insertion of pelvic fins before or just under insertion of pectorals. Supramaxillary bone absent. Number of dorsal finrays never exceeds number of anal finrays by more than five. Five to seven dorsal spines, increasing in length posteriorly. *Psenopsis*, p. 72. Fig. 21

Genus *HYPEROGLYPHE* Günther, 1859

Figure 8

Palinurus DeKay, 1842:118. (Type species: *Coryphaena perciformis* Mitchill, 1818:244, by monotypy. New York Harbor. Preoccupied by *Palinurus* Fabricius, 1798, Crustacea.)

Hyperoglyphe Günther, 1859 (June):337. (Type species: **Diagramma porosa* Richardson, 1845: 26, by monotypy. Coasts of Australia. A synonym of *Perca antarctica* Carmichael, 1818: 501.)

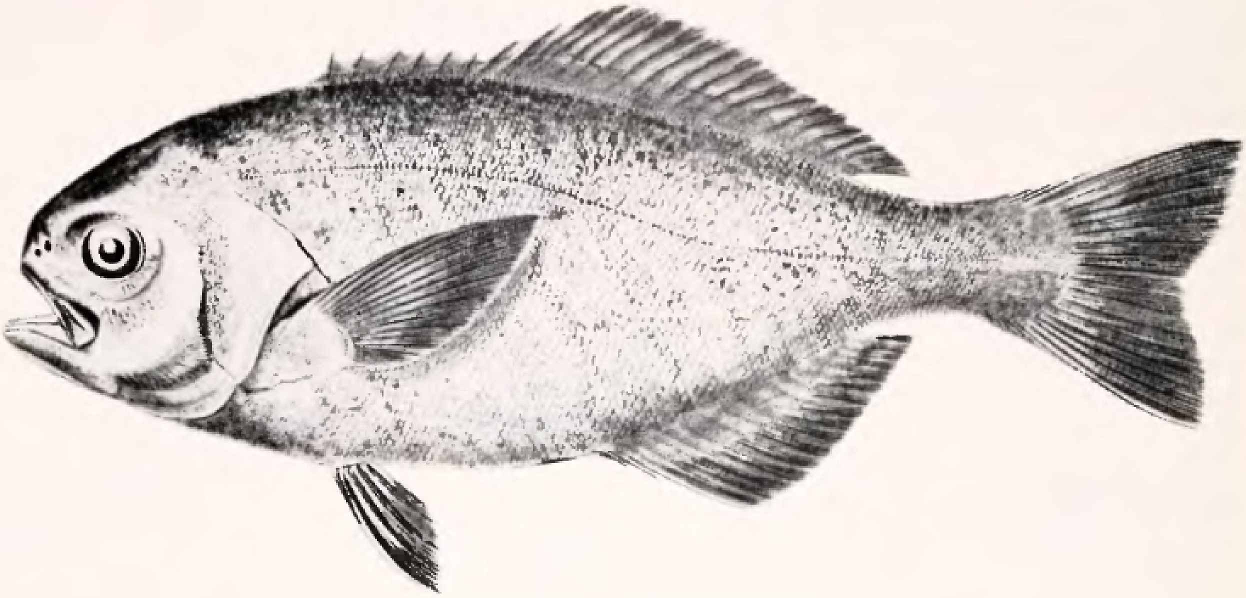

Figure 8. *Hyperoglyphe perciforma*, drawing of an approximately 200-mm specimen, courtesy of the Smithsonian Institution.

Palinurichthys Bleeker, 1859 (November):22. (Substitute name for *Palinurus* DeKay, and therefore taking the same type species, *Coryphaena perciformis* Mitchill, 1818:244.)

Palinurichthys Gill, 1860:20. (Substitute name, proposed independently from Bleeker, for *Palinurus* DeKay, and therefore taking the same type species, *Coryphaena perciformis* Mitchill, 1818:244.)

Pammelas Günther, 1860:485. (Substitute name for *Palinurus* DeKay, and therefore taking the same type species, *Coryphaena perciformis* Mitchill, 1818:244.)

Eurumetopos Morton, 1888:77. (Type species: *Eurumetopos johnstonii* Morton, 1888:77, by monotypy. Tasmania. A synonym of *Perca antarctica* Carmichael, 1818:501.)

Toledia Miranda-Ribeiro, 1915:5. (Type species: *Toledia macrophthalma* Miranda-Ribeiro, 1915:5, by monotypy. Macahé, Brazil.)

Ocycrius Jordan and Hubbs, 1925:226. (Type species: *Centrolophus japonicus* Döderlein *in* Steindachner and Döderlein, 1885:183, by original designation. Tokyo, Japan.)

The combination of less than 25 dorsal finrays, about eight short spines not increasing in length to the rays in the dorsal fin, toothless palate, pelvic insertion under pectoral fin base, supramaxillary bone present, and lateral line arched anteriorly straightening out over the anal fin, distinguishes *Hyperoglyphe* from all other stromateoid genera. The name, a feminine noun, is from the Greek ὑπὲρ, above, + γλυφὴ, groove, in reference to the deep longitudinal groove in the roof of the mouth.

Description. Body moderately deep, maximum depth around 30 to 35 per cent of the standard length; musculature firm. Caudal peduncle broad, of moderate length. Dorsal fin originating over or a little behind insertion of pectoral fins, continuous, six to eight short stout spines not graduating to the longer rays. The longest spine half the length of the longest ray. Anteriormost finrays the longest, those that follow shorter, 19 to 25 finrays in all. Anus at mid-body, in a slit. Anal fin originating a little behind middle of body, three spines precede the 15 to 20 rays. Pectoral fin rounded in the young, pointed in adult. Pelvic fins inserting under end of pectoral fin base, attached to abdomen by a small membrane and folding into a shallow groove. Caudal fin broad, emarginate to moderately forked in adult. Scales cycloid, moderate in size, somewhat deciduous, covering bases of median fins. Lateral line arched anteriorly, straightening out over middle of anal fin and extending onto peduncle. Skin moderately thick; extensive subdermal canal system communicating to the surface through small pores. Head around 33 per cent of the standard length, broad. Top of head not scaled, pores prominent, naked skin projecting backward over nape. Eye moderate to large, no adipose tissue. Nostrils located near tip of obtuse snout, large, the anterior round, the posterior a slit. Angle of gape extending below eye. Premaxillary not protractile. Lacrimal bone partially covering anterior portion of upper jaw when mouth is closed, end of maxillary remaining exposed. Supramaxillary present. Jaw teeth very small, pointed, uniserial, close-set; vomer, palatines, and basibranchials toothless. Opercle and preopercle thin; opercle with two weak flat spines, scaled, margin very finely denticulate or entire; preopercle not scaled, striated, margin with numerous very small spinules. Angle of preopercle rounded, bulging backward slightly. Gillrakers heavy, slightly longer than the filaments, finely toothed on inner edge, spaced, about 16 on lower limb of first arch. Seven branchiostegal rays, five on the ceratohyal, two on the epihyal. Scapula visible. Vertebrae 10 + 15 = 25. Stomach a simple sac; intestine long. Pyloric caeca numerous, in a mass resembling a raspberry.

Base color green-grey or blue-grey to reddish brown. Back dark, sides and below lighter, sometimes silvery. Head dark, iris a golden ring, opercle often silvery. Median fins usually darker than the body. Color pattern irregularly striped, mottled, or clear, changeable in life. Inside of mouth and gill cavity light. Peritoneum light with minute dark speckles.

Natural history. Though *Hyperoglyphe* occurs throughout the world and is fished commercially in Japan, very little is known of its habits. The young commonly occur under flotsam, but usually not under jellyfish, in surface waters near the edge of the continental shelf. The larger adults form shoals in deep water, perhaps fairly near the bottom.

Figure 9. Branchial region of *Hyperaglyphe perciforma*, drawing of a cleared-and-stained preparation from a 173-mm SL specimen. Elements identified in Figure 2.

Small *H. perciforma* two to four inches long occur off the New England coasts under floating objects in great numbers during the summer. By fall, these fish have doubled or even tripled their size. With the approach of cold weather they disappear. Only recently has it been found that adult *H. perciforma* attain three feet in length, and live in deep water off the coast of west Florida (Schwartz, 1963). This discovery bears out an earlier suggestion by Merriman (1945) that the fish observed off New England were the young of a much larger bathypelagic species. In Japan, the large adults had been marketed long before the young were first discovered (Abe, 1955).

Bigelow and Schroeder (1953) reported small fishes and crustacean remains from stomachs of *Hyperoglyphe perciforma.* The fish may also feed occasionally on barnacles (Cornish, 1874; Holt and Byrne, 1903). At times *H. porosa* feeds heavily on the tunicate *Pyrosoma atlanticum* (Cowper, 1960).

Relationships. Hyperoglyphe is the central genus of the Centrolophidae. The mem-

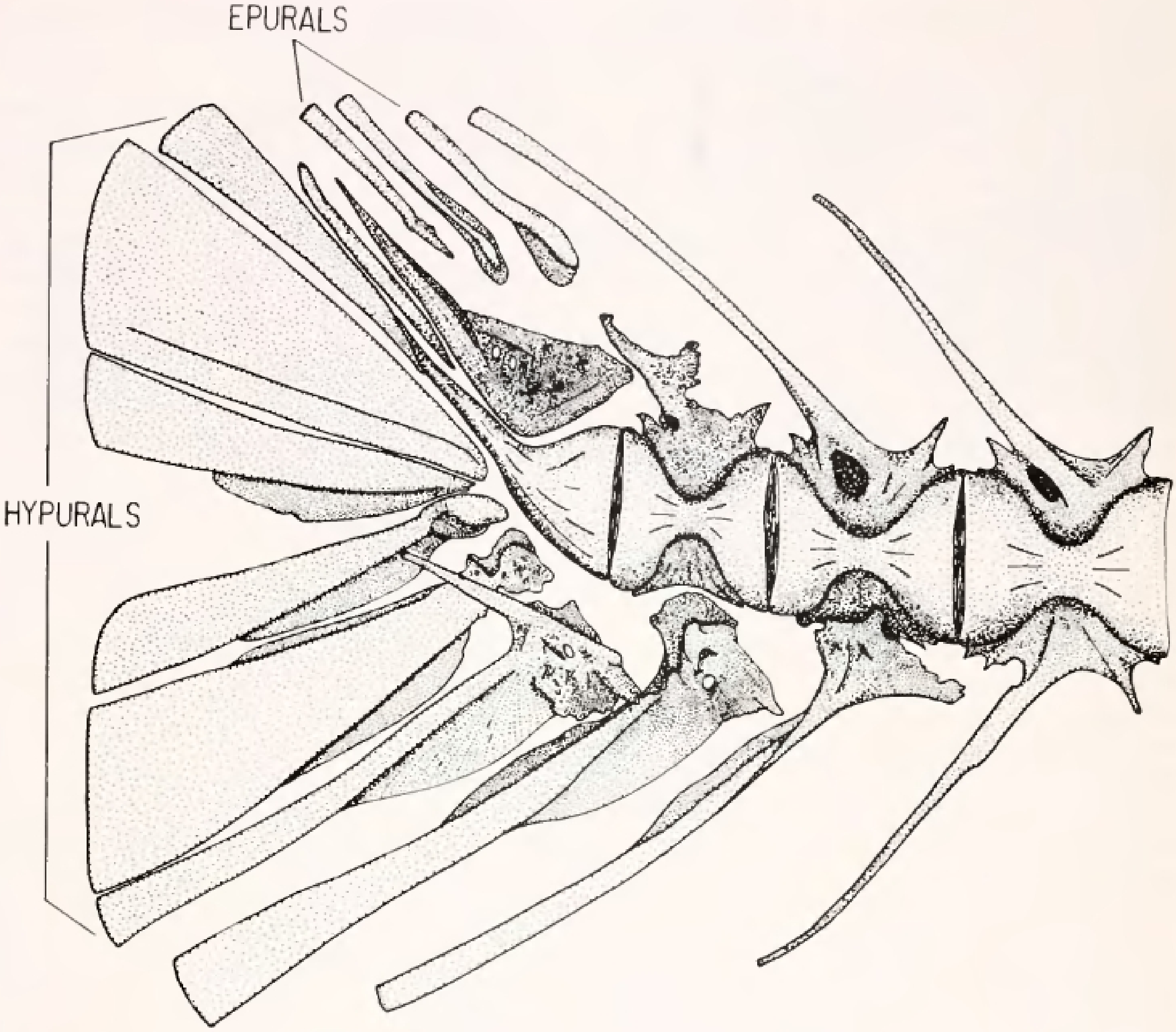

Figure 10. Caudal skeleton of *Hyperaglyphe perciforma*, drawing of a cleared-and-stained preparation from a 50-mm SL specimen. All elements identified in Figure 1.

bers of this genus are the most generalized fishes in the entire suborder, and are probably not unlike the ancestral form. The relatively low number of median finrays, the stout spines in the median fins, the seven blunt branchiostegal rays (Fig. 9), the 25 vertebrae, the spiny preopercle, and the large size attained, are all basal characters. The caudal skeleton (Fig. 10) is of the generalized perciform type.

Hyperoglyphe has given rise, on the one hand, to the more oceanic soft-spined centrolophids, through *Schedophilus* to *Centrolophus* and *Icichthys*. The major change has been the softening of the fin spines and of the tissues in general. On the other hand, *Hyperoglyphe* has given rise to the more coastal, advanced, hard-spined genera *Seriolella* and *Psenopsis*. The change in this direction has been one of slight refinement in the branchial region and a tendency toward fusion of elements in the caudal skeleton.

Species. *Hyperoglyphe* is a wide-ranging genus. The species are found in the slope water off the east coasts of the New World, in the Gulf of Mexico, near St. Helena and Tristan da Cunha, along the west coast of

Africa, in Australia–New Zealand, and in Japan.

There is little problem of synonymy, since the species are fairly distinct from one another. The changes that occur with growth, however, remain a stumbling block. The species in *Hyperoglyphe* are:

Hyperoglyphe antarctica (Carmichael, 1818) = *Perca antarctica* Carmichael. Tristan da Cunha, South Africa, southern Australia, and New Zealand, type locality Tristan da Cunha. D VIII, 19–21. A III 15–16. P 18–20. Gill-rakers 5 + 1 + 14. Vertebrae 10 + 15. This is the most primitive species in *Hyperoglyphe,* and stands nearer to the base of the stromateoid stem than any other fish. It attains a very large size. McCulloch (1914) reports a specimen 1072 mm long. The low median finray counts, large mouth, and a characteristic patch of scales on the otherwise naked occiput distinguish this species from all others. Synonyms are: **Diagramma porosa* Richardson, 1845, from Australia; *Eurumetopos johnstonii* Morton, 1888, from Tasmania; and *Seriolella amplus* Griffin, 1928, from Bay of Plenty, New Zealand.

Hyperoglyphe bythites (Ginsburg, 1954) = **Palinurichthys bythites* Ginsburg. Gulf of Mexico, type locality off Pensacola, Florida. D VII–VIII, 22–25. A III 16–17. P 20–21. Gill-rakers 6–7 + 1 + 15–16. Vertebrae 10 +15. Possibly a synonym of *H. macrophthalma* (Miranda-Ribeiro, 1915). This species has more dorsal finrays and a larger eye than *H. perciforma* (Mitchill, 1818).

Hyperoglyphe perciforma (Mitchill, 1818) = *Coryphaena perciformis* Mitchill. East coast of North America, Florida to Nova Scotia, type locality New York Harbor. D VII–VIII, 19–21. A III 15–17. P 20–22. Gill-rakers 5–7 + 1 + 15–17. Vertebrae 10 + 15 (skel.). This fish is the common "barrelfish" of the offings of New England. Young specimens have followed floating logs across the Atlantic to the British Isles (Holt and Byrne, 1903). *Pimelepterus cornubiensis* Cornish, 1874, is a synonym based on a specimen which floated to Cornwall in a box.

Hyperoglyphe japonica (Döderlein *in* Steindachner and Döderlein, 1885) = *Centrolophus japonicus* Döderlein. Seas of Japan, type locality Tokyo. D VIII, 22–24. A III 17–19. P 21–23. Gill-rakers 6–7 + 1 + 15–16. Vertebrae 10 + 15. This fish is the "medai" of Japanese fisheries literature. It is the subject of a small, deep, hand-line fishery. A probable synonym is **Lirus paucidens* Günther, 1889, based on three small specimens captured by the CHALLENGER somewhere between New Guinea and Japan.

Hyperoglyphe moselii (Cunningham, 1910) = *Leirus moselii* Cunningham. St. Helena, and coasts of Angola and South Africa, type locality St. Helena. D VI, 23–25. A III 19–20. P 20–22. Gill-rakers about 7 + 1 + 15. The type is described as having but one spine and 25 rays in the dorsal fin. The specimen is so large and heavy that I was unable to lift it and its container off the shelf in the British Museum, and hence did not get to examine it closely during my brief visit there. At such a large size, the first five spines in the dorsal may be buried in the skin, where Cunningham could have overlooked them. Probable synonyms are *Palinurichthys pringlei* Smith, 1949, and *Palinurichthys matthewsi* Smith, 1960, both from South Africa.

Hyperoglyphe macrophthalma (Miranda-Ribeiro, 1915) = *Toledia macrophthalma* Miranda-Ribeiro. Brazil, type locality Macahé. D VII, 26. A 20 (from Miranda-Ribeiro, 1915). Known from a single specimen 68 cm long. Possibly a synonym of *H. moselii* (Cunningham, 1910).

Genus *SCHEDOPHILUS* Cocco, 1839

Figure 11

Leirus Lowe, 1833:143. (Type species: **Leirus bennettii* Lowe, 1833:143, by monotypy. Madeira, Atlantic Ocean. Preoccupied by *Leirus* Dahl, 1823, Coleoptera. A junior synonym of **Centrolophus ovalis* Cuvier and Valenciennes, 1833:346.)

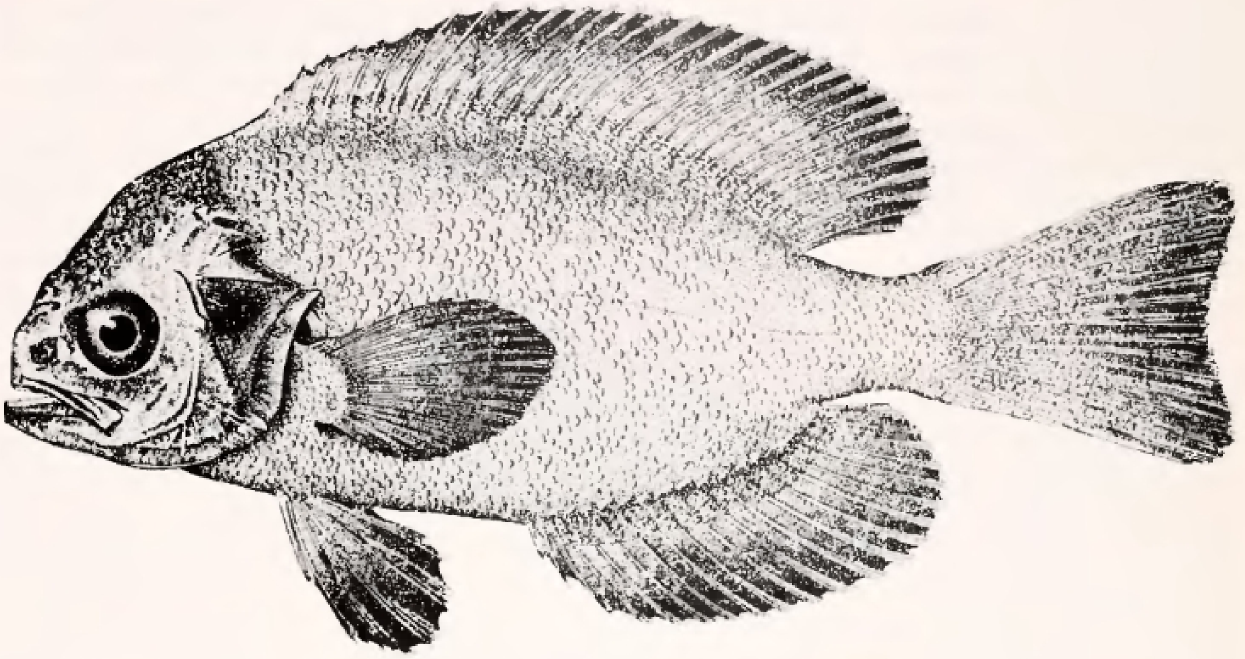

Figure 11. *Schedophilus pemarco*, drawing of a 245-mm specimen, from Poll, 1959.

Schedophilus Cocco, 1839[1]:57. (Type species: *Schedophilus medusophagus* Cocco, 1839:57, by monotypy. Messina.)

Mupus Cocco, 1840[1]:237. (Type species: *Mupus imperialis* Cocco, 1840:237, by monotypy. Messina. A synonym of **Centrolophus ovalis* Cuvier and Valenciennes, 1833:346.)

Lirus Agassiz, 1846:213. (Emendation of *Leirus* Lowe, 1833:143, and therefore taking the same type species, **Leirus bennettii* Lowe, 1833:143, a junior synonym of **Centrolophus ovalis* Cuvier and Valenciennes, 1833: 346.)

Crius Valenciennes, 1848:43. (Type species: **Crius bertheloti* Valenciennes, 1848:45, by original designation. Canary Islands, Atlantic Ocean. A synonym of **Centrolophus ovalis* Cuvier and Valenciennes, 1833:346.)

Hoplocoryphis Gill, 1862:127. (Type species: **Schedophilus maculatus* Günther, 1860:412, by original designation. Seas of China.)

Eucrotus T. H. Bean, 1912:123. (Type species: *Eucrotus ventralis* T. H. Bean, 1912:123, by monotypy. Bermuda, Atlantic Ocean.)

Tubbia Whitley, 1943:178. (Type species: *Tubbia tasmanica* Whitley, 1943:179, by original designation. Eastern Tasmania.)

The combination of deep body, broad deep head, large eye, continuous dorsal fin with weak spines graduating to the rays and originating before the pectoral insertion, toothless palate, and prominent spines on the preopercular margin distinguishes *Schedophilus* from all other stromateoid genera. The name, a masculine noun, is from the Greek *σχεδία*, raft, + *φίλος*, friend, in reference to the fish's common association with floating objects.

Description. Body deep, maximum depth generally greater than 35 per cent of the standard length; musculature soft. Peduncle fairly broad, short. Dorsal fin originating before (or over in very large specimens) insertion of pectoral fins, continuous, three to seven weak spines graduating to the 23 to 50 rays. Anus and genital pore at midbody, in a slit. Anal fin originating behind middle of body, three long weak spines preceding the 16 to 30 rays. Median fins with compressed fleshy bases. Pectoral fin rounded in the young, pointed in adult, relative length decreasing with growth. Pelvic fins inserting under end of pectoral fin base, reaching to anus in young and juveniles, attached to abdomen by a membrane and folding into a shallow groove; relative length of fin decreasing markedly

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[1] Tortonese (1959) has clarified the confusion surrounding the publication dates of Cocco's names.

with growth. Caudal fin broad, forked. Scales small to moderate, cycloid, or with one or two minute cteni in young *Schedophilus medusophagus*, deciduous, covering fleshy bases of the median fins. Lateral line arched anteriorly, straightening out about mid-body and extending onto peduncle. Skin thin; extensive subdermal canal system communicating to the surface through small pores. Head soft, broad and deep, usually greater than 25 per cent of the standard length, not scaled, naked skin projecting slightly backward over the nape. Eye large, no adipose tissue. Nostrils located near tip of obtuse snout, anterior nostril round, the posterior a slit. Angle of gape extending below eye. Premaxillary not protractile. Lacrimal bone covering anterior portion of upper jaw when mouth is closed, end of maxillary remaining exposed. Slender supramaxillary present. Jaw teeth very small, pointed, uniserial, close-set; vomer, palatines, and basibranchials toothless. Opercle and preopercle thin; opercle with two weak flat spines, scaled, margin denticulate; preopercle not scaled, margin set with nine to eighteen prominent spines, angle of preopercle rounded, bulging back slightly. Gillrakers heavy, about half the length of the filaments, toothed on inner edge, spaced; 10 to 16 on lower limb of first arch; a few rudimentary rakers present under large pseudobranch. Seven branchiostegal rays, five on the ceratohyal, two on the epihyal. Scapula visible. Vertebrae 10 + 15, 16 or 20 = 25, 26 or 30, or 12 + 17 = 29. Stomach a simple sac; intestine long. Pyloric caeca numerous, dendritic.

Base color brown, bluish, or silvery. Median fins, pectorals, and pelvics usually darker than the body. Color pattern irregularly striped, mottled, or clear. Young of some have dark vertical stripes.

Natural history. Most species in *Schedophilus* are oceanic, rare, and, consequently, little is known concerning their biology. The young of *S. medusophagus* occurs commonly with jellyfish. The fish may feed very largely on medusae, but will also take small crustaceans. At a length of about 200 mm, *S. medusophagus* deserts its coelenterate companion, and descends to deeper water.

Adult *Schedophilus* appear very different from the younger stages. The relative length of the paired fins is greatly decreased, the body is much more elongate, and the mottled or barred pattern, typical of juveniles, is gone.

Relationships. Schedophilus provides the link between the soft-spined and the hard-spined centrolophids. The range of variation in the genus is great, and the species grade from the one condition to the other. The caudal skeleton (Fig. 12) is most like that of *Centrolophus* and *Icichthys*. The pharyngeal sacs and teeth are intermediate between those of *Centrolophus* and *Hyperoglyphe*. *Schedophilus ovalis* has fairly stout spines ahead of the median fins; in *S. medusophagus* the spines are soft and flexible.

Schedophilus is derived from the central *Hyperoglyphe* stock. As it has moved into a more oceanic environment, the spines on the preopercle have become more pronounced, while the fin spines and the body in general have become softer.

Species. The species in *Schedophilus* are in general well differentiated. Almost all descriptions are based on young specimens. The large adults differ greatly in appearance from the young. Adults are so very rarely seen that only three have entered the literature, two of them assigned to other genera. Unfortunately, the species from the Australian region are very poorly known. Because of their isolated geographic distribution, critical examination of these species will doubtless provide much insight into the evolution of the soft-spined centrolophids.

The species in the genus are:

Schedophilus ovalis (Cuvier and Valenciennes, 1833) = **Centrolophus ovalis* Cuvier and Valenciennes. Eastern Atlantic Ocean from Spain to South Africa and Mediterranean Sea, type locality Nice. D

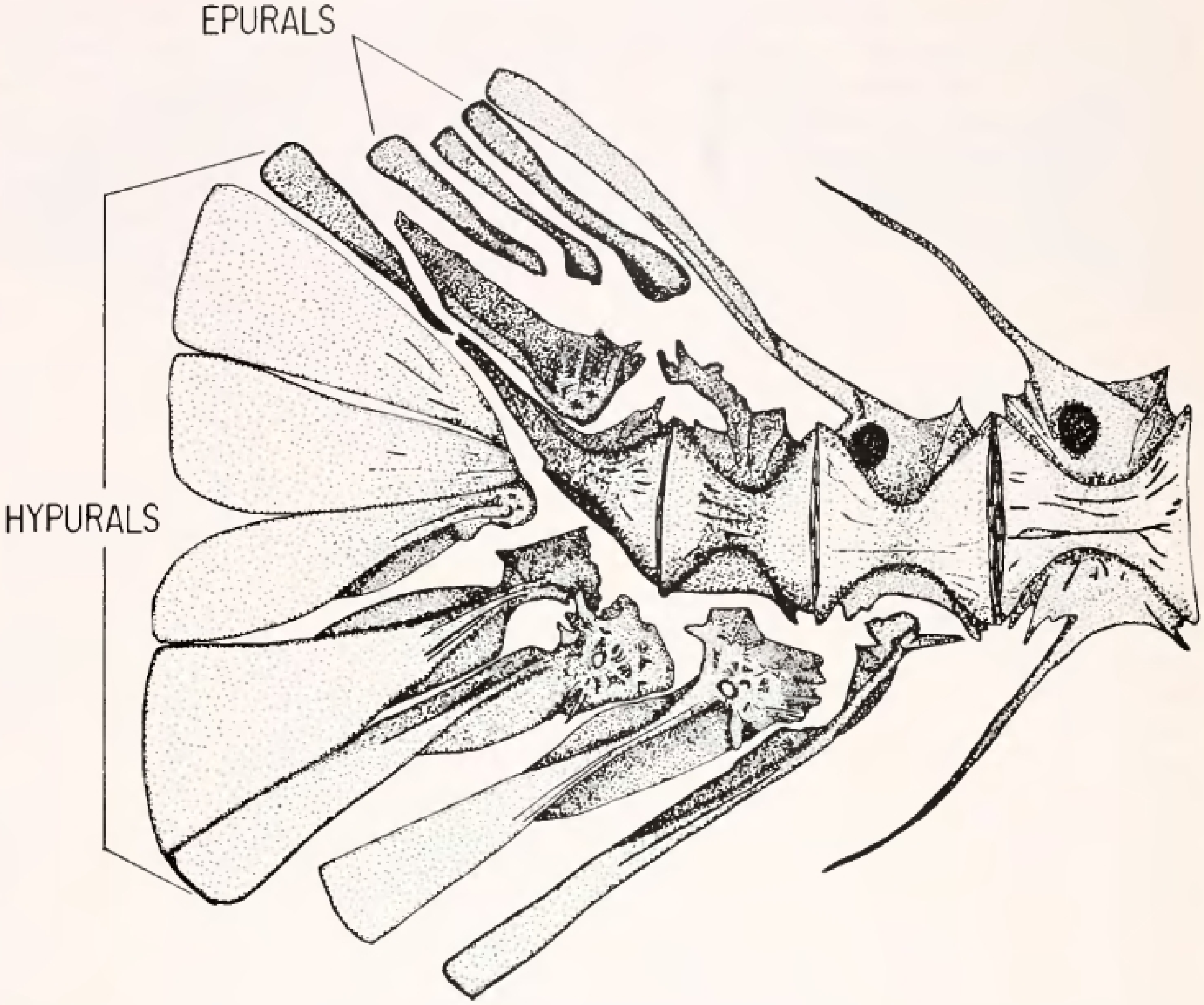

Figure 12. Caudal skeleton of *Schedophilus medusophagus*, drawing of a cleared-and-stained preparation from a 39-mm SL specimen. All elements identified in Figure 1.

VI–VIII, 30–32. A III 20–24. P 21–22. Gill-rakers around 6 + 1 + 16. Vertebrae 10 + 15. Silvery to greenish. Synonyms are: *Centrolophus crassus* Cuvier and Valenciennes, 1833, from west of the Azores; **Leirus bennettii* Lowe, 1833, from Madeira; *Mupus imperialis* Cocco, 1840, from the Mediterranean; **Crius bertheloti* Valenciennes, 1848, from the Canary Islands; *Centrolophus rotundicauda* Costa, 1866, from Naples; *Centrolophus porosissimus* Canestrini, 1865, and *Schedophilus botteri* Steindachner, 1868, from Barcelona.

Schedophilus medusophagus Cocco, 1839. Atlantic Ocean and western Mediterranean Sea, type locality Messina. D 44–50 (total elements). A 28–31 (total elements). P 18–21. Gill-rakers around 5 + 1 + 11. Vertebrae 10 + 15. Major preopercular spines usually about 12. Lateral line scales 160–230, increasing in number with growth. Brown, often mottled. The report of this species from the South Pacific (Günther, 1876), is undoubtedly that of a closely related form, *Schedophilus huttoni* (Waite, 1910). The adult of *S. medusophagus* has long been known under the name **Centrolophus britannicus* Günther, 1860a.

**Schedophilus maculatus* Günther, 1860. China Seas. D 36 (total elements). A 27 (total elements). P 19. Gill-rakers 5 + 1 + 13. Vertebrae 10 + 15. Major preopercular spines 13. This species is known only from the type, a 37-mm SL specimen that is soft and in poor condition.

**Schedophilus marmoratus* Kner and Steindachner, 1866. "Südsee," presumably near Australia. D 38 (total elements). A 27 (total elements). Vertebrae 12 + 17. This species is usually treated as a synonym of *S. maculatus* Günther, 1860. A probable synonym is *Hoplocoryphis physaliarum* Whitley, 1933, from New South Wales.

Schedophilus huttoni (Waite, 1910) = *Centrolophus huttoni* Waite. Seas of New Zealand, eastern Australia, and Tasmania, type locality Sumner, New Zealand. D 57 (total elements). A 38 (total elements). Gill-rakers 5 + 12. Vertebrae 10 + 20. Lateral line scales in the 776-mm holotype near 240. Brownish. As in *S. medusophagus*, the number of lateral line scales probably increases with age. A probable synonym is *Tubbia tasmanica* Whitley, 1943, from Tasmania, known only from a 10-cm specimen reported as having 144 scales in the lateral line.

Schedophilus ventralis (Bean, 1912) = *Eucrotus ventralis* Bean. Bermuda. D IV–VII, 31–34. A III 20–23. P 22. Gill-rakers around 5 + 1 + 16. Vertebrae 10 + 15. Major preopercular spines about 9. The type is apparently lost. This nominal species has been synonymized with *S. ovalis* (Cuvier and Valenciennes, 1833) by Fowler (1936).

Schedophilus griseolineatus (Norman, 1937) = **Palinurichthys griseolineatus* Norman. Southern Atlantic Ocean, type locality 49°00'S 61°58'W. D VII–VIII, 31–33. A III 20–21. P 19–21. Gill-rakers around 6 + 1 + 14. Vertebrae 10 + 16. Lateral line scales about 120. Major preopercular spines around 14. Blue-brown, horizontally striped. This species can be distinguished at once by the increased number of caudal vertebrae. The large specimens which Norman (1937) doubtfully referred to "*Palinurichthys caeruleus*" belong to this species.

Schedophilus pemarco (Poll, 1959) = *Palinurichthys pemarco* Poll. Gulf of Guinea, tropical Atlantic Ocean. D V–VII, 23–26. A III 16–18. P 19–22. Gill-rakers around 5 + 1 + 16. Vertebrae 10 + 15. Lateral line scales about 95. Major preopercular spines 15–19. Blue-brown, horizontally striped. The median finray counts in this species are lower than in any other.

Genus *CENTROLOPHUS* Lacépède, 1803

Figure 13

Centrolophus Lacépède, 1803:441. (Type species: *Perca nigra* Gmelin, 1788:132, by monotypy. "Rivers of Cornwall.")

Acentrolophus Nardo, 1827:28. (Substitute name for *Centrolophus* Lacépède, 1803, and therefore taking the same type species, *Perca nigra* Gmelin, 1788:132. *Centrolophus* deemed inapplicable.)

Gymnocephalus (*non* Bloch, 1793:24) Cocco, 1838:26. (Type species: *Gymnocephalus messinensis* Cocco, 1838:26, by monotypy. Messina. A synonym of *Perca nigra* Gmelin, 1788:132.) (*Vide* Jordan, 1923.)

Pompilus Lowe, 1839:81. (Type species: **Centrolophus morio* Cuvier and Valenciennes, 1833: 342, by absolute tautonymy, *C. pompilus* [= *P. pompilus*] Cuvier and Valenciennes, 1833: 334, considered a synonym. Madeira. A synonym of *Perca nigra* Gmelin, 1788:132. Preoccupied in *Pompilus* Schneider, 1784, Cephalopoda.)

Centrolophodes Gilchrist and von Bonde, 1923:2. (Type species: *Centrolophodes irwini* Gilchrist and von Bonde, 1923:3, by monotypy. South Africa. A synonym of *Perca nigra* Gmelin, 1788:132.)

The combination of elongate body, small head with prominent pores, continuous dorsal fin with very weak spines graduating to the rays, toothless palate, very small scales, and 160 to 230 scales in the lateral line, distinguishes *Centrolophus* from all other stromateoid genera. The name, a masculine noun, is from the Greek *κέντρον*, spine, + *λοφος*, crest of a helmet, probably in reference to the manner in which the dorsal fin rises from the back.

Description. Body elongate, maximum depth rarely exceeding 30 per cent of the standard length except in very small specimens; musculature firm. Peduncle broad,

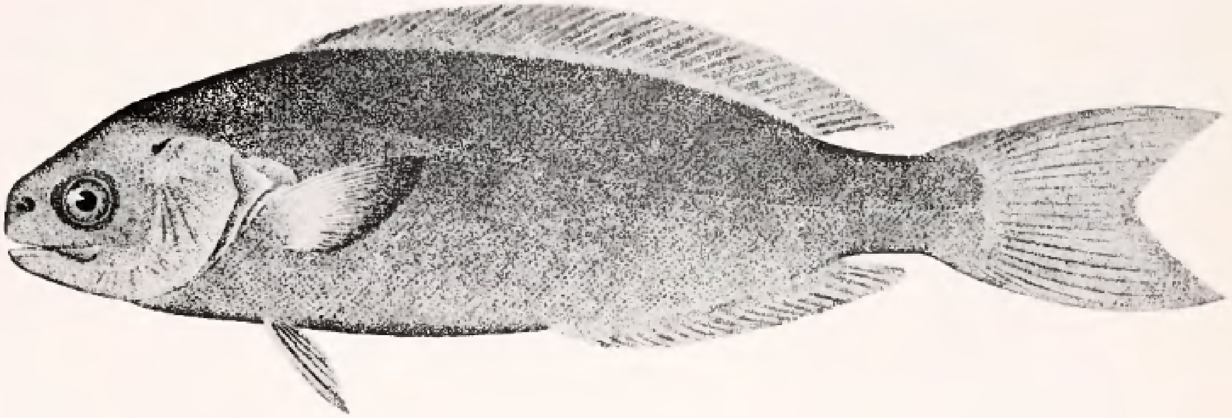

Figure 13. *Centrolophus niger*, drawing of a 223-mm specimen, USNM 44440, courtesy of the Smithsonian Institution.

thick, long. Dorsal fin originating a little behind insertion of pectoral fins, continuous, about five very weak spines graduating to the 32 to 37 rays. Anus and genital pore at mid-body, in a slit. Anal fin originating a little behind middle of body, three weak spines precede the 20 to 23 rays. Pectoral fin rounded in the young, pointed in adult, relative length decreasing slightly with growth. Pelvic fins inserting under posterior portion of pectoral fin base, attached to the abdomen by a small membrane and folding into a shallow groove. Caudal fin broad, moderately forked. Very small cycloid scales, deciduous, covering fleshy bases of the median fins. Lateral line slightly arched anteriorly, straightening out about mid-body and extending onto peduncle; lateral line scales around 190. Skin fairly thick; extensive subdermal canal system communicating to the surface through small pores. Head usually less than 25 per cent of the standard length, not scaled, pores very prominent, naked skin not projecting backward over the nape. Eye of moderate size, no adipose tissue. Nostrils near tip of rounded snout, the anterior round, the posterior a slit. Angle of gape extending below eye. Premaxillary not protractile. Upper jaw covered completely by lacrimal bone when mouth is closed. Slender supramaxillary present. Jaw teeth small, pointed, uniserial, spaced, increasing in number with growth; vomer, palatines, and basibranchials toothless. Opercle and preopercle thin, margins finely denticulate; opercle with two weak flat spines, scaled; angle of preopercle rounded, bulging back slightly; preopercle and cheek not scaled. Gill-rakers heavy, about half the length of the filaments, toothed on inner edge, spaced, about 13 on lower limb of first arch; rudimentary rakers present under large pseudobranch. Seven branchiostegal rays, five on the ceratohyal, two on the epihyal. Scapula prominent. Vertebrae 10 + 15 = 25. Caudal skeleton with six hypurals and three epurals. Stomach a simple sac; intestine long. Pyloric caeca about 10, digitiform.

Base color brown. Range is from russet through chocolate to dark bluish. Median fins and pelvics darker than the body. No pattern, hardly any countershading in adults; young have three or four dark vertical stripes.

Natural history. Young *Centrolophus* have been taken under jellyfish (Collett, 1896) and swimming with *Mola* (Munro, 1958). Some described as "small" were found in the stomachs of bottom-living hake trawled west of the British Isles (Blacker, 1962). Presumably these *Centrolophus* had not been in association with pelagic medusae. While young fish are found near the surface, the large fish are taken at depth.

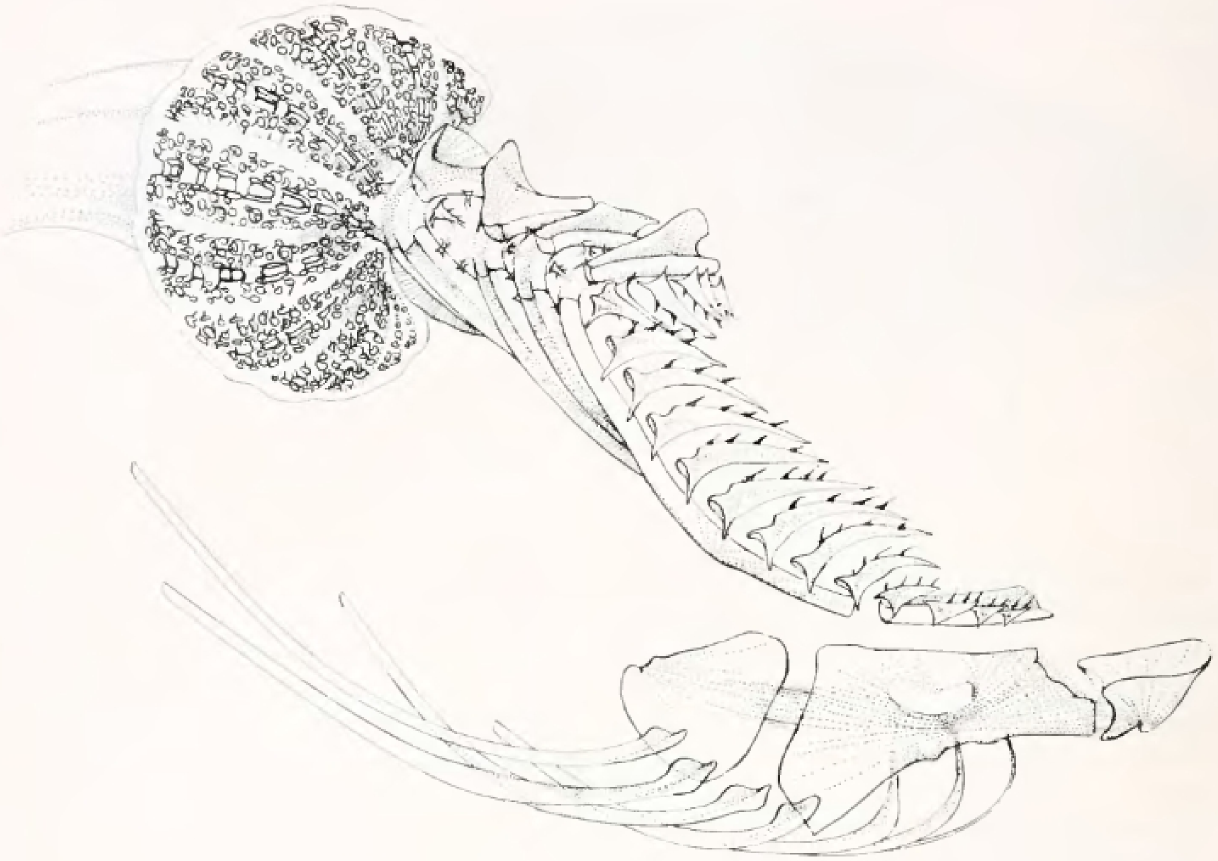

Figure 14. Branchial region of *Centrolophus niger*, drawing of a cleared-and-stained preparation from a 190-mm specimen. Elements identified in Figure 2.

In the North Atlantic, the adults seem widespread, but the young have been found only in the eastern Atlantic and Mediterranean areas. A spawned-out female, however, has been caught south of New England (Templeman and Haedrich, 1966).

The young are at first vertically banded, but by the time they are about 100 millimeters long they have become a uniform brown. Growth is very rapid; from December to May, five months, a Mediterranean specimen grew from 20 to 170 millimeters (Padoa, 1956). Growth is regular and the allometry is not marked. The number of jaw teeth does increase, however, from about 17 in a 150-millimeter specimen to near 100 in one of 1,200 millimeters.

Centrolophus is one of the largest stromateoids known. Specimens a meter or more in length have been taken in Australia (Mees, 1962), South Africa (Barnard, 1948), and the western North Atlantic.

Autumn spawning, from October into winter, is indicated by the occurrence of eggs and very small fish at this time in the Mediterranean (Padoa, 1956) and by the capture of a large, recently spawned-out female in December 1963 in the western North Atlantic. Fraser-Brunner (1935) noted dimorphism in the coloring of the sexes, the females said to be lighter than the males. This difference, however, is not always observed.

Lo Bianco (1909) observed young *Centrolophus* feeding on medusae, but Chabanaud and Tregouboff (1930) found that their aquarium specimen preferred small fish and plankton. It never attempted to eat the medusae which were present in the tank.

The large specimen from south of New England was taken on a long-line baited with squid. Fish and large crustacean remains occurred most often in stomachs examined, and, on one occasion, bits of potato and an onion were found.

As Nielsen (1963) has suggested, in reporting the seining of five near Skagen, *Centrolophus* may school. Blacker (1962) reports several hundredweight trawled off Ireland. Potentially a good fish with fine white meat, those offered experimentally in Milford Market found no sale (Blacker, 1962).

Relationships. Centrolophus is one of the most primitive stromateoids. The small pharyngeal sac with few rows of large papillae (Fig. 14), the heavy blunt-ended branchiostegal rays, and the large size attained, are all primitive characters. *Centrolophus* shows much affinity of form towards *Icichthys*, from which it differs mainly in having far fewer vertebrae.

Centrolophus, *Icichthys*, and *Schedophilus* are the soft-spined centrolophids. This group is in general a little more primitive than the hard-spined centrolophids, *Hyperoglyphe*, *Seriolella*, and *Psenopsis*. The soft-spined centrolophids usually have smaller sacs with fewer papillae, coarser jaw teeth, and attain a larger size than the hard-spined centrolophids.

Species. Centrolophus is known from the Australian region, from South Africa, and from the North Atlantic, where numerous species have been described. The counts of the Southern Hemisphere specimens, of which only a handful are known, overlap the range of those for the North Atlantic species. Some differences may exist in relative proportions, but these are only at certain stages of growth. Lacking comparative material, the safest course is to follow Waite (1910) and Mees (1962) in recognizing but one bipolar species:

**Centrolophus niger* (Gmelin, 1788) = *Perca nigra* Gmelin, 1788. North Atlantic, western Mediterranean Sea, Adriatic Sea, South Africa, southern Australia, and New Zealand, type locality "Rivers of Cornwall." D 37–41 (total elements). A III 20–23. P 19–22. Gill-rakers 5–6 + 1 + 12–15, usually 19 total. Vertebrae 10 + 15. The name *Centrolophus pompilus* (Linnaeus, 1758) is often used for this fish. Linnaeus's *Coryphaena pompilus*, however, is too poorly characterized, and differs too much in certain respects to be considered the same species. Gmelin's (1788) *Perca nigra* is the first available name. Synonyms from the North Atlantic are: *Centrolophus liparis* Risso, 1826, from Nice; *Acentrolophus maculosus* Nardo, 1827, from the Adriatic Sea; **Centrolophus pompilus* Cuvier and Valenciennes, 1833, from Marseille; **Centrolophus morio* Cuvier and Valenciennes, 1833 (ascribed to Lacépède), from the Mediterranean Sea; **Schedophilus elongatus* Johnson, 1862, from Madeira; and **Centrolophus valenciennesi* Moreau, 1881, from Marseille.

The two species described from the Southern Hemisphere, here considered synonyms of *niger*, are: *Centrolophus maoricus* Ogilby, 1893, Australia and New Zealand. Counts made on two specimens of this nominal species fell at the high end of the range for *C. niger*, as do the counts for one small specimen reported by Regan (1914).

Centrolophus irwini (Gilchrist and von Bonde, 1923) = *Centrolophodes irwini* Gilchrist and von Bonde. South Africa. The counts reported for the holotype likewise fall at the high end of the range for *C. niger*. *Mupus bifasciatus* Smith, 1961, based on two small specimens, is almost certainly the same fish. There is little cause to doubt that the South African and Australian forms belong to the same population.

Genus *ICICHTHYS* Jordan and Gilbert, 1880

Figure 15

Icichthys Jordan and Gilbert, 1880:305. (Type species: **Icichthys lockingtoni* Jordan and Gilbert, 1880:305, by original designation. Point Reyes, California.)

The combination of elongate soft body, continuous dorsal fin originating well be-

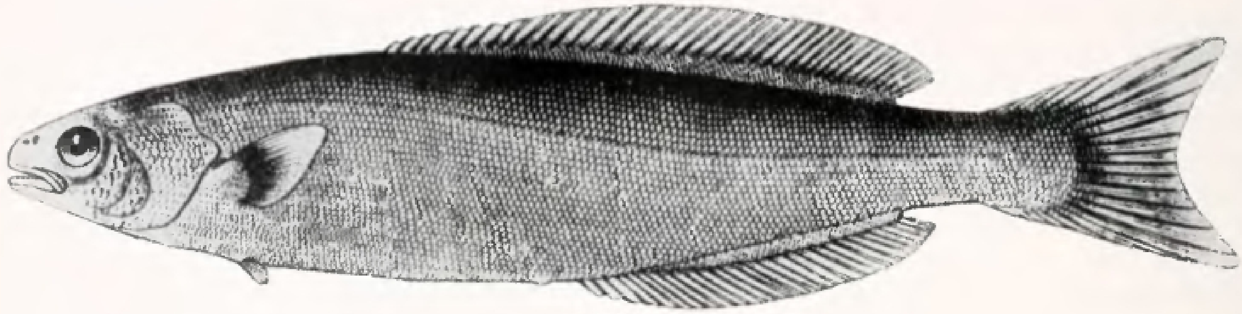

Figure 15. *Icichthys lockingtoni*, drawing of a 390-mm specimen, from Parin, 1958.

hind pectoral insertion, toothless palate, moderate scales covering opercles and cheek, 100 to 130 scales in the lateral line, and 50 to 60 vertebrae, distinguishes *Icichthys* from all other stromateoid genera. The name, a masculine noun, is from the Greek *εἴκω*, to yield, + *ἰχθύς*, fish, in reference to the fish's flexible soft body.

Description. Body elongate, maximum depth less than 25 per cent of the standard length except in small specimens; musculature soft. Peduncle broad, compressed, of moderate length. Dorsal fin originating well behind insertion of pectoral fins, continuous, a few very weak spines graduating to the rays, 39–43 elements in all. A mid-dorsal ridge preceding the fin. Anus at about mid-body. Anal fin originating slightly behind middle of body, three weak spines precede the rays, 27 to 32 elements in all. Median fins with compressed fleshy bases. Pectoral fin rounded, base fleshy. Pelvic fins small, inserting directly under insertion of pectoral fins, not attached to abdomen with a membrane, folding into an insignificant groove. Caudal fin broad, slightly rounded or emarginate. Moderate cycloid scales with prominent circuli, not especially deciduous, covering bases of median fins. Lateral line slightly arched anteriorly, straightening out over anterior part of anal fin and extending onto peduncle; lateral line scales around 120. Skin fairly thick; subdermal canal system not well developed, pores very small. Head around 25 per cent of the standard length, its profile sloping and the pores not prominent. Top of head not scaled, naked skin not projecting backward over the nape. Eye of moderate size, no adipose tissue. Nostrils near tip of truncate snout, both round. Angle of gape extending below eye. Premaxillary not protractile. Only upper margin of upper jaw covered by lacrimal bone when mouth is closed. Very slender supramaxillary present. Jaw teeth minute, pointed, uniserial, close-set; vomer, palatines, and basibranchials toothless. Opercle and preopercle thin, both well scaled, margins with very fine spinules; opercle with two weak flat spines; angle of preopercle rounded, bulging backward. Cheek scaled. Gill-rakers heavy, a little shorter than the filaments, toothed on inner edge, spaced, about 10 on lower limb of first arch. Pseudobranch small. Seven branchiostegal rays, five on the ceratohyal, two on the epihyal. Scapula not prominent. Vertebrae 50 to 60. Caudal skeleton with three autogenous haemal spines, six hypurals, and two or three epurals. Stomach a simple sac; intestine long. Pyloric caeca about 10, digitiform, slender.

Color in preservative tan to dark brown, the median fins and pelvics darker than the body. No pattern, slight countershading.

Natural history. Young *Icichthys* are commonly found swimming under or within medusae (Jordan, 1923a; Hobbs, 1929; Fitch, 1949), and sometimes appear in fair number off the California coast. Large adults have been taken by drift-nets (Parin,

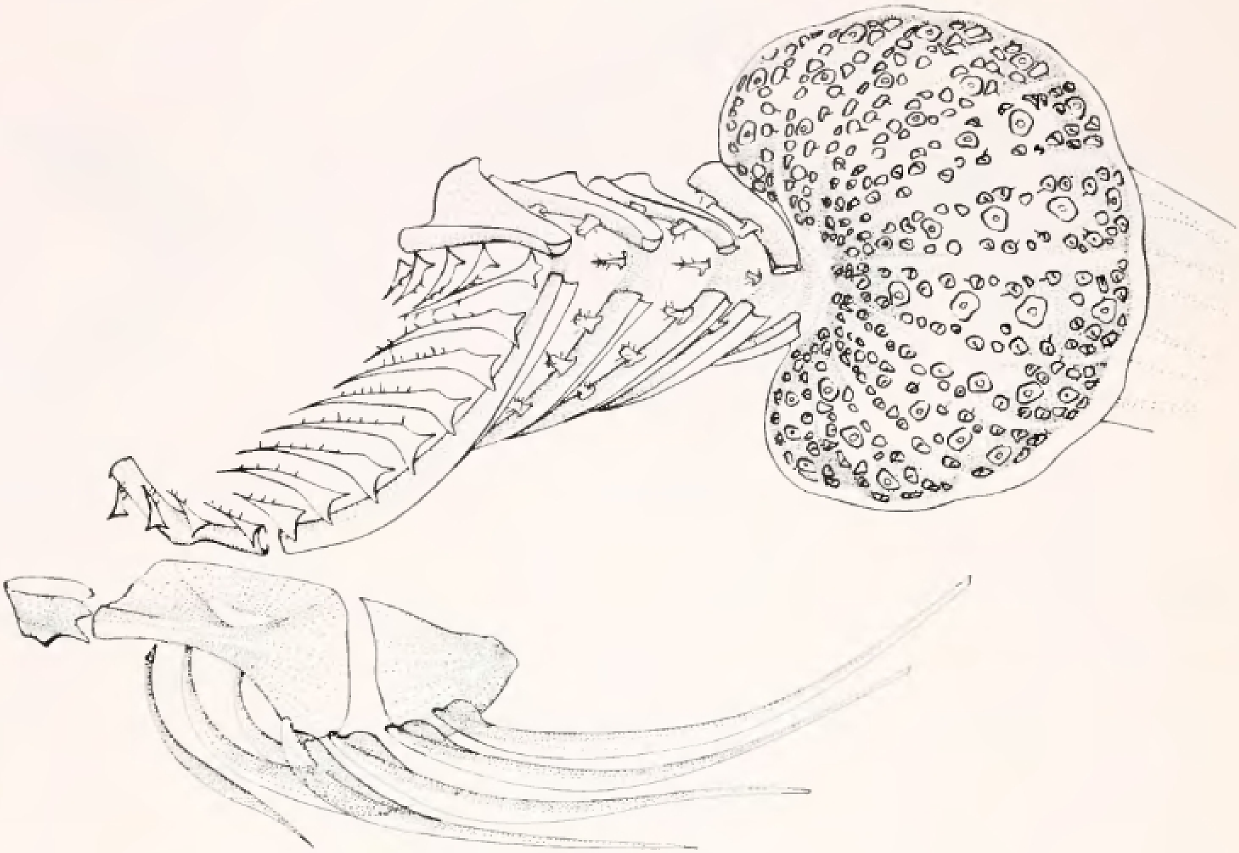

Figure 16. Branchial region of *Icichthys lockingtoni*, drawing of a cleared-and-stained preparation from a 173-mm specimen. Elements identified in Figure 2.

1958) and by deep trawl (Ueno, 1954), but are very rare. All recorded captures are from deep water. *Icichthys* is certainly oceanic, and, judging from its soft tissues, somber color, and rare occurrence, it may well live as an adult in the bathypelagic realms. Ueno's (1954) 362-mm SL specimen is the largest known.

Icichthys is found in cool waters. The appearance of twelve small specimens off the Cape of Manazuru, Japan, in the spring of 1963 corresponded with an unusual influx of *ca.* 15°C water in this normally warmer area (Abe, 1963).

Relationships. Externally, *Icichthys* very closely resembles *Centrolophus*, with which it has been synonymized by Parin (1958). However, in several respects—the scalation on the cheeks, the caudal skeleton, and the greatly increased number of vertebrae—*Icichthys* differs from *Centrolophus* enough to warrant generic recognition.

The structure of the pharyngeal sacs (Fig. 16, *cf.* Fig. 14) and the general appearance of *Icichthys* suggest a very close relationship with *Centrolophus*. *Icichthys* has lost an epural in the caudal skeleton (Fig. 17), and is almost certainly the derived form. But *Centrolophus*, having lost the cheek scales retained in *Icichthys*, cannot be the direct ancestor. Both must have branched from a common stem. It is perhaps significant that the ranges of the two genera complement each other nicely (Fig. 52).

Icichthys, a member of the most primitive group of stromateoids, has a very high number of vertebrae, an advanced condition. The number, between 50 and 60, is slightly more than twice the basic perciform number, 25, found in other centrolophids.

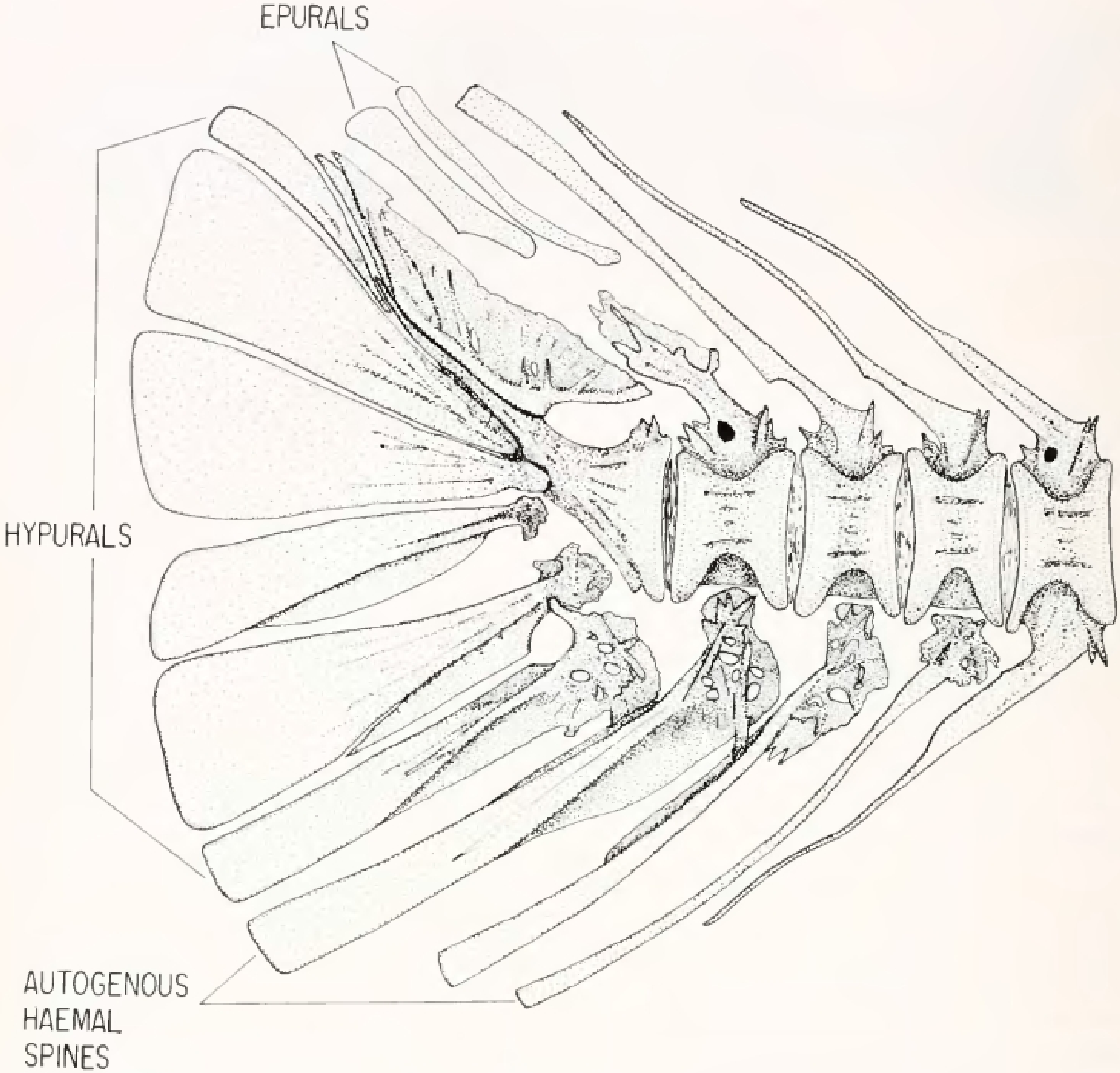

Figure 17. Caudal skeleton of *Icichthys lockingtoni*, drawing of a cleared-and-stained preparation from a 43-mm specimen, SU 41028. All elements identified in Figure 1.

The number of elements in the median fins is about the same as in *Centrolophus*, but there are more than twice the number of free interneurals ahead of the dorsal fin. The evidence is at least suggestive that *Icichthys* may have arisen by polyploidy; chromosome counts would be most instructive. The three autogenous haemal spines in the tail (Fig. 17), in contrast to the two of all other perciforms (Gosline, 1961a), are undoubtedly a by-product of the increased number of vertebrae.

Species. The genus is restricted to the cooler waters of the North Pacific and of New Zealand, from whence a new species is being described (Haedrich, in press). Abe (1963) reports more pyloric caeca and slightly fewer vertebrae for his Japanese specimens than are found in specimens from off California. Many more specimens will be needed to see whether these differences are significant. From knowledge of *Icichthys*' apparent bathypelagic habitat, it

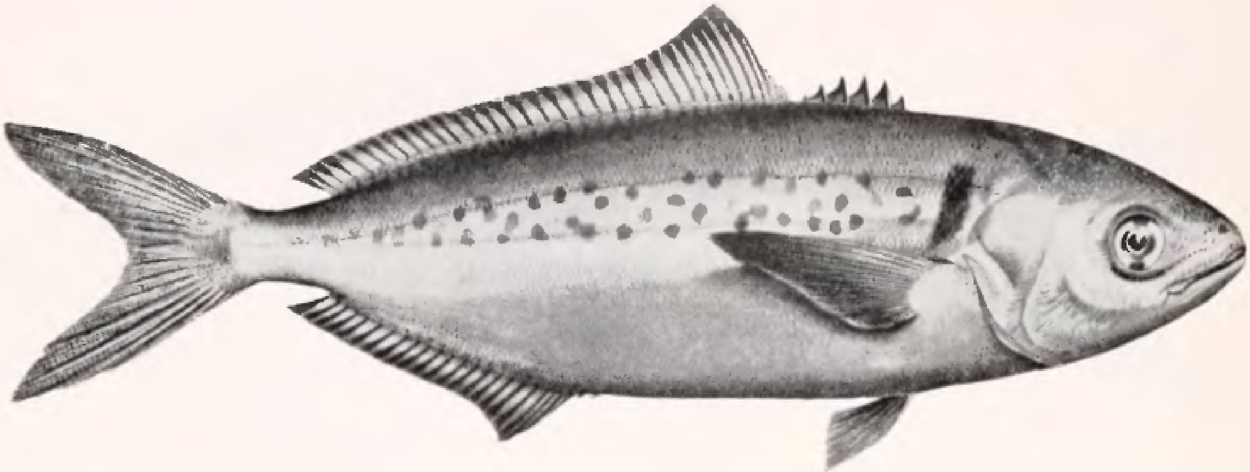

Figure 18. *Seriolella punctata*, an elongate species, drawing of an approximately 250-mm specimen, from McCulloch, 1911.

seems best for the time being to recognize but one North Pacific species:

**Icichthys lockingtoni* Jordan and Gilbert, 1880. California to Japan, type locality Point Reyes, California. D 39–43 (total elements). A 27–32 (total elements). P 18–21. Gill-rakers 4–6 + 1 + 11–13, usually 18 total. Vertebrae 56–60. Synonyms, both based on small specimens from the coast of California, are **Schedophilus heathi* Gilbert, 1904, and **Centrolophus californicus* Hobbs, 1929.

Genus *SERIOLELLA* Guichenot, 1848

Figures 18, 19

Seriolella Guichenot, 1848:238. (Type species: *Seriolella porosa* Guichenot, 1848:239, by subsequent designation of Jordan, 1923:238. Chile.)

Neptomenus Günther, 1860:389. (Type species: *Neptomenus brama* Günther, 1860:340, by original designation. New Zealand.)

The combination of at least seven more dorsal than anal finrays, short stout spines not increasing in length to the rays in the dorsal fin, toothless palate, pelvic insertion behind the pectoral insertion, supramaxillary bone present, and lateral line following the dorsal profile, distinguishes *Seriolella* from all other stromateoid genera. The name, a feminine noun, is the diminutive of *Seriola*, a carangid genus. Ultimately from the Latin *seria*, an oblong earthen vessel, it doubtless refers to the shape of the fish.

Description. Body moderately deep to elongate, maximum depth 25 to 40 per cent of the standard length, compressed but fairly thick; musculature firm. Peduncle stout. Two dorsal fins, the first originating over or slightly behind insertion of pectoral fins, with seven to nine short spines. Usually the third, fourth, and fifth spines are the longest, the longest spine less than half the length of the longest dorsal finray. Second dorsal with 25 to 40 finrays, the anteriormost the longest. Anal and genital pore slightly before or behind mid-body, in a slit. Anal fin originating at or behind mid-body, three spines increase in length to the 18 to 25 rays, the anteriormost finrays the longest. Number of dorsal finrays exceeds number of anal finrays by more than seven. Pectoral fins rounded in the young, long and falcate in the adult. Pelvic fins inserting just under end of or behind pectoral fin base, attached to the abdomen by a small membrane and folding into a shallow groove. Caudal fin broad and forked. Large cycloid scales, very deciduous, covering fleshy bases of the median fins. Lateral line moderately high, following dorsal profile and extending onto peduncle. Skin thin; main subdermal canal along inter-

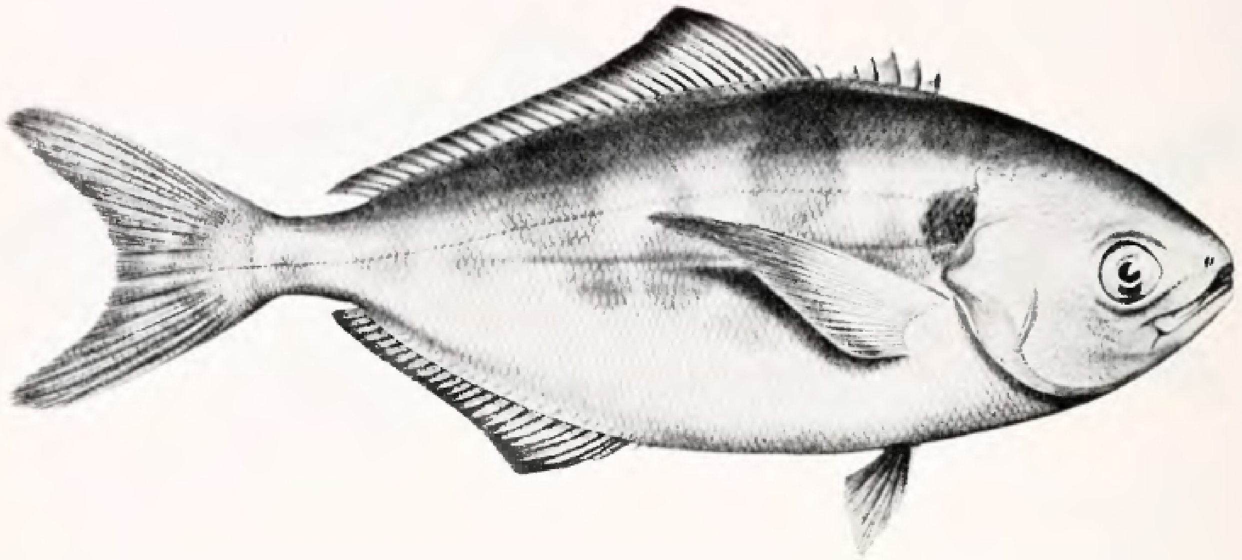

Figure 19. *Seriolella brama*, a deep-bodied species, drawing of an approximately 250-mm specimen, from McCulloch, 1911.

muscular septum and side branches usually visible, pores small. Head about 30 to 35 per cent of the standard length. Top of head naked, fine canal network and small pores usually visible, naked skin projecting backwards over the nape. Eye moderate to large. Adipose tissue around eye well developed and extending forward around the nostrils. Nostrils near tip of pointed or truncate snout, small, the anterior round, the posterior a vertical slit. Maxillary extending below eye but angle of gape before eye. Premaxillary not protractile. Lacrimal bone partially covering upper jaw when mouth is closed, ventral border of premaxillary and end of maxillary remaining exposed. Supramaxillary present. Jaw teeth small to minute, pointed, uniserial, close-set or slightly spaced, covered laterally by a membrane; vomer, palatines, and basibranchials toothless. Opercle and preopercle thin, margins entire or finely denticulate; opercle with two weak flat spines, scaled, the scales covered by skin; preopercle not scaled, angle rounded, bulging backward. Cheek scaled, the scales covered by thick skin and not visible without dissection. Gill-rakers one-half to one-third the length of the filaments, toothed on inner edge, slightly spaced, 14 to 18 on lower limb of first arch; no rudimentary rakers under the small pseudobranch. Seven branchiostegal rays, five on the ceratohyal, two on the epihyal, the tips of the branchiostegals pointed. Posterior border of scapula free from the body. Vertebrae 10 + 15, or 11 + 14 = 25. In the adult, hypurals 2 + 3 and 4 + 5 closely conjoined or even partially fused, three epurals. Sclerotic bones well ossified, subocular shelf present on second suborbital. Stomach a simple sac; intestine long. Pyloric caeca numerous and forming a dendritic mass.

Color in preservative brown or bluish, darker above than below, the sides sometimes with a silvery overlay. Usually a prominent dark blotch on the shoulder at the beginning of the lateral line; smaller spots often present on sides. Fins usually a little lighter than the body, but black-edged. Inside of mouth and gill cavity light.

Natural history. In contrast to most other centrolophids, the species of *Seriolella* are coastal fishes. Schools of them occur from 150 fathoms in towards the coasts, and some species even enter estuaries (Munro, 1958). Others live in kelp beds, apparently not deeper than 40 fathoms (Scott, 1962).

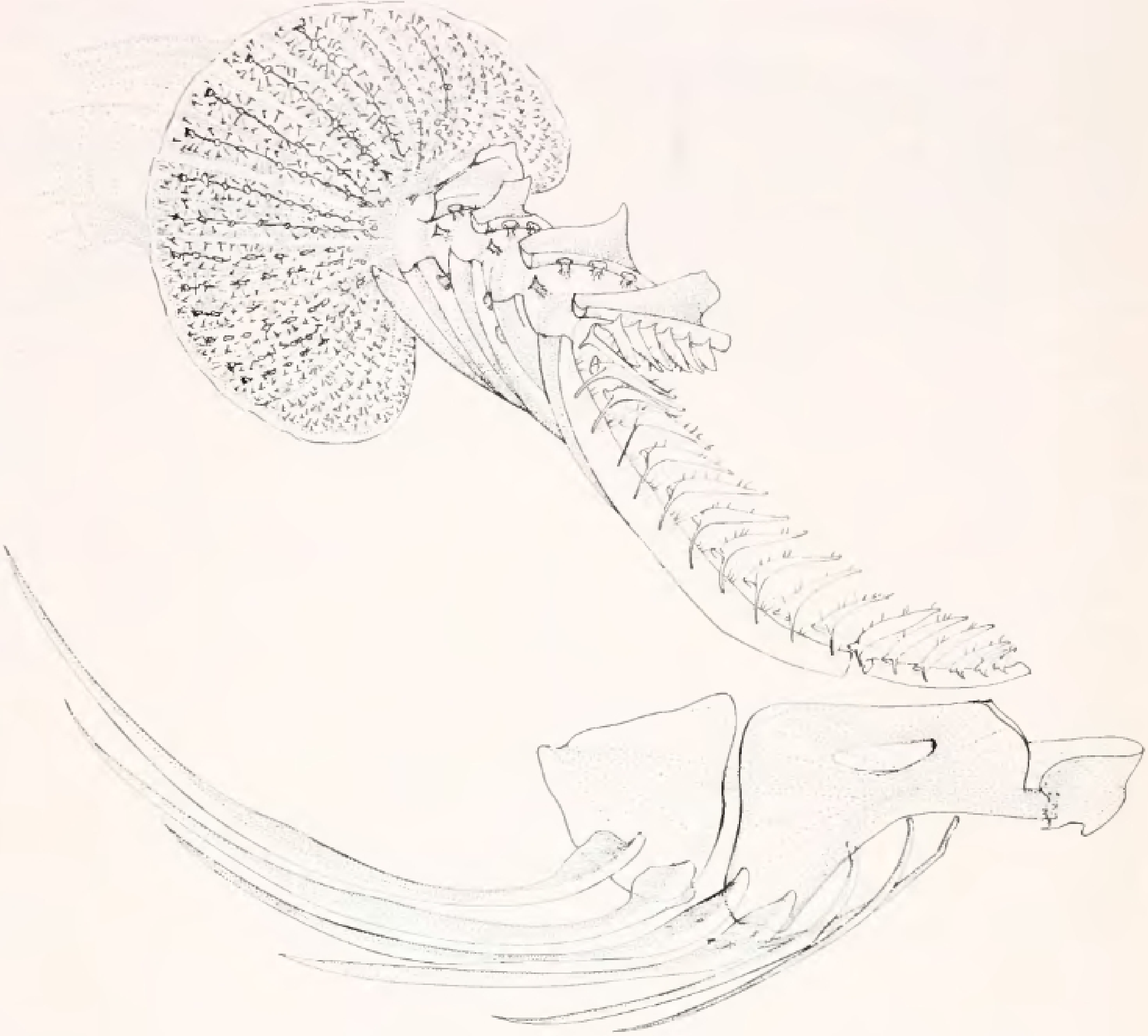

Figure 20. Branchial region of *Seriolella violacea*, drawing of a cleared-and-stained preparation from a 188-mm specimen, USNM 77593. Elements identified in Figure 2.

Nichols and Murphy (1922) report a young Peruvian specimen from under a jellyfish.

Seriolella is the subject of a modest fishery in Chile (Mann, 1953). In Peru, nine- or ten-inch specimens are at times so common that they are caught by jigging (Nichols and Murphy, 1922). These fish are occasionally taken by fishermen in Australia and New Zealand, but apparently are not sought-after commercial species there.

Relationships. Seriolella, with its probable off-shoot *Psenopsis*, represents the advanced condition among centrolophids. *Seriolella* is derived from a *Hyperoglyphe*-like stock, with which it shares the short stout spines in the dorsal fin and the fluted first haemal spine curving backward to meet the first interhaemal. The slender pointed branchiostegal rays (Fig. 20), the numerous bands of small papillae in the pharyngeal sacs, the well ossified sclerotic bones, and the partial fusion of hypurals 2 + 3 and 4 + 5 with growth are all advanced characters, and approach the nomeid grade. *S. violacea*, from Peru, comes near to bridging the gap between *Hyperoglyphe* and *Seriolella.*

Seriolella has given rise to *Psenopsis.* The pharyngeal sacs and caudal skeleton of both are very similar. Both genera have, in most species, well ossified sclerotic bones and a dark blotch on the shoulder. *Seriolella*, however, is closer to *Hyperoglyphe* in the possession of a supramaxillary, which has been lost in *Psenopsis.*

Species. Seriolella is restricted to the cool temperate waters of the Southern Hemisphere. About a dozen species have been described; the majority are known to me only from published descriptions. I have been able to examine only a few *Seriolella*, most of them from South America. The nominal species in the genus are:

Seriolella punctata (Bloch and Schneider, 1801) = *Scomber punctatus* Bloch and Schneider. Southern Australia, Tasmania, and New Zealand. Elongate. D VI–VII, 34–39. A III 21–24. P 19–22. Gill-rakers usually 6 + 1 + 14–15. Vertebrae 10 + 15. Synonyms are **Neptomenus dobula* Günther, 1869, from Tasmania, and *Neptomenus bilineatus* Hutton, 1872, from Wellington Harbor, New Zealand.

Seriolella violacea Guichenot, 1848. Chile and Peru, type locality Valparaiso. Moderately deep. D VII–VIII, 25–28. A III 18–20. P 21–22. Gill-rakers 5–7 + 1 + 16–18. Vertebrae 11 + 14. This fish is the "cojinoba" of Chilean fisheries literature (Mann, 1953). Synonyms are *Centrolophus peruanus* Steindachner, 1874, from Callao, Peru, and **Neptomenus crassus* Starks, 1906, also from Callao.

Seriolella porosa Guichenot, 1848. Chile and Peru, type locality Valparaiso. Elongate. D VI–VIII, 34–38. A III 22–23. P 19–21. Gill-rakers usually 6 + 1 + 14–15. Vertebrae 10 + 15. This species has the same counts as S. *punctata* (Bloch and Schneider, 1801), and was synonymized with S. *dobula* (Günther, 1869) [here considered = S. *punctata*] by Regan (1902). It is unlikely that an essentially coastal fish such as *Seriolella* would regularly cross the broad expanse of ocean between South America and Australia. With closer study S. *porosa*, S. *punctata*, and possibly S. *dobula* will probably prove distinct.

Seriolella brama (Günther, 1860) = *Neptomenus brama* Günther. Southern Australia and New Zealand, type locality New Zealand. Deep-bodied. D VI–VIII, 26–33. A III 21–23. P 20–21. Gill-rakers 7 + 1 + 16. Vertebrae 10 + 15. *Neptomenus travale* Castelnau, 1872, from New Zealand is a synonym.

Seriolella velaini Sauvage, 1879. Island of St. Paul, Indian Ocean. Moderately deep. D VIII, 27. A III 20. (From Regan, 1902.)

Seriolella christopherseni Sivertsen, 1945. Tristan da Cunha. Atlantic Ocean. D VI, 28. A III 20. Moderately deep. (From Sivertsen, 1945.)

Seriolella noel Whitley, 1958, is based on one battered specimen from Sydney, Australia, standard length 331 mm. The counts given are D X + 31?; A 2–30; P 14; gill-rakers 8 + 16; lateral line scales 95 + 8. The description is inadequate to tell even to what genus this fish belongs, but it is decidedly not a *Seriolella.* The ten dorsal spines indicate it may belong in the family Nomeidae.

Genus *PSENOPSIS* Gill, 1862

Figure 21

Psenopsis Gill, 1862:127. (Type species: *Trachinotus anomalus* Temminck and Schlegel, 1850: 107, by monotypy. Japan.)

Bathyseriola Alcock, 1890:202. (Type species: **Bathyseriola cyanea* Alcock, 1890:202, by monotypy. Ganjam Coast, India.)

The combination of dorsal and anal fin-rays in almost equal numbers, spines graduating to the rays, toothless palate, pelvic insertion directly under the pectoral insertion, broad forward scoop in the opercle below the second opercular spine, and no supramaxillary distinguishes *Psenopsis* from all other stromateoid genera. The name, a feminine noun, is from the Greek ψήνη, *Psenes* + ὄψις, appearance, drawing atten-

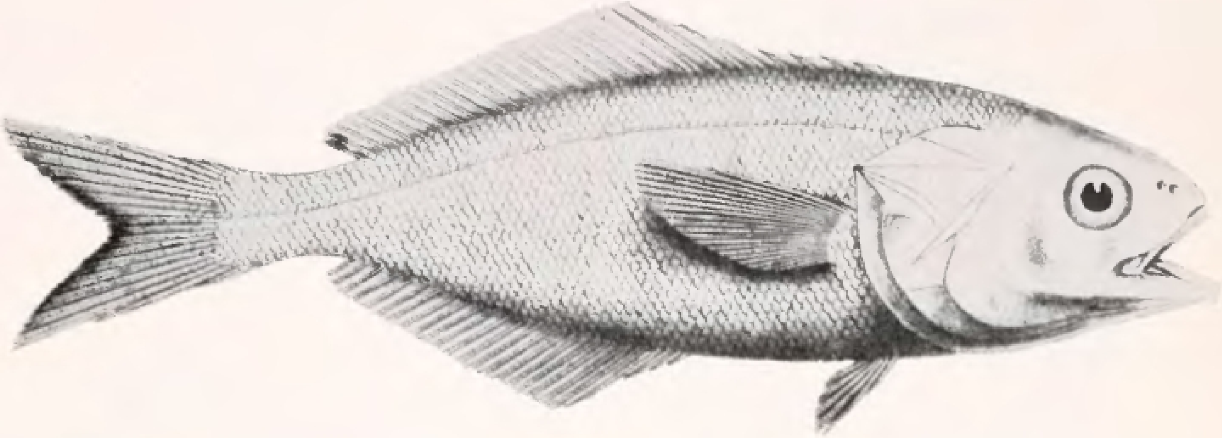

Figure 21. *Psenopsis cyanea*, an elongate species, drawing of a 139-mm specimen, BMNH 1890. 11. 28. 9, from Alcock, 1892.

tion to the superficial similarity between these two genera.

Description. Body moderately deep to deep, maximum depth 30 to 45 per cent of the standard length, compressed but fairly thick; musculature soft. Peduncle short, deep, and compressed. Dorsal fin originating over or slightly behind insertion of pectoral fins, continuous, with five to seven short spines increasing in length to the 27 to 32 rays. The last spine the longest, but less than half the length of the longest dorsal finray. Anal and genital pore well before or at mid-body, in a slit. Anal fin originating well before or slightly behind mid-body, three spines increase in length to the 22 to 29 rays. Number of dorsal finrays never exceeds number of anal finrays by more than five. Pectoral fins rounded in the young, usually produced in the adult. Pelvic fins inserting directly under origin of the pectoral fin, attached to the abdomen by a small membrane and folding into a groove which reaches to the anus. Caudal fin broad, slightly forked. Small cycloid scales, very deciduous, covering fleshy bases of the median fins. Lateral line moderately high, following dorsal profile and extending onto peduncle. Skin very thin; main subdermal canal along intermuscular septum and side branches clearly visible, canals particularly dense on back, pores very small. Head around 30 per cent of the standard length. Top of head naked, minute pores faintly visible, naked skin not projecting or projecting only slightly backwards over the nape. Eye moderate to large. Adipose tissue around eye developed and extending forward around the nostrils. Nostrils near tip of truncate snout, moderate in size, the anterior round, the posterior a slit. Maxillary extending below eye, angle of gape at anterior border of eye. Premaxillary not protractile. Upper jaw covered completely by lacrimal bone when mouth is closed. Supramaxillary absent. Jaw teeth minute, pointed, uniserial, close-set, covered laterally by a membrane; vomer, palatines, and basibranchials toothless. Opercle and preopercle thin, not scaled, margins entire or finely denticulate; opercle with two weak flat spines; under the second spine the bone is Ƨ-shaped, the upper indentation reaching almost to the preopercle and covered with uncalcified membrane; angle of preopercle rounded, bulging backwards significantly, the margin scalloped in very small specimens. Gill-rakers about half the length of the filaments, toothed on inner edge, spaced, about 13 on lower limb of first arch; no rudimentary rakers under small pseudobranch. Seven branchiostegal rays, five on the ceratohyal, two on the epihyal, the tips of the branchi-

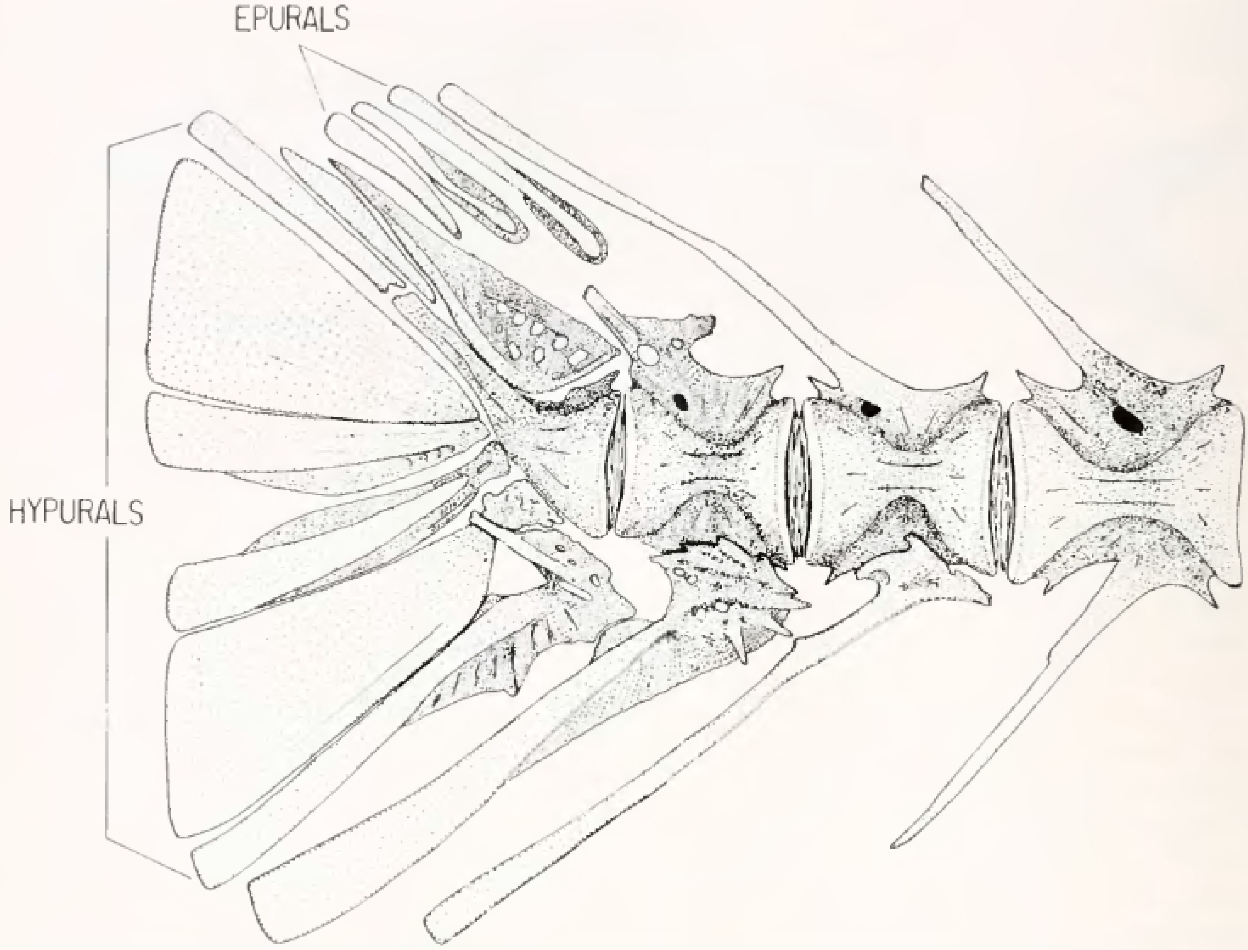

Figure 22. Caudal skeleton of *Psenopsis anomala*, drawing of a cleared-and-stained preparation from a 40-mm specimen, ABE 62-656. All elements identified in Figure 1.

ostegals pointed. Scapula visible. Vertebrae 10 + 15 = 25. In the adult, hypurals 2 + 3 and 4 + 5 closely conjoined, three epurals. Sclerotic bones well ossified, subocular shelf present on second suborbital. Stomach a simple sac; intestine long. Pyloric caeca very numerous, in a mass resembling a raspberry.

Color in preservative brown or bluish, deep-bodied form often with a silvery or whitish overlay. Deep-bodied form countershaded, others uniform. Usually a prominent black spot on shoulder at beginning of lateral line. Fins a little lighter than the body. Opercles and peritoneum silvery or blackish. Inside of mouth light, gill cavity dark.

Natural history. Though fished commercially in Japan, very little is known of the habits of these fishes. Young *Psenopsis* have been reported in association with medusae (Shojima, 1961). The adults of *P. anomala*, at least, live nearer the coasts and in shallower water than most centrolophids. Large schools are taken by near-shore trap nets in Japan. Adult specimens of *P. cyanea* were taken off Cananore in 1½ fathoms.

Psenopsis is one of the smaller centrolophids. Specimens of 180 mm SL are fully mature. Few exceed 200 mm.

Relationships. Psenopsis, with *Seriolella*, is the most evolutionarily advanced centrolophid. The slender tapering branchiostegal rays and the conjunction of hypurals 2 + 4 and 4 + 5 (Fig. 22) with growth

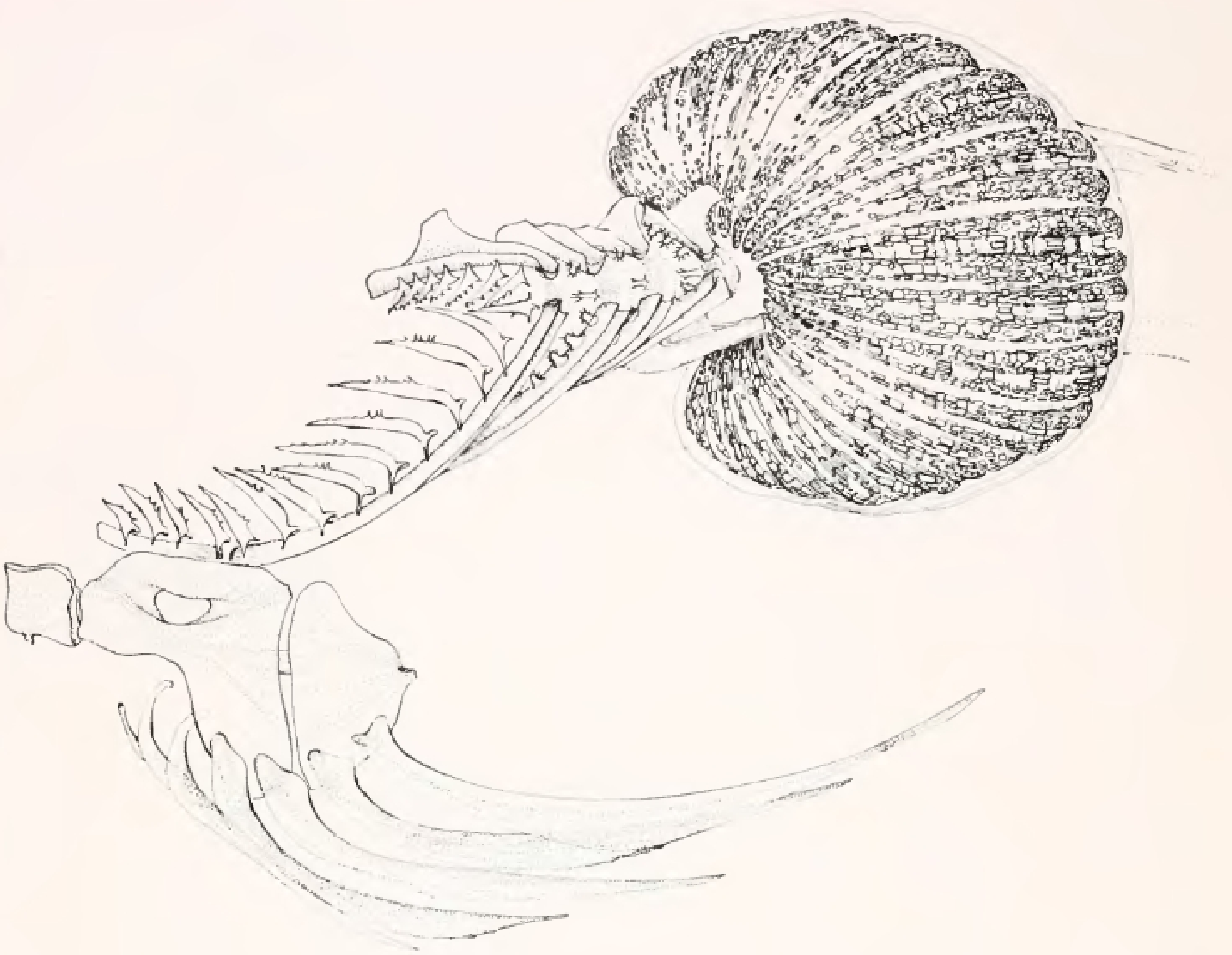

Figure 23. Branchial region of *Psenopsis anomala*, drawing of a cleared-and-stained preparation from a 150-mm specimen. Elements identified in Figure 2.

approach the nomeid grade. The pharyngeal sacs (Fig. 23) are larger, and there are more numerous bands of small papillae than are found in *Hyperoglyphe* or *Centrolophus*. The well ossified sclerotic bones, the absence of a supramaxillary bone, the smallish mouth, the deciduous scales, and the dorsal fin with only slightly more fin-rays than the anal suggest that *Psenopsis* may be near the base of the line leading to the Stromateidae. *Seriolella*, which retains the supramaxillary lost in *Psenopsis*, is its closest relative within the centrolophids.

Species. *Psenopsis* is an Indo-Pacific genus, found in India, Japan, northwest Australia, and the East Indies. There are four allopatric species, one of them undescribed. Little confusion has arisen regarding the identification of these fishes, and there are no problems of synonymy. The species are:

Psenopsis anomala (Temminck and Schlegel, 1850) = *Trachinotus anomalus* Temminck and Schlegel. China and southern Japan, type locality Tokyo. Deep-bodied. D V–VII, 27–32. A III 25–29. P 20–23. Gill-rakers usually 6 + 1 + 13, 12–15 on lower limb of first arch, 18–21 total. Vertebrae 10 + 15 (skel.). This species is the "ibodai" of Japanese fisheries literature, and is common from Hong Kong to Tokyo and into the Sea of Japan as far north as Hokkaido. It forms the basis of an important fishery. *P. shojimai* Ochiai and Mori,

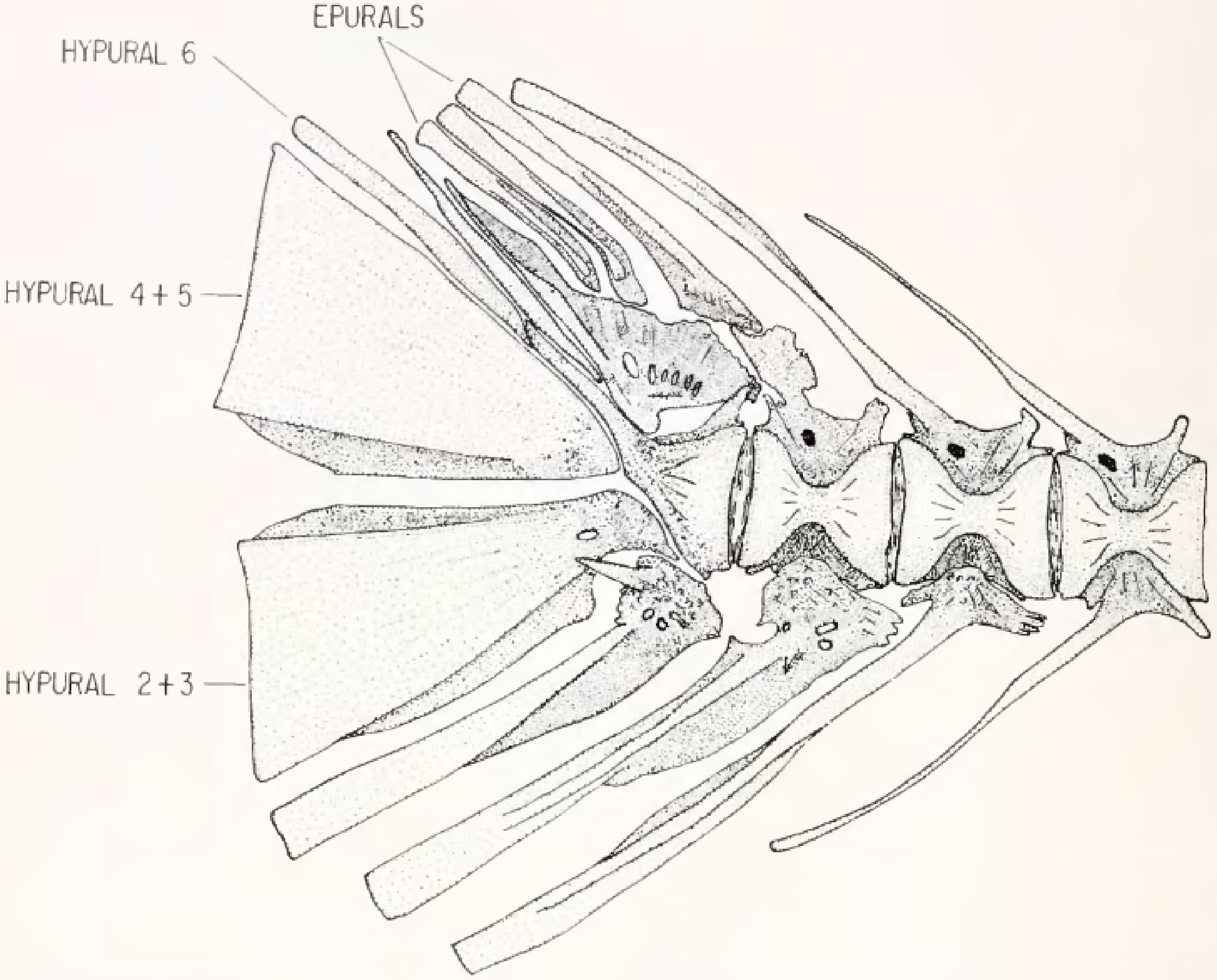

Figure 24. Caudal skeleton of *Nomeus gronovii*, drawing of a cleared-and-stained preparation from an 87-mm specimen. All elements identified in Figure 1.

1965, from the Sea of Japan is a probable synonym.

Psenopsis humerosa Munro, 1958. Dampier Archipelago, N. W. Australia. Deep-bodied. D VII, 28. A III 25. P 22. Gill-rakers 12 on lower limb of first arch (from Munro, 1958). Probably a good species, little differentiated from *P. anomala*.

Psenopsis cyanea (Alcock, 1890) = **Bathyseriola cyanea* Alcock, type locality, Ganjam Coast, India. Elongate. D VI, 25–26. A III 22–23. P 20. Gill-rakers 5 + 1 + 14. Vertebrae 10 + 15.

Family NOMEIDAE

Type genus: *Nomeus* Cuvier, 1817

Pasteurs. Cuvier and Valenciennes, 1833:242 (descr.).

Nomeina. Günther, 1860:387 (in part, def.).

Nomeidae. Günther, 1880:455 (in part, def.). Jordan and Gilbert, 1882:448 (descr.). Jordan and Evermann, 1896:948 (descr., North America). Jordan, 1923:183 (in part, list). Berg, 1940:323 (in part, dist.); 1955:249 (in part, dist.). Norman, 1957:503 (in part, def., genera listed).

Psenidae. Auctorum.

Diagnosis. Stromateoid fishes with pelvic fins present in adults, two dorsal fins, teeth on vomer and palatines, six branchiostegal rays, and four hypural and three epural bones in the tail. The papillae in the pharyngeal sacs with stellate bases, arranged in about five broad longitudinal bands.

Description. Body slender to deep, compressed. Two dorsal fins, the first with about ten slender spines folding into a

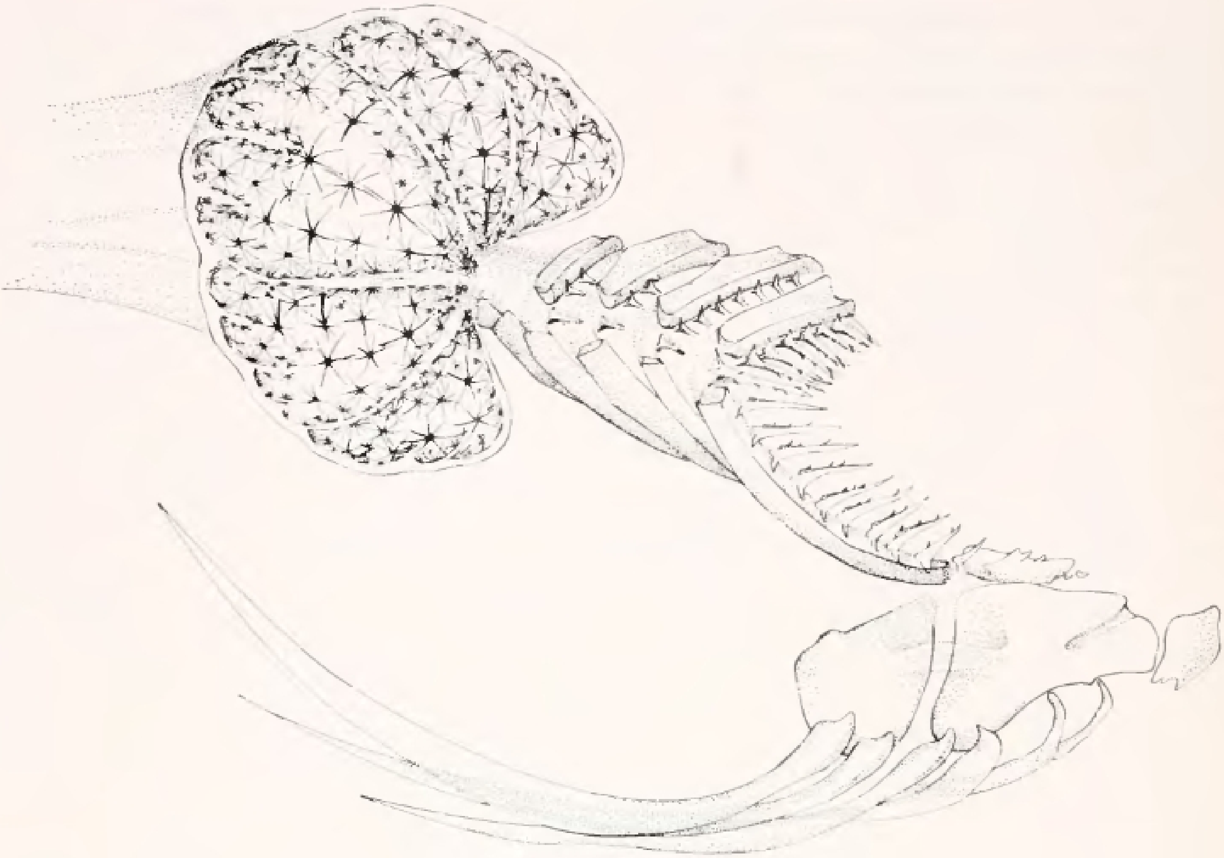

Figure 25. Branchial region of *Nomeus gronovii*, drawing of a cleared-and-stained preparation from a 187-mm specimen, MCZ 35327. Elements identified in Figure 2.

groove, the longest spine at least as long as the longest ray of the second dorsal fin. One to three anal spines, not separated from the rays. Soft dorsal and anal fins approximately the same length. Bases of median fins sheathed by scales. Pelvic fins attached to the abdomen by a thin membrane, folding into a narrow groove, the fins greatly produced and expanded in young *Nomeus* and some *Psenes*. Scales small to very large, cycloid or with very small weak cteni, thin, extremely deciduous. Lateral line high, following dorsal profile and often not extending onto peduncle. Skin thin; subdermal mucous canal system well developed and visible in most; the main canal down the side of the body may be mistaken for a lateral line. Opercular and preopercular margins entire or finely denticulate. Opercle very thin, with two flat, weak spines. Six branchiostegal rays. Mouth small, maxillary rarely extending to below eye. Teeth small, conical, or cusped in some *Psenes*, approximately uniserial in the jaws, present on vomer, palatines, and basibranchials. Supramaxillary absent. Adipose tissue around eye only moderately developed in most. Vertebrae 30 to 38, 41, or 42. Caudal skeleton with four hypurals and three epurals. Pharyngeal sacs with papillae in upper and lower sections, papillae in five to seven broad longitudinal bands. Bases of the papillae stellate, teeth seated on top of a central stalk. Adults usually about a foot long, although a giant *Cubiceps* may exceed three feet. Silvery to bluish-brown, some with conspicuous striped or blotched pattern.

Distribution. Nomeids are oceanic fishes of tropical and subtropical waters. They occur in the Gulf of Mexico, the Caribbean Sea, the Atlantic Ocean, the western Mediterranean Sea, the Indian Ocean, and across the Pacific. Numerous in the waters of the Philippines and southern Japan, they do not seem to enter the shallow South China Sea (Fig. 54).

Relationships. From an evolutionary standpoint, the nomeids are a grade above the centrolophids. There are more vertebrae, fusions have occurred in the hypural fan (Fig. 24), a branchiostegal ray has been lost, and the papillae in the pharyngeal sacs have stellate bases (Fig. 25). Nomeids have teeth on the palate and basibranchials, however, which precludes their derivation from a centrolophid. Probably both families have a common ancestor, and development has been somewhat parallel. The palatal dentition, lost in the Centrolophidae, remains in nomeids. The Nomeidae have passed through the centrolophid stage without leaving living representatives at that level.

The Nomeidae have given rise to two other families, each with a single genus. The tetragonurids, a very highly specialized group, arose early, perhaps from the same line which produced *Psenes*. The similarity between the teeth of *Tetragonurus* and *Psenes pellucidus* is striking, but need not imply too close a relationship. The reappearance of characters in divergent lines of common ancestry is not an unusual phenomenon (Simpson, 1953), and seems widespread in stromateoids.

The ariommids may have been derived more recently. Superficially, they resemble nomeids very much, but the teeth on the palate have been lost, further fusions have taken place in the caudal skeleton, and the pharyngeal sacs are strikingly divergent. The species of the *Cubiceps pauciradiatus* group may share a common ancestor with the Ariommidae. These show a tendency toward the ariommid condition in the reduced palatal dentition, and share with them the very large, deciduous scales and the extremely slender (sometimes even absent) bridge over the anterior vertical canal in the ear.

Key to Nomeid Genera

1 (4). Body elongate, maximum depth usually less than 35 per cent of the standard length, greatest in small specimens. Origin of dorsal fin behind, or directly over in very small specimens, insertion of pectoral fins. 2

2 (3). Anal count I-III 14–25. Insertion of pelvic fins under end or behind base of pectoral fin. An oval patch of knoblike teeth on the tongue. Vertebrae 30 to 33. *Cubiceps*, p. 78. Fig. 26

3 (2). Anal count I-II 24–29. Insertion of pelvic fins before or under insertion of pectoral fin, possibly behind in very large specimens. No patch of teeth on the tongue. Vertebrae 41. .... *Nomeus*, p. 81. Fig. 27

4 (1). Body deep, maximum depth usually greater than 40 per cent of the standard length, but possibly less in very large specimens. Origin of dorsal fin before, or directly over in large specimens, insertion of pectoral fins. .... *Psenes*, p. 84. Fig. 28

Genus *CUBICEPS* Lowe, 1843

Figure 26

Cubiceps Lowe, 1843:82. (Type species: *Seriola*[1] *gracilis* Lowe, 1843:82, by subsequent designation of Jordan and Evermann, 1896:950. Madeira.)

Atimostoma A. Smith, 1849, plate XXIV. (Type species: *Atimostoma capensis* Smith, 1849, plate XXIV, by monotypy. South Africa.)

Navarchus Filippi and Verany, 1859:187. (Type species: *Navarchus sulcatus* Filippi and Verany, 1859:187, by monotypy. Mediterranean. A synonym of *Cubiceps gracilis* Lowe, 1843: 82.)

Trachelocirrhus Doumet, 1863:220. (Type species: *Trachelocirrhus mediterraneus* Doumet, 1863: 222, by monotypy. Sète, France. A synonym of *Cubiceps gracilis* Lowe, 1843:82.)

Mulichthys Lloyd, 1909:156. (Type species: *Mulichthys squamiceps* Lloyd, 1909:158, by monotypy. Arabian Sea.)

Mandelichthys Nichols and Murphy, 1944:247. (Subgenus. Type species: *Cubiceps carinatus* Nichols and Murphy, 1944:245, by monotypy. 180 miles SW of Cape Mala, Panama.)

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[1] Lowe described his fish as a species in the genus *Seriola*, but noted (p. 82), "Still it is not unlikely that a comparison of the two fishes [*gracilis* and *S. bipinnulata* (Quoy and Gaimard)] may warrant . . . their separation from *Seriola* into a genus, which may be called *Cubiceps*."

The combination of elongate body, long winglike pectoral fins, insertion of pelvics behind pectoral fin base, scales on top of head, cheeks, and opercles, and a patch of teeth on the tongue distinguishes *Cubiceps* from all other stromateoid genera. The name, a masculine noun, is from the Greek κύβος, cube, + κεφαλή, head, in reference to the square profile of the fish's head.

Description. Body elongate, maximum depth 25 to 30 per cent of the standard length; musculature firm. Peduncle short, deep, and compressed. Two dorsal fins, scarcely divided. First dorsal originating behind insertion of pectoral fins, with about ten stiff spines folding into a groove, the longest spine longer than the longest ray of the second dorsal. Anterior rays of the second dorsal the longest, those that follow decreasing in length, 14 to 23 finrays in all. Anal and genital papillae behind midbody, in a slit. Anal fin originating behind origin of second dorsal fin, one to three short spines preceding the rays. Anterior rays the longest, those that follow decreasing in length, 14 to 21 finrays in all. Pectoral fin pointed, becoming very long and winglike, the relative length increasing markedly with growth; base of the fin inclined at an angle of 45°. Pelvic fins inserting just under end of or behind pectoral fin base, attached to the abdomen by a small membrane and folding into a deep groove. Expanded coracoid often forming a conspicuous keel along mid-ventral line ahead of pelvics. Caudal fin forked, the lobes often folding over one another. Scales large, cycloid, very deciduous, covering bases of the median fins. Simple tubed scales of lateral line high, following dorsal profile and ending under last dorsal finray or extending onto peduncle. Skin thin; subdermal canals on flanks easily traced. Main canal may be confused with lateral line. Pores to surface small. Head around 32 per cent of the standard length. Top of snout naked, minute pores in naked skin. Scales extending forward on top of head almost to level of the nostrils. Eye large, bony supraorbital ridge pronounced. Adipose tissue around eye well developed, extending forward around the nostrils. Nostrils near tip of blunt snout, small, both round. Maxillary ending under anterior border of eye, angle of gape well before eye. Premaxillary not protractile. Lacrimal bone completely covering upper jaw when mouth is closed, ventral border of maxillary sometimes remaining exposed. Supramaxillary absent. Jaw teeth small, pointed, slightly recurved, usually spaced. Very small teeth usually present on vomer and in a single series on the palatines and basibranchials. An oval patch of low knoblike teeth on the glossohyal. Opercle and preopercle thin, scaled, margins entire or finely denticulate; opercle with two weak flat spines; angle of preopercle slightly rounded, not bulging backward. Cheeks scaled. Gillrakers slender, almost the length of the filaments, toothed on inner edge, fairly close set, 14 to 18 on lower limb of first arch; no rudimentary rakers under the large pseudobranch. Scapula prominent. Vertebrae $13 + 17$ to $15 + 18 = 30$ to 33. Sclerotic bones usually well ossified in adults. Stomach a simple sac; intestine of moderate length. Pyloric caeca very numerous, in a large dendritic mass.

Color in preservative either brownish, darker on the back than on the sides, or bluish above and silvery on the sides. First dorsal blackish, other fins usually the same color as the body, caudal dusky. Iris greyish, often with golden semicircles at anterior and posterior borders. Inside of mouth, gill cavity, and peritoneum dark.

Natural history. All the nomeids are oceanic. Most species are very rarely seen, and little is known of their habits.

Small *Cubiceps gracilis* are very numerous near the Azores, where they are taken in surface nets and from under medusae. By the time these fishes reach about 200 mm SL, they are mature. With the attainment of maturity growth does not stop, but

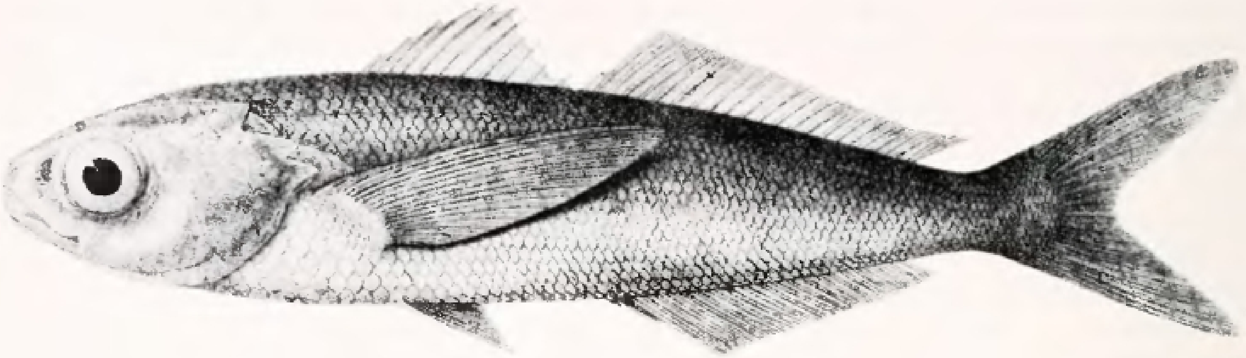

Figure 26. *Cubiceps gracilis*, drawing of a 164-mm specimen, from Günther, 1889.

continues significantly. Specimens near 800 mm SL have been reported from the Mediterranean (Ariola, 1912). With growth, the relative length of the pectoral fin increases markedly.

In the Philippines, *Cubiceps* is caught by using night-lights and lift-nets (Herre and Herald, 1950). Large specimens are taken occasionally by the near-shore winter long-line fishery for swordfish off southern Japan.

Relationships. *Cubiceps* occupies the central position in nomeid evolution. The two other nomeid genera, *Nomeus* and *Psenes*, are certainly derived from *Cubiceps*. In both derived genera the patch of teeth on the tongue has been lost, and there has been a tendency towards an increase in the number of vertebrae and finrays. The papillae in the pharyngeal sacs of *Cubiceps* are very similar to those of *Nomeus* (Fig. 25), but those of *Psenes* are in general smaller (Figs. 29, 30). The caudal skeletons of all three genera are almost identical (Fig. 24).

The Ariommidae have probably evolved from a *Cubiceps*, although the systematic position of the family is far from clear. The ariommids do share certain characters, however, with the fishes of the *Cubiceps pauciradiatus* group, as discussed on pages 77 and 90.

Cubiceps and the tetragonurids both have patches of teeth on the tongue. The jaw teeth, the pharyngeal sacs, and the scales, however, are very different in these two groups. It seems likely that the Tetragonuridae branched off very early from the nomeid stem, but their ancestor may have been a fish similar in many respects to the present-day *Cubiceps*.

Species. *Cubiceps* is found in the temperate and tropical waters of the Atlantic, Pacific, and Indian oceans. It also occurs in the western Mediterranean Sea, and the Gulf of Mexico and Caribbean Sea.

Much confusion surrounds the species of *Cubiceps*. The counts of all described are fairly close. Lacking sufficient comparative material, it is difficult to evaluate the small differences which do occur, for example in vertebral number. There seems to be a great differential in the size attained by the adult. The species of the *Cubiceps pauciradiatus* group may never exceed 200 mm SL (Haedrich, 1965), whereas fishes allied to *Cubiceps gracilis* are reported (Smith, 1849; Ariola, 1912; Abe, 1955a) to approach a meter in length.

The nominal species in the genus *Cubiceps* are:

Cubiceps gracilis (Lowe, 1843) = *Seriola gracilis* Lowe. Atlantic Ocean and western Mediterranean, type locality Madeira, perhaps a world-wide species. D IX–XI, I–II 20–22. A II–III 20–23. P 20–24. Gill-rakers 8–9 + 1 + 14–17. Vertebrae 15 + 18. Synonyms are: *Navarchus sulcatus* Filippi and Verany, 1859, from the Mediterranean; *Trachelocirrhus mediterraneus* Doumet, 1863, from Sète; *Cubiceps lowei* Osorio, 1909, from the Cape Verde Islands; and *Aphareus obtusirostris* Borodin, 1930, from the Azores.

Cubiceps capensis (A. Smith, 1849) = **Atimostoma capensis* Smith. Type locality South Africa. D IX–X, I–III 24–26. A II 22–23. P 16–18. Gill-rakers 8–9 + 1 + 16–17. Vertebrae 14 + 17. The stuffed type is about 900 mm SL. The margin of the opercle between the two flat opercular spines may be strongly serrate in this species. A probable synonym is *Cubiceps niger* Franca, 1957, from Angola.

**Cubiceps pauciradiatus* Günther, 1872. Central and western Pacific Ocean, type locality Misol Island. D X–XII, I 16–18. A I–II 14–17. P 18–19. Gill-rakers 8–9 + 1 + 16. This is a diminutive species, rarely exceeding 160 mm SL. Closely related forms are: **C. longimanus* Fowler, 1934a, *C. carinatus* Nichols and Murphy, 1944, and **C. athenae* Haedrich, 1965. **Cubiceps nesiotes* Fowler, 1938, from Christmas Island, Central Pacific, is a probable synonym.

Cubiceps squamiceps (Lloyd, 1909) = *Mulichthys squamiceps* Lloyd. South Africa to Japan, type locality Arabian Sea. D IX–XI, I–II 19–21. A II–III 18–21. P 18–20. Gill-rakers 8–9 + 1 + 16–17. This is a chunky-looking fish, with a very short peduncle and broad, winglike pectoral. **Cubiceps natalensis* Gilchrist and von Bonde, 1923, is probably a synonym.

**Cubiceps caeruleus* Regan, 1914a. Tasman Sea, type locality Three Kings Island. D X–XI, I–II 21–24. A II–III 21–24. P 19–21. Gill-rakers 7 + 1 + 16–17. Vertebrae 13 + 18. A few of the jaw teeth on the types are long and project like fangs. *Cubiceps baxteri* McCulloch, 1923, based on a damaged specimen 371 mm long, may be the adult.

**Cubiceps longimanus* Fowler, 1934. Western Indian Ocean, type locality Durban. D X–XI, I 15–16. A I–II 15. P 18–20. Gill-rakers 9 + 1 +14. All specimens known are less than 50 mm SL long.

Cubiceps carinatus Nichols and Murphy, 1944. Pacific Coast of Central America, type locality Gulf of Panama. D IX–X, I 14–16. A II 14–15. P 17–19. Gill-rakers 7–8 + 1 + 14–16. Vertebrae 13 + 17. This species has fewer median finrays than the closely related *C. pauciradiatus* Günther, 1872, from the Central and Western Pacific.

**Cubiceps athenae* Haedrich, 1965. East coast of North America. D X–XI, I 15–16. A II 14–15. P 18–19. Gill-rakers 8 + 1 + 16–17. Vertebrae 13 + 18.

Genus *NOMEUS* Cuvier, 1817

Figure 27

Nomeus Cuvier, 1817:315. (Type species: *Gobius gronovii* Gmelin, 1788:1205, by subsequent designation of Jordan and Gilbert, 1882:449.[1] Atlantic Ocean.)

The combination of elongate body, black fanlike pelvic fins with the full length of the trailing edge attached to the abdomen, insertion of the pelvics (usually) ahead of the pectorals, blotched and spotted pattern, and 41 vertebrae distinguishes *Nomeus* from all other stromateoid genera. The name, a masculine noun, is from the Greek *νομεὺς*, herdsman, a translation of the Dutch vernacular "Harder" (Marcgrave, 1648), probably in reference to the fishes' habit of following *Physalia*.

Description. Body elongate, maximum depth around 30 per cent of the standard length; musculature firm. Peduncle slightly tapered, compressed. Two dorsal fins, scarcely divided. First dorsal fin originating over or a little behind insertion of the pectoral fin, with about ten soft spines folding into a deep groove, the longest

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[1] Cuvier and Valenciennes (1833:242) designated *Nomeus mauritii* Cuvier (1817:315) type for the genus. Cuvier's species, however, based on the "Harder" of Marcgrave (1648:153), appeared in name only, the description being later supplied by Cuvier and Valenciennes (1833:243). Under the International Code, a *nomen nudum* is unavailable as a type, and *Nomeus mauritii* Cuvier, 1817, is thus rejected. *Nomeus mauritii* (*non* Cuvier, 1817) Cuvier and Valenciennes, 1833, is a synonym of *Nomeus gronovii* (Gmelin, 1788).

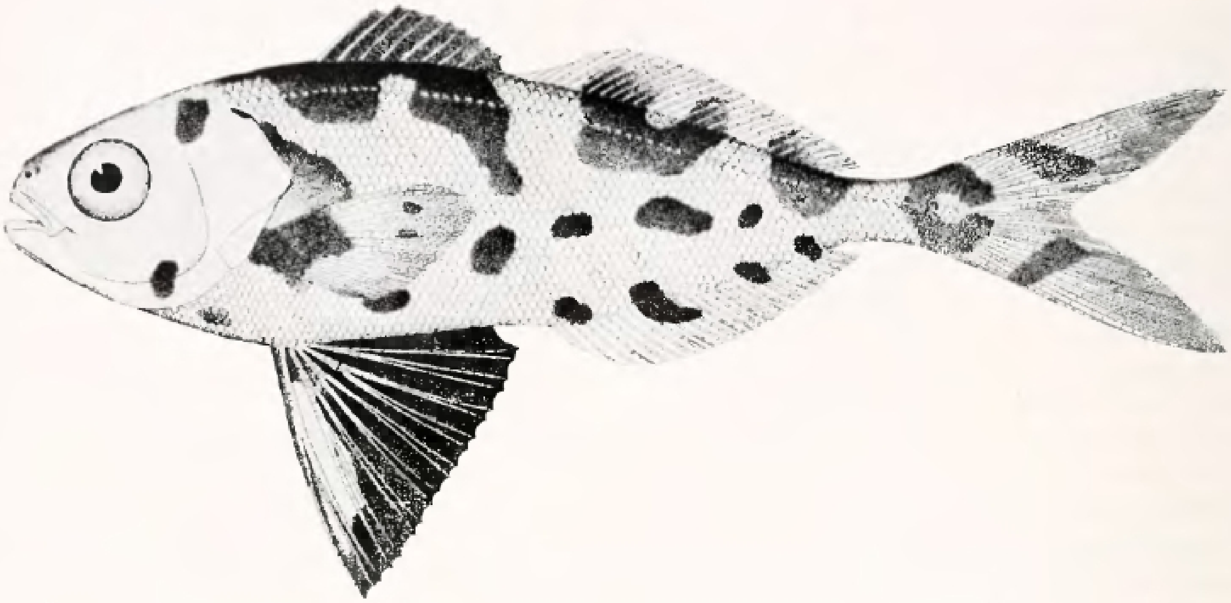

Figure 27. *Nomeus gronovii*, drawing of an approximately 40-mm specimen, courtesy of the Smithsonian Institution.

spine slightly longer than the longest ray of the second dorsal. Anterior rays of the second dorsal fin the longest, those that follow shorter, subequal, 24 to 28 finrays in all. Anal and genital papilla at mid-body, in a deep slit. Anal fin originating under or slightly behind origin of second dorsal fin, one or two weak spines preceding the rays. Anteriormost rays the longest, those that follow shorter, subequal. Pectoral fin rounded in the young, pointed, winglike, in the adult; the relative length increases markedly with growth. Pelvic fins inserting before, or in large specimens under, pectoral fin base, fan-shaped, innermost ray the longest, attached to the abdomen for its entire length by a strong membrane and folding into a deep groove which reaches to the anus. Relative length of the fin decreasing markedly with growth. Caudal fin deeply forked, lobes very long. Scales small, cycloid, very thin, deciduous, covering bases of median fins. Simple tubed scales of lateral line high, following dorsal profile and not appearing to extend onto peduncle. End of lateral line under last dorsal finray in most specimens (in the single large specimen known, the lateral line reaches the caudal base). Skin thin; subdermal canals on flanks easily traced. Main canal may be confused with lateral line. Pores to surface minute. Head around 30 per cent of the standard length. Top of snout naked, minute pores visible in naked skin. Scales extending forward over nape to level of anterior border of the eye. Interorbital space and top of snout covered with adipose tissue. Eye of moderate size, bony supraorbital ridge pronounced. Adipose tissue around eye very well developed, extending forward to cover the lacrimal and surrounding the nostrils. Nostrils on tip of truncate snout, small, the anterior round, the posterior a slit. Maxillary ends under, or before in large specimens, anterior border of the eye, angle of gape well before eye. Premaxillary not protractile. Lacrimal bone almost completely covering upper jaw when mouth is closed, ventral border of maxillary remaining exposed. Supramaxillary absent. Jaw teeth small, pointed, slightly recurved, spaced. Small recurved teeth present on vomer and in a single series on the palatines and basibranchials. No teeth on the glossohyal. Opercle and preopercle thin, scaled, margins very finely denticulate or entire; opercle with two weak hardly defined flat spines; angle of preopercle rounded, bulging backward in large specimens. Cheeks scaled. Gill-rakers slender, half the length of the filaments, toothed on inner edge, fairly close-set, about 16 on lower limb of first arch; sometimes a few rudimentary rakers under the large pseudobranch. Six branchiostegal rays, four on the ceratohyal, two on the epihyal. Scapula prominent. Vertebrae 15 + 26 = 41. In the single large specimen known, the sclerotic bones are well ossified. Stomach a simple sac; intestine of moderate length. Pyloric caeca numerous, in a small dendritic mass.

Color in life bright blue above, blotched and spotted with blue on the brilliant silvery sides. In preservative, the base color is tan, the blotches and spots appearing dark brown. Median fins with about three dark stripes. First dorsal and pelvics black, pectorals light. The single large specimen known is uniform dark brown. Eye usually greyish; in the large specimen the iris is golden, divided by a dark vertical bar. Inside of mouth, gill cavity, and peritoneum light.

Natural history. The association between *Nomeus* and *Physalia* is commonly cited as an example of commensalism, but actually very little is known about the true nature of the association or about the life histories of the animals involved. *Nomeus* has been observed eating *Physalia* (Kato, 1933) and *vice versa* (Garman, 1896). In comparison to other fishes, however, *Nomeus* is relatively immune to the toxin of the siphonophore (Lane, 1960).

The eggs and larvae of *Nomeus* are not known. Fishes of 10-mm SL have been taken from under *Physalia*, however, indicating that the association must form early in the fish's life. I have seen 150-mm SL specimens also taken with *Physalia*. These fishes appeared to be adults, but none were ripe. The largest known specimen of *Nomeus* was taken with a bottom trawl in the Caribbean Sea. This 225-mm specimen was apparently not in association with *Physalia*, was living fairly deep in the water, and was a uniform dark brown instead of blotched like smaller specimens. This fish appeared to be a mature male. Many young stromateoids live with jellyfishes, have a blotched or mottled color pattern, and both desert their coelenterate host and become uniformly colored with growth. The discovery of this large, dark *Nomeus* suggests that the familiar small, blotched *Nomeus* found under *Physalia* may only be the young form of a bigger fish which lives in the depths.

Relationships. *Nomeus* is derived from the central *Cubiceps* stock. It is very similar in appearance to *Cubiceps*. The differences between the two are slight, but sufficient to consider *Nomeus* a genus in its own right. In *Nomeus* the pelvic bones have become much shortened, the patch of teeth on the glossohyal has disappeared, the number of vertebrae and finrays has increased, and there are only two spines preceding the anal finrays.

Nomeus lives in a very specialized environment, under *Physalia*. The features which distinguish it from *Cubiceps* doubtless reflect the demands of this unusual habitat. Adapted to a particular way of life, *Nomeus* has given rise to no other forms.

Species. *Nomeus* is a wide-ranging genus, found in the temperate and tropical waters of all the major oceans. It does not occur, however, in the eastern Atlantic or the Mediterranean. I have examined specimens from the Atlantic Ocean, the Gulf of Mexico and Caribbean Sea, the Indian Ocean, and the central and western Pacific Ocean. The counts of all these are essentially the same. I cannot but conclude that in the genus *Nomeus* there is but one species:

Nomeus gronovii (Gmelin, 1788) = *Gobius gronovii* Gmelin. Temperate and tropical regions of the Atlantic, Pacific, and Indian Oceans, Gulf of Mexico and Caribbean Sea, type locality "American Ocean in the Torrid Zone." D IX–XII, 24–28. A I–II 24–29. P 21–23. Gill-rakers 8–9 + 1 + 15–18. Vertebrae 41. Synonyms are: *Eleotris mauritii*

Bloch and Schneider, 1801, from Mauritius; *Nomeus maculosus* Bennett, 1831, from the Atlantic coast of North Africa; *Nomeus maculatus* Valenciennes, 1836; *Nomeus oxyurus* Poey, 1861, from Cuba; and *Nomeus dyscritus* Whitley, 1931, from New South Wales. **Nomeus peronii* Cuvier and Valenciennes, 1833, from the seas of Java is known only from three specimens in very poor condition. It is hard to be certain that these fish belong to *Nomeus*, though they are almost surely nomeids. I was able to make counts on only one. The counts were D IX, 30; A 31 (total elements); P 21; gillrakers 8 + 1 + 16. No subsequent material has appeared, and I consider **N. peronii* a synonym of *N. gronovii*.

Genus *PSENES* Cuvier and Valenciennes, 1833

Figure 28

Psenes Cuvier and Valenciennes, 1833:259. (Type species: **Psenes cyanophrys* Cuvier and Valenciennes, 1833:260, by original designation. New Ireland, western Pacific Ocean.)

Icticus Jordan and Thompson, 1914:242. (Type species: **Icticus ischanus* Jordan and Thompson, 1914:242, by original designation. Okinawa, western Pacific Ocean. A synonym of **Psenes pellucidus* Lütken, 1880:516.)

Papyrichthys J. L. B. Smith, 1934:90. (Type species: **Psenes pellucidus* Lütken, 1880:516, by original designation. Straits of Surabaja, Java.)

Thecopsenes Fowler, 1944a:63. (Type species: **Psenes chapmani* Fowler, 1906:119, by original designation. Cape Verde Islands, Atlantic Ocean. A synonym of **Psenes cyanophrys* Cuvier and Valenciennes, 1833:260.)

Caristioides Whitley, 1948:87. (Type species: *Caristioides amplipinnis* Whitley, 1948:88, by monotypy. Lord Howe Island, Tasman Sea. A synonym of **Psenes pellucidus* Lütken, 1880:516.)

Parapsenes J. L. B. Smith, 1949a:847. (Type species: *Psenes rotundus* Smith, 1949:307, by original designation. Dassen Island, South Africa.)

The combination of two dorsal fins, the first dorsal fin originating before or over the pectoral insertion, pelvic fins present, deep body, teeth on the palatines and basibranchials, and no teeth on the glossohyal distinguishes *Psenes* from all other stromateoid genera. The name, a feminine noun, is from the Greek ψήνη, the osprey *Pandion*, the allusion not evident. The authors of the name, Cuvier and Valenciennes (1833), may have been impressed by the resemblance of the "sourcil bleu" on their little fish to the similar brow of the fish hawk.

Description. Body deep, maximum depth usually greater than 40 per cent of the standard length, but sometimes less in large specimens; musculature firm to soft and flabby. Regions at bases of median fins may be very compressed and translucent. Peduncle short, compressed, may be fairly slender. Two dorsal fins, scarcely divided. First dorsal fin originating before insertion of pectoral fins, with about ten soft spines folding into a deeper groove. Rays of the second dorsal fin nearly as long as the longest D_1 spine, all approximately the same length or decreasing in length posteriorly, 18 to 30 finrays in all. Anal papilla a little before mid-body, in a depression. Anal fin originating at mid-body, slightly behind origin of second dorsal fin, two or three weak spines preceding the 17 to 30 rays. Pectoral fin rounded or winglike; relative length of fin decreasing slightly or increasing markedly with growth. Pelvic fins inserting under posterior portion of pectoral fin base, attached to the abdomen by a small membrane and folding into a groove. Pelvics very long in the young of some, the relative length decreasing markedly with growth. Caudal fin deeply forked. Scales small to minute, with a few weak cteni, very thin, deciduous, covering bases of median fins. Simple tubed scales of lateral line high, following dorsal profile and ending under last dorsal finray or extending onto peduncle. Skin thin; main subdermal canals along intermuscular septum apparent, may be confused with lateral line, side branches not visible. Pores to surface minute or absent. Head around 30 per cent of the standard length. Top of snout naked, minute pores in naked skin. Scales extending forward on top of head almost to level

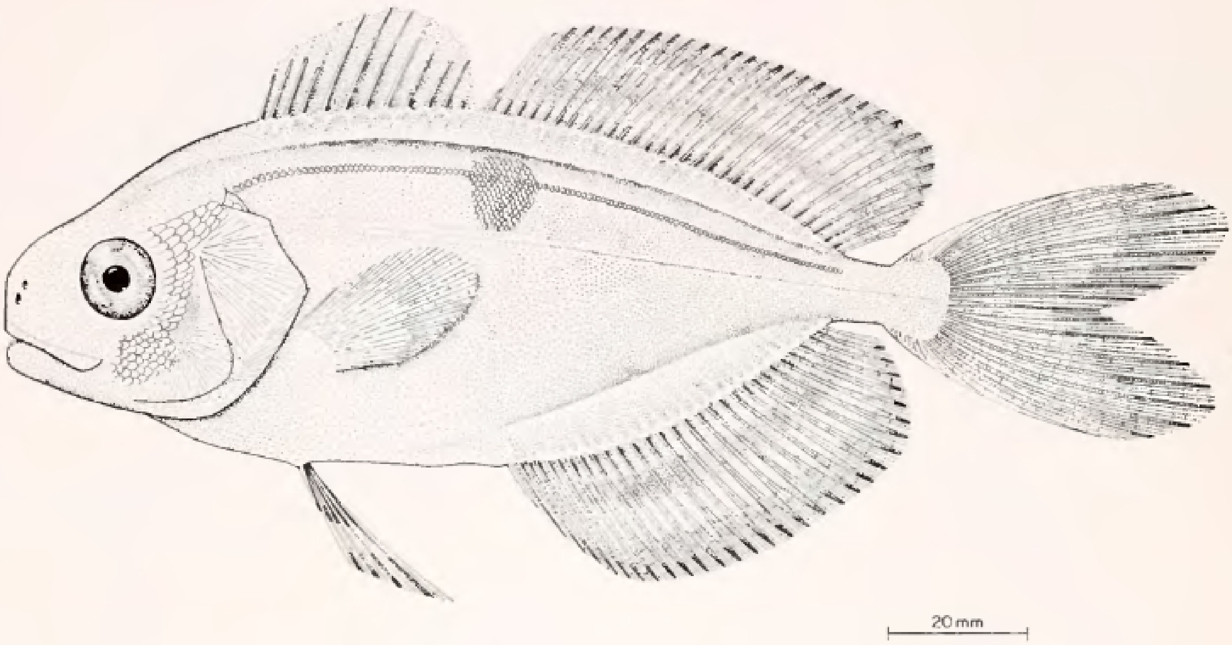

Figure 28. *Psenes pellucidus*, drawing of a 130-mm specimen by Margaret Bradbury.

of anterior border of the eye. Eye moderate to large. Adipose tissue around eye moderately developed. Nostrils near tip of truncate snout, small, the anterior one round, the posterior a slit. Maxillary ending under anterior portion of the eye. Premaxillary not protractile. Lacrimal bone almost completely covering upper jaw when mouth is closed, ventral border of maxillary remaining exposed. Supramaxillary absent. Teeth in both jaws uniserial, pointed; teeth in upper jaw small, slightly recurved, spaced; teeth in lower jaw larger, may be long and bladelike with small cusps, close-set. A few small recurved teeth in a patch on the head of the vomer and in a single series on each palatine and on the basibranchials. Opercle and preopercle thin, scaled, margins very finely denticulate or entire; opercle with two weak, hardly defined, flat spines; angle of preopercle rounded, projecting backward very slightly. Gill-rakers slender, a little shorter than the filaments, toothed on inner edge, moderately spaced, 14 to 19 on lower limb of first arch; sometimes a few rudimentary rakers under the long pseudobranch. Six branchiostegal rays, four on the ceratohyal, two on the epihyal. Scapula not prominent. Vertebrae 13 to 15 + 18 to 23 = 31 to 38, or 15 + 26 or 27 = 41 or 42. Stomach a simple sac; intestine very long. Pyloric caeca numerous, in a dendritic mass.

Color in preservative brown to yellowish, some species with a conspicuous, dark, blotched or longitudinally striped pattern. Median fins and pelvics often darker than the body. Region at bases of median fins translucent in *P. pellucidus*. Inside of mouth light brown, gill cavity usually darker. Peritoneum dark or light.

Natural history. The young of *Psenes* are fairly common in the surface layers on the high seas. They do not seem to associate with jellyfishes to any extent, but are very often dipnetted from under floating *Sargassum*. The larger adults, as with most other stromateoids, probably live deeper in the water. Most species in *Psenes* are strictly oceanic, and large specimens are rarely seen. Longley and Hildebrand (1941) report the remains of 120-mm *P. cyanophrys* from bird rookeries in the Tortugas. Other species found there included *Monacanthus*

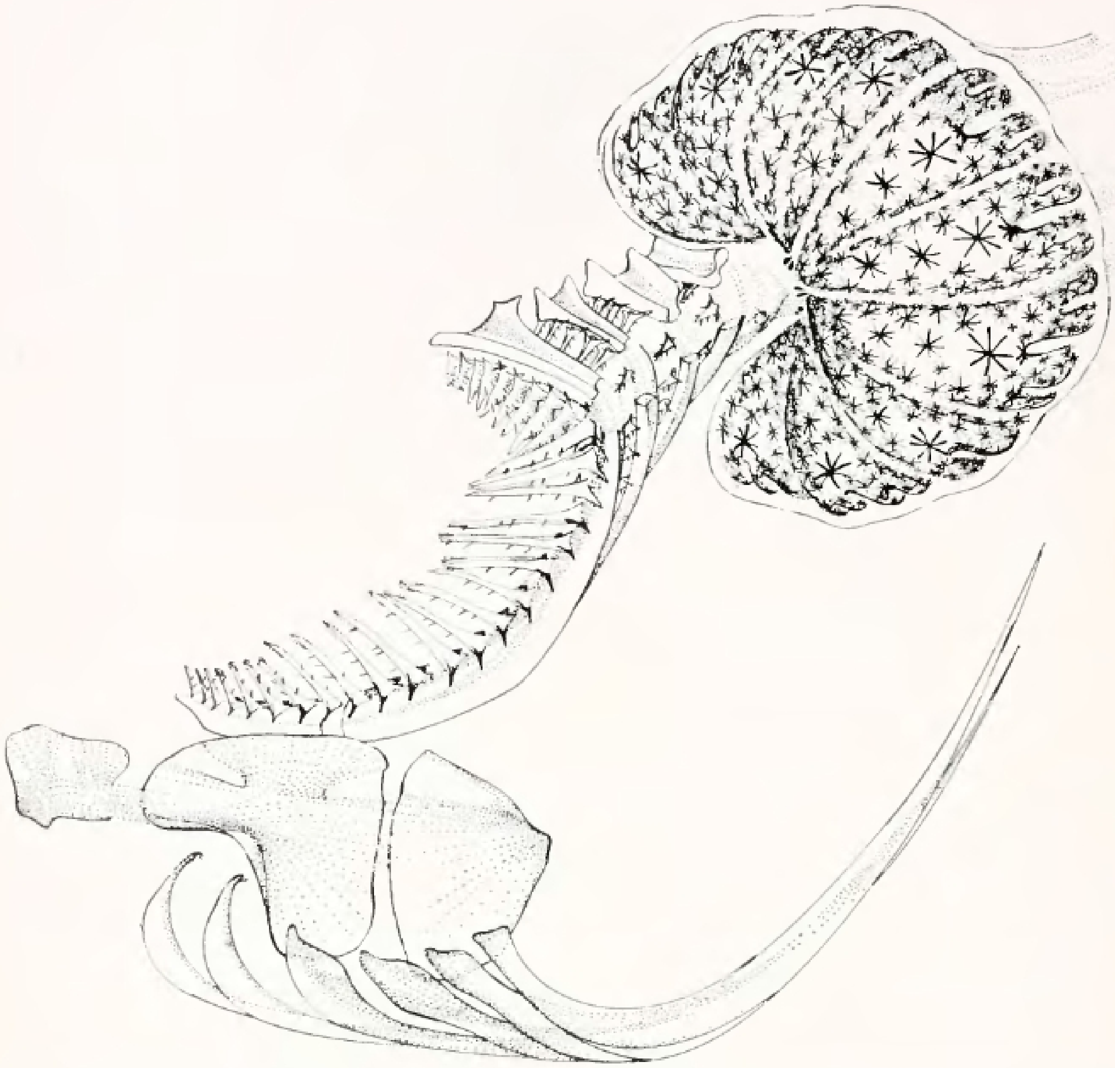

Figure 29. Branchial region of *Psenes cyanophrys*, drawing of a cleared-and-stained preparation from a 128-mm specimen. Elements identified in Figure 2.

hispidus, *Trachurops crumenopthalma*, and *Caranx ruber*, all fishes commonly associated with floating Gulf weed.

In the Caribbean area, the monthly distribution of post-larval and juvenile *Psenes cyanophrys* suggested that spawning occurred from March through October (Legaspi, 1956). The young fish fed at first on copepods, but later a variety of foods—copepods, amphipods, chaetognaths, fish eggs and larvae—was taken (Lloyd, 1909; Legaspi, 1956). In large *P. pellucidus*, a sombre-colored probably mesopelagic species, I have found gonostomatids of the genus *Maurolicus*.

Relationships. *Psenes*, like *Nomeus*, is a derivative of the central *Cubiceps* stock. In *Psenes*, the number of median finrays and vertebrae has tended to increase, the first interhaemal has moved forward forming an abrupt angle with the haemal process of the first precaudal vertebra, the teeth on the glossohyal have disappeared, the toothbases in the pharyngeal sac have become smaller, and the body has become deeper. In the meso- or bathypelagic species the teeth are highly differentiated. Those in the lower jaw are long and knifelike, while those in the upper jaw are small and strongly recurved. In many species of

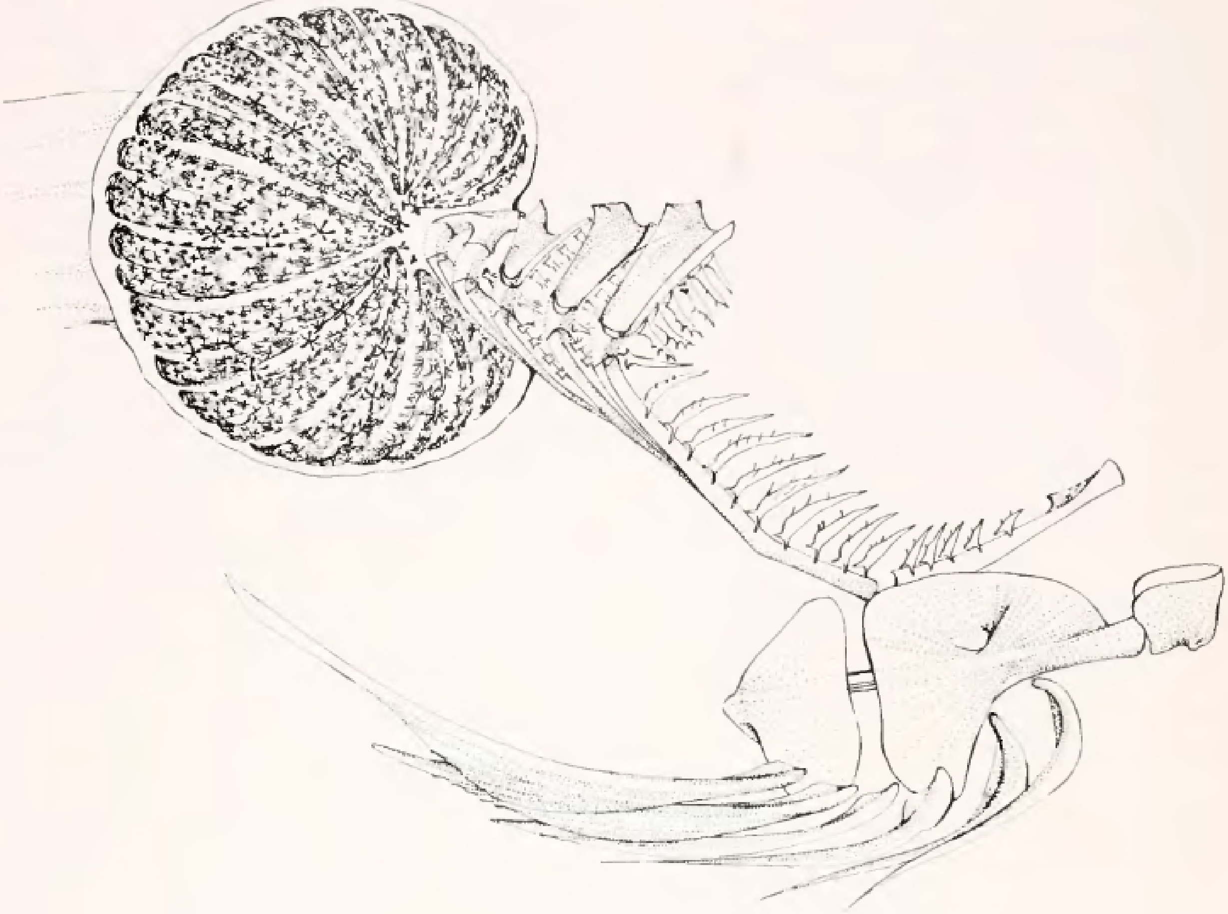

Figure 30. Branchial region of *Psenes pellucidus*, the type species for the nominal genus *Icticus*, drawing of a cleared-and-stained preparation from a 166-mm specimen, ABE 60-106. Elements identified in Figure 2.

Psenes, the teeth in the lower jaw are cusped.

Psenes has given rise to no other forms, although species such as *Psenes pellucidus*, which have entered the bathypelagic realm, seem to be diverging rapidly from the central bauplan. This fish has been described as a separate genus, *Icticus*. Were it not for the great similarity between the structure of the pharyngeal sacs of this nominal genus and *Psenes* (Figs. 29, 30), and for the presence of species intermediate in other characters, *Icticus* would stand as a genus derived from *Psenes*.

Species. *Psenes* is widespread in the temperate and tropical parts of the Atlantic, Pacific, and Indian oceans. There are numerous records of the genus from the Gulf of Mexico and the Caribbean, but none from the Mediterranean Sea.

As in *Cubiceps*, there is some confusion surrounding the species of *Psenes*. Most seem to be world-wide, with minor differences from ocean to ocean. Larger collections and more extensive series than those now available are necessary for proper comment on the significance of these differences.

The nominal species in the genus are:

**Psenes cyanophrys* Cuvier and Valenciennes, 1833. Atlantic, Pacific, and Indian oceans, type locality New Ireland. D IX–XI, 24–28. A III 24–28. P 17–20. Gill-rakers 8–9 + 1 + 19. Vertebrae 13 + 18. The counts recorded for specimens from the Gulf of Mexico (Legaspi, 1956) are modally higher than those of Pacific specimens. A very characteristic feature of this species is the numerous longitudinal streaks on the sides. According to Le Danois (1962), the following are synonyms: *Psenes javanicus* Cuvier and Valenciennes, 1833, from Java, *Psenes auratus* Cuvier and Valenciennes, 1833, from Guam, and *Psenes fuscus* Guichenot, 1866, from Madagascar. *Psenes leucurus* Cuvier and Valenciennes, the color of which is described by the authors (1833:265) as "jaunâtre, marbré de noirâtre et finement rayé de traits longitudinaux noirâtres," is also probably a synonym, but Le Danois (1962) does not agree. Other synonyms are: **Cubiceps multiradiatus* Günther, 1871, from Manado, Philippines; *Psenes chapmani* Fowler, 1906, from the Cape Verde Islands; *Psenes pacificus* Meek and Hildebrand, 1925, from the Bay of Panama; and *Psenes kamoharai* Abe, Kojima, and Kosakai, 1963, from Kyushu.

**Psenes pellucidus* Lütken, 1880. Atlantic, Pacific, and Indian oceans, type locality Surabaja Strait, Java Sea. D X–XI, I–II 27–32. A III 26–31. P 18–20. Gill-rakers 8–9 + 1 + 14–16. Vertebrae 15 + 26–27. This meso- or bathypelagic species is immediately recognizable by the soft, flabby musculature, the long knifelike teeth in the lower jaw, the sombre coloration, and the high vertebral and median finray counts. With growth, this species becomes quite slender. Synonyms are: **Psenes edwardsii* Eigenmann, 1902, from the Atlantic Ocean south of Rhode Island; **Icticus ischanus* Jordan and Thompson, 1914, from Okinawa; *Caristioides amplipinnis* Whitley, 1948, from Lord Howe Island, and *Cubiceps ismaelensis* Dieuzeide and Roland, 1955, from the coast of Algeria.

**Psenes maculatus* Lütken 1880. Atlantic, Pacific, and Indian oceans, type locality central Atlantic Ocean. D IX–XI, I 22–24. A III 21–23. P 20–21. Vertebrae 15 + 18–20. *Psenes nigrescens* Lloyd, 1909, from the Andaman Sea is a possible synonym.

**Psenes arafurensis* Günther, 1889. Atlantic, Pacific, and Indian oceans, type locality Arafura Sea. D X–XI, I–II 19–21. A III 20–21. P 18–20. Gill-rakers 7–9 + 1 + 15–16. Vertebrae 13 + 18. This species is very similar to **P. maculatus* Lütken, 1880, but the body is deeper at comparable sizes. The teeth in the lower jaws of both nominal species are like those of **P. pellucidus*. *P. rotundus* Smith, 1949, from South Africa is a probable synonym.

Psenes whiteleggii Waite, 1894. Coasts of New South Wales, type locality Maroubra Bay. D XI, I 19. A III 18. P 18. (From Waite, 1894.) *Psenes hillii* Ogilby, 1915, from Queensland is a probable synonym.

Psenes guttatus Fowler, 1934a. Coast of Natal. D XI, I 20. A III 18. Gill-rakers 7 + 18. (From Fowler, 1934a). This name appears as a *nomen nudum* in Fowler (1906). *Psenes stigmapleuron* Fowler, 1939, is a synonym. Perhaps a synonym of *P. whiteleggii* Waite, 1894.

**Psenes benardi* Rossignol and Blache, 1961. Gulf of Guinea. D XI, I 19–20. A III 21–22. P 19. Gill-rakers 9 + 1 + 16–17. **P. arafurensis* Günther, 1889, has a much deeper body, and is striped and mottled on the sides. *P. benardi* is uniform light brown. It is perhaps a synonym of *P. guttatus* Fowler, 1934a.

Family ARIOMMIDAE, new family

Type genus: *Ariomma* Jordan and Snyder, 1904

Diagnosis. Stromateoid fishes with pelvic fins present in adults, two dorsal fins, toothless palate, six branchiostegal rays, two hypural bones in the tail, and well ossified sclerotic bones. Bases of papillae in the pharyngeal sacs round; papillae not in bands and in upper halves of the sacs only.

Description. Body slender or deep, rounded to compressed. Peduncle slender, with two low fleshy lateral keels on each side. Two dorsal fins. The first dorsal with about ten slender spines folding into a groove. The longest spine twice the length of the longest ray of the second dorsal fin. Three anal spines, not separated from the rays. Soft dorsal and anal fins approxi-

Figure 31. Branchial region of *Ariomma* cf. *nigriargentea*, an elongate species, drawing of a cleared-and-stained preparation from a 140-mm specimen. Elements identified in Figure 2.

Figure 32. Branchial region of *Ariomma indica*, a deep-bodied species, drawing of a cleared-and-stained preparation from a 164-mm specimen, NTU 51942. Elements identified in Figure 2.

mately the same length, each with 14 or 15 finrays, the large basals protruding into the body profile. Bases of median fins not sheathed by scales. Pelvic fins attached to the abdomen by a thin membrane and folding into a groove. Scales large, cycloid, thin, extremely deciduous. Lateral line high, following dorsal profile and not extending onto peduncle; tubes in the lateral line scales sometimes branched. A branch of the lateral line extending forward over the eye in a bony tract. Skin thin; subdermal mucous canal system well developed. Opercular and preopercular margins entire or very finely denticulate. Opercle very thin, brittle, with two weak, ill-defined, flat spines. Six branchiostegal rays. Mouth small, maxillary barely extending to below eye. Teeth small, simple or three-cusped, uniserial in the jaws. Vomer, palatines, and basibranchials toothless. Supramaxillary bone absent. Eye large, adipose tissue well developed and covering the lacrimal bone. Sclerotic bones well ossified. Vertebrae 29 to 32. Caudal skeleton with two hypurals and three epurals. Pharyngeal sacs with papillae in the upper halves only. The papillae not in bands, their bases rounded with a stalk with teeth seated all along it arising off-center. Adults usually about a foot long, but in some species exceeding two feet. Silvery to blue-brownish, some species with conspicuous spotted or counter-shaded pattern.

Distribution. Ariommids apparently live near bottom in deep water of the subtropics and tropics. They occur along the east coast of North America, in the Gulf of Mexico and Caribbean Sea, along the coasts of West and South Africa, along Asian coasts from the Red Sea to Japan, and off Hawaii (Fig. 55).

Relationships. Ariomma, the single genus in the family, superficially appears to be a nomeid. The two dorsal fins, persistent pelvics, and six branchiostegal rays have been the cause for placement in this group close to *Cubiceps* (Psenidae of Jordan and Snyder, 1907; Nomeidae of Katayama, 1952). Some authors (Regan, 1914a; Jordan, 1923) have even considered *Ariomma* a synonym of *Cubiceps*. But the complete absence of teeth on the vomer, palatines, and basibranchials in *Ariomma* contrasts with the situation in the Nomeidae. The structure of the caudal skeleton (Fig. 33) and of the pharyngeal sacs (Figs. 31, 32) in *Ariomma* is unique among stromateoids, and divergent enough from any others to warrant separation at the family level. The unique

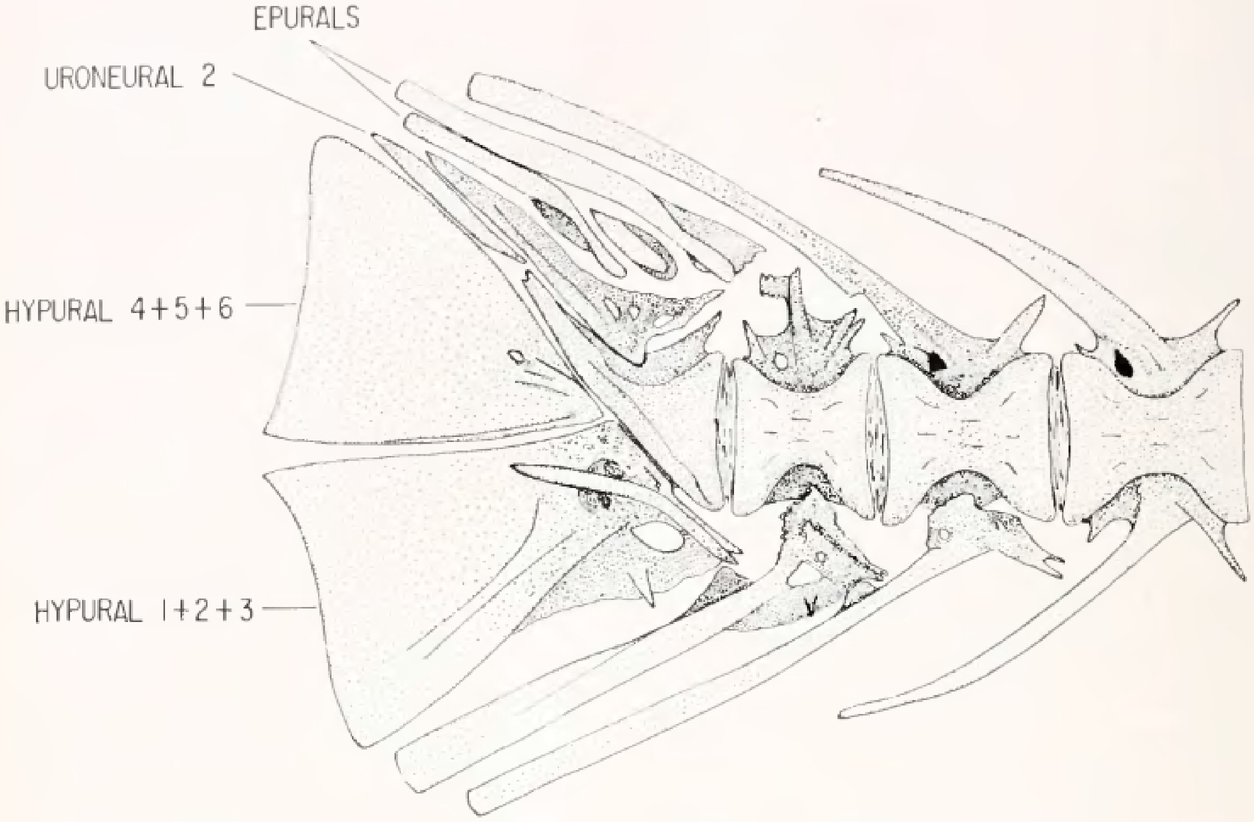

Figure 33. Caudal skeleton of *Ariomma* cf. *nigriargentea*, drawing of a cleared-and-stained preparation from a 28-mm specimen. All elements identified in Figure 1.

characters of the family, far from the condition of others in the suborder, are probably due to the shift the ariommids have made to an adaptive zone atypical for stromateoids (see below: *Natural history*, p. 93).

Ariomma presents a confusing array of characters which could suggest affinities with the centrolophids, the nomeids, or the stromateids. The well ossified sclerotic bones, minute body pores, and extremely deciduous scales are characters held in common with the advanced *Seriolella* group of the centrolophids and the diminutive *Cubiceps pauciradiatus* group of the nomeids and the stromateids. The teeth on the papillae occur all along the bony stalk, and the jaw teeth of *Ariomma indica* are cusped. Both characters are typical of stromateids. The general body shape is like *Seriolella*. The complete absence of palatal dentition suggests an affiliation with the line connecting the advanced centrolophids with the stromateids.

However, *Ariomma* has two distinct dorsal fins and very large scales, and the bony bridge over the anterior vertical canal of the ear is either very reduced or absent, all in marked contrast to the situation in centrolophids and stromateids. These conditions are found in the *Cubiceps pauciradiatus* group, nomeids which in addition have reduced palatal dentition. The Ariommidae are probably derived from somewhere in this line, and have lost the teeth on the palate and basibranchials.

Genus *ARIOMMA* Jordan and Snyder, 1904

Figures 34, 35

Ariomma Jordan and Snyder, 1904:942. (Type species: *Ariomma lurida* Jordan and Snyder, 1904:943, by original designation. Honolulu, Hawaii.)

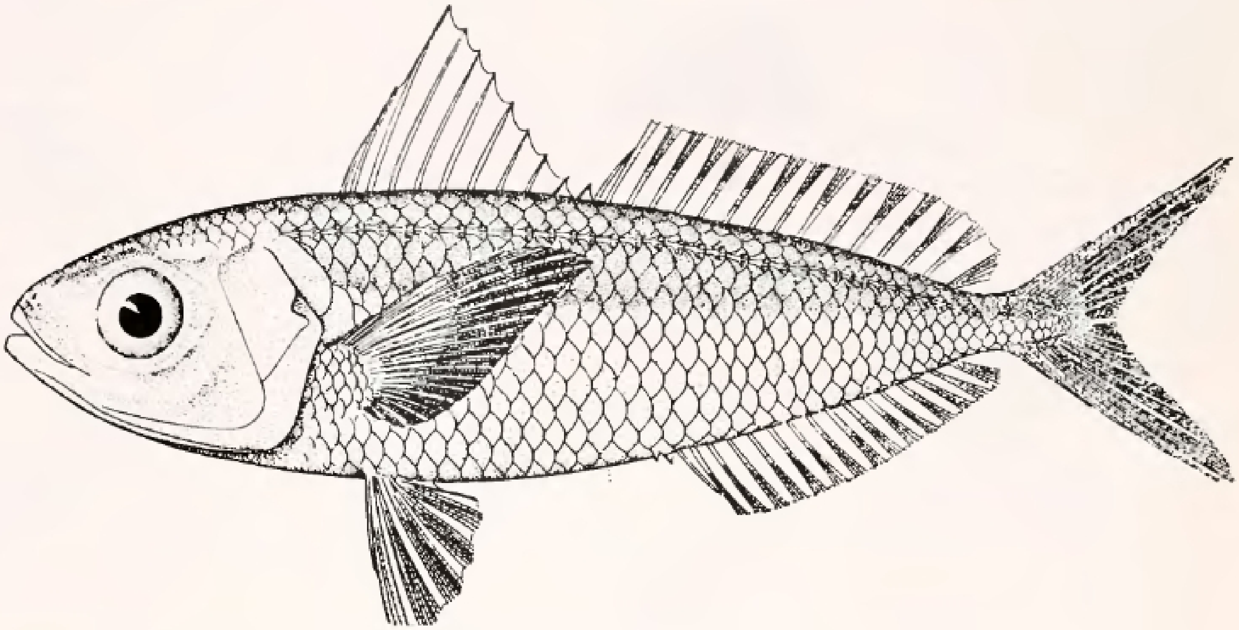

Figure 34. *Ariomma ledanoisi*, an elongate species, drawing of a 189-mm specimen, from Poll, 1959.

Paracubiceps Belloc, 1937:356. (Type species: *Paracubiceps ledanoisi* Belloc, 1937:356, by original designation. Coast of West Africa.)

The combination of slender caudal peduncle with lateral keels, deeply forked, stiff caudal fin, about fifteen dorsal and anal finrays with their basal elements pronounced and entering into the body profile, well-developed adipose tissue around the eye, two dorsal fins, and toothless palate distinguishes *Ariomma* from all other stromateoid genera. The name is a feminine noun of unknown derivation.

Description. Body either elongate, maximum depth about 25 per cent of the standard length, rounded, or deep, maximum depth 40 per cent of the standard length, compressed; musculature firm, often oily. Peduncle short, slender, square in cross-section, with two ill-defined, low, fleshy keels on each side at base of caudal fin. Two dorsal fins, scarcely separated. First dorsal originating directly over, or a little before, insertion of pectoral fin, with about ten long, brittle spines, folding into a deep groove. Second dorsal fin with 14 or 15 rays, each about half as long as the longest D_1 spine; the anterior rays a little longer than those which follow. Anal papilla a little behind mid-body, in a slit. Anal fin originating behind middle of body and behind origin of the second dorsal fin, two or three spines preceding the 14 to 15 rays; rays short, the anterior ones the longest. Rays of the median fins close-set anteriorly, becoming more widely spaced posteriorly. Basals of the finrays often projecting above the body profile. Pectoral fin rounded in the young, becoming pointed with growth; relative length decreasing slightly with growth of elongate form but increasing markedly with growth of deep-bodied form. Pelvic fins inserting under end or behind base of pectoral fin, attached to abdomen with a membrane and folding into a pronounced groove which reaches to the anus. Caudal fin stiff, deeply forked, rays on the leading edge stiff and spinelike. Scales large, cycloid, very thin, extremely deciduous, not covering bases of the median fins. Scales of the lateral line with branched tubes, located high on the body, following dorsal profile and not extending onto peduncle. A branch of the lateral line extend-

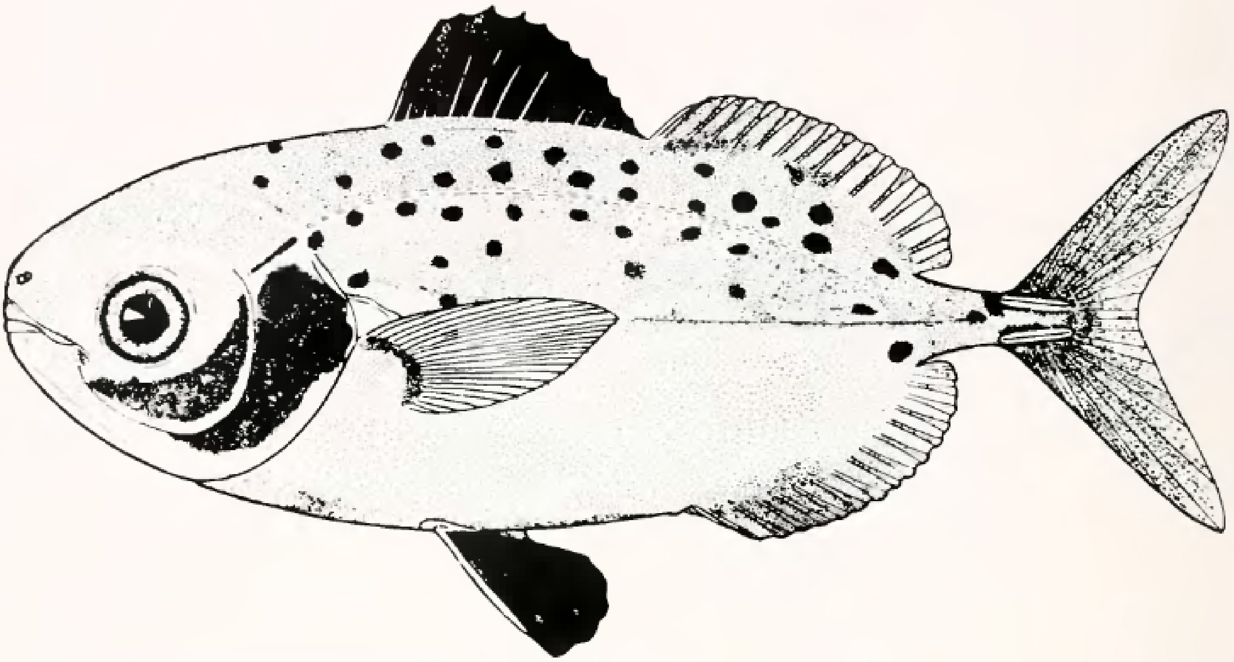

Figure 35. *Ariomma regulus*, a deep-bodied species, from McKenney, 1961.

ing forward over the eye in a bony tract from the head of the hyomandibular. Skin thin; main subdermal canal along intermuscular septum very apparent, may be confused with lateral line; side branches not as conspicuous, pores to surface seem to be wanting. Head around 30 per cent of the standard length. Top of snout naked, pores and subdermal canals barely visible. Scales extending forward over nape to level of anterior border of the eye. Eye large, bony supraorbital ridge pronounced. Adipose tissue around eye well developed, extending forward over the lacrimal and around the nostrils. Nostrils near tip of the obtuse snout, small, the anterior round, the posterior a slit. Maxillary scarcely reaching to under eye, angle of gape well before eye and nearer to tip of snout. Premaxillary not protractile. Lacrimal bone transparent, almost completely covering upper jaw when mouth is closed, the ventral border of the maxillary remaining exposed. Supramaxillary absent. Jaw teeth minute, covered basally with a membrane, usually pointed but three-cusped in a few deep-bodied forms, uniserial, close set or slightly spaced; vomer, palatines, and basibranchials toothless. Opercle and preopercle thin, brittle, margins very finely denticulate or entire; opercle rounded, with two weak, ill-defined, flat spines; angle of preopercle rounded and not bulging backward. Gill-rakers slender, half the length of the filaments, toothed on inner edge, fairly close set, about 19 on lower limb of first arch; no rudimentary rakers under the well-developed pseudobranch. Six branchiostegal rays, four on the ceratohyal, two on the epihyal. Scapula prominent. Vertebrae 12 to 14 + 17 or 18 = 29 to 32. Two hypurals and three epurals. Sclerotic bones well ossified. Stomach large, a simple sac; intestine very long. Pyloric caeca numerous, in a dendritic mass. Air bladder present, extending the length of the abdominal cavity.

Color in preservative brown, bluish, or silvery. First dorsal blackish, pelvic fins dark or clear, other fins usually light. Color pattern may be blue above, silvery below, the shades not intergrading, uniformly dark, or light with dark spots. Young have three to five dark vertical stripes. Opercles silvery or blackish. Iris usually golden, divided by a dark vertical bar. Mouth and gill cavity light or dark. Peritoneum silvery.

Natural history. Most stromateoids are pelagic, but *Ariomma* is a bottom or near-bottom fish of deep water. Very small *Ariomma* are pelagic, for they are taken in surface collections, but all large specimens reported have been taken in bottom trawls, usually at depths in excess of 100 meters (Lowe, 1962; McKenney, 1961; Poll, 1959). *Ariomma* apparently schools, for single net hauls contain numerous specimens (Poll, 1959).

The pharyngeal sacs, but not the stomachs, of most specimens dissected contained grit and mud, indicative of a bottom-feeding habit. This habit could account for the relatively high number of gill-rakers, around 30, found in *Ariomma*. The stomachs of specimens examined by Poll (1959) contained bits of crustaceans and unidentifiable meat. The thick adipose tissue on the head probably protects the eyes and nostrils as the fish scoops its prey from the sea floor.

Most *Ariomma* mature around 160 to 180 mm SL (*A. regula* [McKenney, 1961]; *A. ledanoisi* [Poll, 1959]; *A. indica*; *A. nigriargentea*), and probably do not grow much larger than this. Very large specimens are known from the Red Sea (800 mm, Klunzinger, 1884), Japan (356 mm SL, Abe, 1954), and Hawaii (635 mm, Fowler, 1923). The Japanese species, at least, does not seem to mature before reaching this size.

Species. The problem of delineating the species of *Ariomma* is one of the most perplexing in the entire suborder. Fourteen have been described, but all of these, from the Gulf of Mexico to Hawaii, have almost the same numbers of finrays and gill-rakers. Reports of lateral line scale counts vary slightly, but the scales are so deciduous in *Ariomma* that this information must be viewed with caution.

The species of *Ariomma*, with one intermediate exception, are either elongate, with the maximum depth less than 30 per cent of the standard length, or deep-bodied, with the maximum depth greater than 40 per cent of the standard length. It is possible that these two groups warrant subgeneric recognition, but, pending further study, this action is deferred.

The nominal species in *Ariomma* are:

Ariomma regulus (Poey, 1868) = *Psenes regulus* Poey. Gulf of Mexico to British Guiana, type locality Cuba. Deep-bodied. D XI, I 15. A III 15. P 21–24. Gill-rakers usually 7 + 1 + 15. (From McKenney, 1961.) Spotted. Teeth not cusped.

Ariomma indica (Day, 1870) = **Psenes indicus* Day. India to southern Japan, type locality Madras. Deep-bodied. D XI–XII, 14–15. A III 14–15. P 21–23. Gill-rakers usually 7 + 1 + 15. Vertebrae 12 or 13 + 18. The pectoral fin of this silvery species becomes produced, up to 35 per cent of the standard length, with growth. The teeth in the hind part of the lower jaw are three-cusped; the rest are simple. *Psenes extraneus* Herre, 1950, known from a single Philippine specimen, is very likely a synonym.

Ariomma brevimanus (Klunzinger, 1884) = *Cubiceps brevimanus* Klunzinger. Red Sea. Elongate, known from a single specimen 800 mm long. D XI, 15. A II 15. P 24. (From Klunzinger, 1884.)

**Ariomma lurida* Jordan and Snyder, 1904. Hawaii. Elongate. D XI–XII, 14–15. A III 13–14. P 20–21. Gill-rakers 9 + 1 + 20. Vertebrae 14 + 18. This species is distinguished from **A. evermanni* Jordan and Snyder, 1907, by the large eye, greater than 30 per cent of the length of the head, and fewer pectoral finrays.

**Ariomma evermanni* Jordan and Snyder, 1907. Hawaii. Elongate. D XI–XII. 15. A III 14. P 25. Gill-rakers 9 + 20. Vertebrae 13 + 18. Eye is less than 28 per cent of the length of the head. Attains a large size; *Cubiceps thompsoni* Fowler, 1923 (type 635 mm long), is a probable synonym.

Ariomma africana (Gilchrist and von Bonde, 1923) = **Psenes africanus* Gilchrist and von Bonde. South Africa. Deep-bodied. D IX–X, 15. A III 16. P 22. Gill-rakers 8

+ 1 + 16. Vertebrae 13 + 18. Very similar to *A. regulus* (Poey, 1868). Spotted. Teeth not cusped.

Ariomma dollfusi (Chabanaud, 1930) = **Cubiceps dollfusi* Chabanaud. Gulf of Suez. Intermediate, maximum depth of cotype 32 per cent of the standard length (112 mm). D XI–XII, 15. A III 15. P 22. Gill-rakers 7 + 1 + 14. Vertebrae 12 + 18. The teeth are said to be "comprimées . . . et crenelées" (Chabanaud, 1930:520), suggesting close relationship or synonymy with *A. indica* (Day, 1870).

**Ariomma bondi* Fowler, 1930. Grenada, British West Indies. Elongate, known from the holotype, 79 mm TL. D XI–XII, 14. A II 15. Gill-rakers 8 + 15. Lateral line scales 43. Dark above, light on sides. (From Fowler, 1930.) Possible synonyms are **A. nigriargentea* and/or **A. melana*, both of Ginsburg, 1954.

Ariomma ledanoisi (Belloc, 1937) = *Paracubiceps ledanoisi* Belloc. West equatorial Africa. Elongate. D XI–XII, 14–15. A III 14–15. P 20–22. Gill-rakers ? + ? + 16–17. (From Poll, 1959.)

Ariomma nigriargentea (Ginsburg, 1954) = **Cubiceps nigriargenteus* Ginsburg. Gulf of Mexico, Caribbean, and north to Cape Cod, type locality Cape Romain, South Carolina. Elongate. D XI–XII, 15–16. A III 15. P 21–22. Gill-rakers 9–10 + 17–19. (From Ginsburg, 1954.) Vertebrae 13 + 17. Said to differ from *A. melana* (Ginsburg, 1954) by the smaller scales (62 to 68 in lateral line), color (blue above, silvery below), less scalation on the head, and shorter maxillary. These characters, however, seem to intergrade.

Ariomma melana (Ginsburg, 1954) = **Cubiceps melanus* Ginsburg. Gulf of Mexico, Caribbean, and north to Cape Hatteras, type locality Mississippi Delta. Elongate. D XI–XII, 15. A III 14–15. P 21–22. Gill-rakers 9–11 + 18–20. Lateral line scales 39–56. (From Ginsburg, 1954.) Vertebrae apparently 15 + 16. Uniform dusky brown.

Ariomma multisquamis (Marchal, 1961) = **Paracubiceps multisquamis* Marchal. West equatorial Africa. Elongate. D XI–XII, 15–16. A III 14–16. P 21–23. (From Marchal, 1961.) Gill-rakers 9 + 1 + 18. Said to differ from *A. ledanoisi* (Belloc, 1937) by having more scales in the lateral line (61–63 *vs.* 36–40).

Family TETRAGONURIDAE

Type genus: *Tetragonurus* Risso, 1810

Tetragonuridae. Risso, 1826:382 (def.). Lütken, 1880:437 (disc., rel. to scombroids). Ramsay and Ogilby, 1888:9 (disc., rel. to Atherinidae). Regan, 1902:206 (rel. to Stromateidae). Boulenger, 1904:642 (popular account). Grey, 1955:1 (world-wide revision).

Tetragonurina. Günther, 1861:407 (def., rel. to Atherinidae).

Tetragonuroidei. Berg, 1940:323 (definition); 1955: 247 (definition). Smith, 1953:53 (review).

Diagnosis. Elongate stromateoid fishes with pelvic fins present in the adults, two dorsal fins, teeth on vomer and palatines, five or six branchiostegal rays, heavy adherent keeled scales, and four hypural and two epural bones in the tail. Papillae in the pharyngeal sacs with rounded bases, not in bands.

Description. Body slender, rounded. Peduncle thick, square in cross-section, with modified scales forming two prominent lateral keels on each side. Two dorsal fins, the first with 10 to 20 short spines, folding into a groove; the base of the fin as long as or longer than the base of the second dorsal. One anal spine, not separated from the rays. Soft dorsal and anal fins approximately the same length, with 10 to 17 fin-rays. Last ray of pelvic fin attached to abdomen for its entire length, fin folding into a depression. Scales moderate in size, ctenoid, with heavy longitudinal ridges, very adherent, arranged in a geodesic pattern around the body. Lateral line slightly arched forward, descending to run along middle of side and extending onto peduncle; no tubed scales. Skin thick; subdermal mucous canal system well developed, but barely visible. Opercular and preopercular margins entire or finely denticulate. Opercle thick, spines not apparent. Five or six

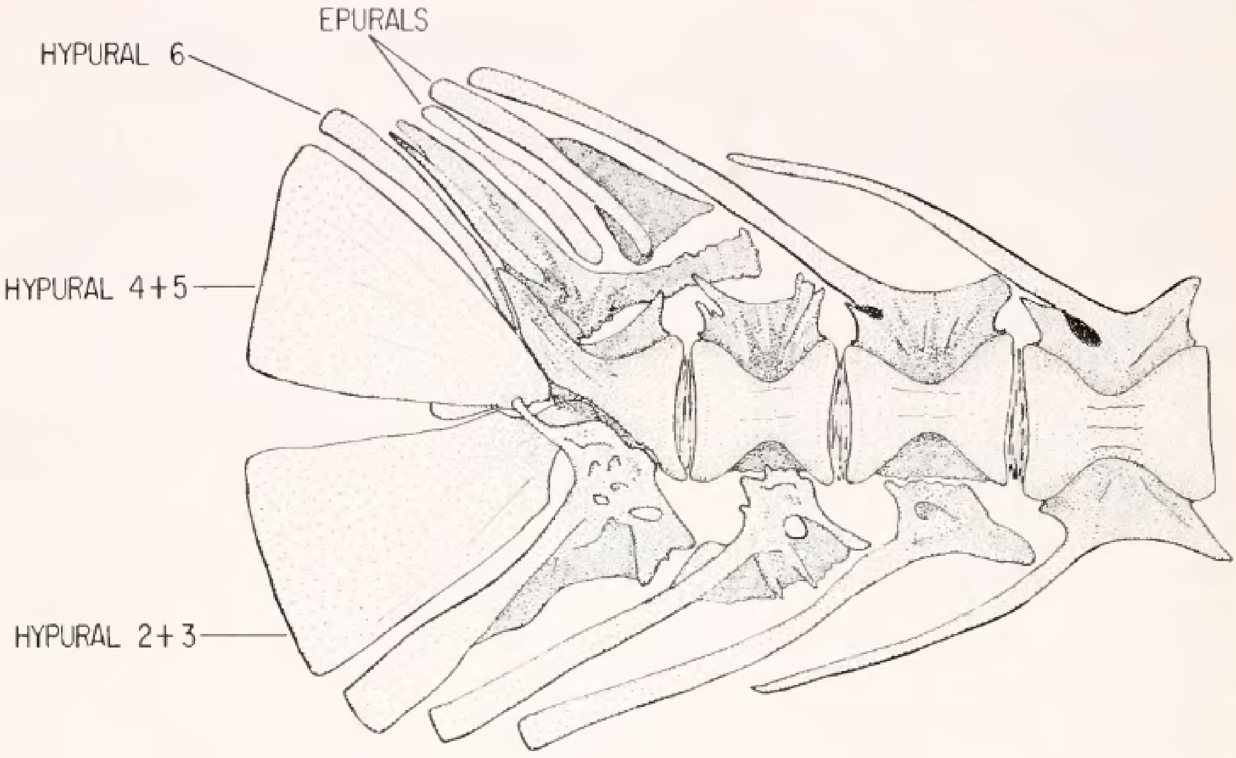

Figure 36. Caudal skeleton of *Tetragonurus atlanticus*, drawing of a cleared-and-stained preparation from a 66-mm specimen, MCZ 41791. All elements identified in Figure 1.

branchiostegal rays. Mouth large, maxillary extending below eye. Teeth moderate to large, simple and cusped, uniserial in the jaws. Vomer, palatines, basibranchials, and usually the tongue with teeth. Supramaxillary bone absent. Eye large, no adipose tissue. Sclerotic bones not well ossified. Vertebrae 43 to 58. Caudal skeleton with four hypurals and two epurals. Pharyngeal sacs with small papillae in upper and lower halves; bases of papillae not in bands, rounded, central stalk with a few teeth. Adults one to two feet in length. Uniform dark brown, with no pattern or countershading.

Distribution. The distribution of the Tetragonuridae largely parallels that of the nomeids (Fig. 54). Tetragonurids are oceanic fishes of tropical, subtropical, and temperate seas. None have been taken in the eastern Mediterranean Sea, the Red Sea, and the South and East China seas.

Relationships. Tetragonurus, the single genus in the family, has teeth on the vomer, palatines, and basibranchials. Thus, it is affiliated with the nomeid stock. The caudal skeleton (Fig. 36) is similar to that of the nomeids, but is advanced an evolutionary grade in having lost one of the epurals. The pharyngeal sacs (Fig. 37) and the heavy, keeled scales of *Tetragonurus*, however, are markedly different from the sacs and scales of the nomeids. The pharyngeal sacs are exceedingly elongate. The papillae are poorly ossified and are very reduced in size. The bases of the papillae are rounded, as they are in the Ariommidae, but there are less than six teeth seated on top of a short stalk. The fourth pharyngobranchial is very elongate and is fused to the third pharyngobranchial. This long bone is studded with teeth and extends well backward into the sac, where it no doubt aids both in shredding the food and in supporting the sacs. All nomeids have six branchi-

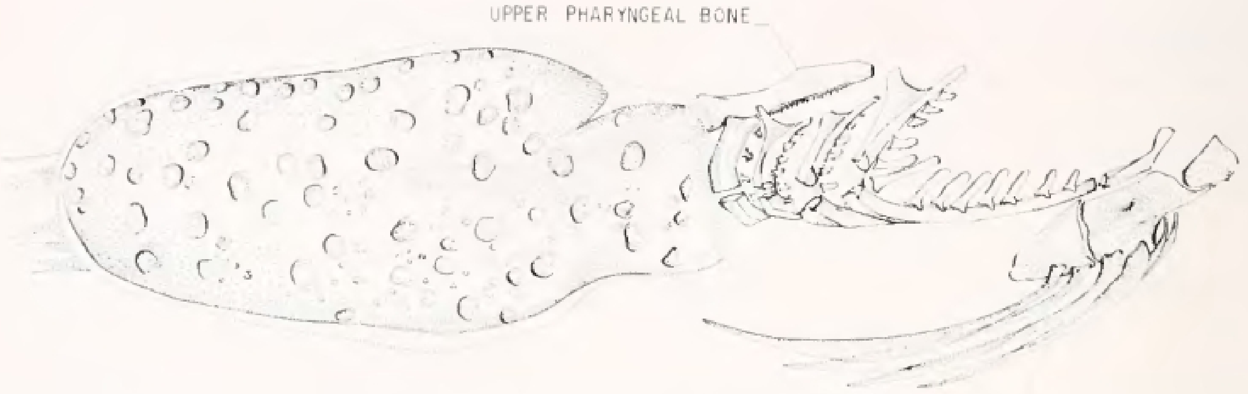

Figure 37. Branchial region of *Tetragonurus cuvieri*, drawing of a cleared-and-stained preparation from a 340-mm specimen, CNHM 64218. Elements identified in Figure 2. The upper pharyngeal bone is formed by the fusion of the third and fourth pharyngobranchials.

ostegal rays; tetragonurids have either six or five.

The highly differentiated jaw teeth of *Tetragonurus* are very similar to those of certain species in the genus *Psenes*. But *Tetragonurus* has teeth on the tongue, and cannot be derived from *Psenes*. It is very likely that *Tetragonurus* branched off fairly early from the nomeid stem and is derived from no living nomeid genus. The loss of an epural and a branchiostegal ray, the heavy keeled scales, the very elongate pharyngeal sacs with the reduced papillae, and the greatly increased number of vertebrae are quite divergent from the situation in nomeids, and together imply that evolution has proceeded independently in these two groups for some time.

The divergent characters of *Tetragonurus* are part of its adaptation to a very particular mode of life. *Tetragonurus* is certainly a derived form, and is probably quite unlike the ancestral nomeid. The central nomeid genus *Cubiceps*, like *Tetragonurus*, has teeth on the tongue. The nomeid stock from which *Tetragonurus* arose may have been in many respects similar to the present-day *Cubiceps*.

Genus *TETRAGONURUS* Risso, 1810

Figure 38

Tetragonurus Risso, 1810:347. (Type species: *Tetragonurus cuvieri* Risso, 1810:347, by monotypy. Mediterranean.)

Ctenodax Macleay, 1885:718. (Type species: *Ctenodax wilkinsoni* Macleay, 1885:718, by monotypy. Lord Howe Island, Tasman Sea. A synonym of **Tetragonurus atlanticus* Lowe, 1839:79.)

The combination of elongate body and peduncle, modified scales forming two keels on the peduncle, origin of first dorsal slightly to well behind pectoral insertion, base of first dorsal longer than base of second dorsal, heavy keeled scales, and peculiar lower jaw with heavy knifelike teeth distinguishes *Tetragonurus* from all other stromateoid genera. The name, a masculine noun, is from the Greek τετράγωνος, with four angles, + οὐρά, tail, in reference to the shape of the caudal peduncle.

Description. Body very elongate, maximum depth less than 20 per cent of the standard length, rounded; musculature firm. Peduncle long, thick, with modified scales forming two prominent keels at base of caudal fin. Two dorsal fins, scarcely divided. First dorsal originating slightly to well behind insertion of pectoral fins, with 10 to 21 stiff spines folding into a groove, the longest spine half the length of the longest ray of the second dorsal. Anterior rays of the second dorsal the longest, those that follow decreasing slightly in length, 10 to 17 finrays in all. Anus well behind midbody, in a depression. Anal fin originating slightly behind origin of second dorsal fin,

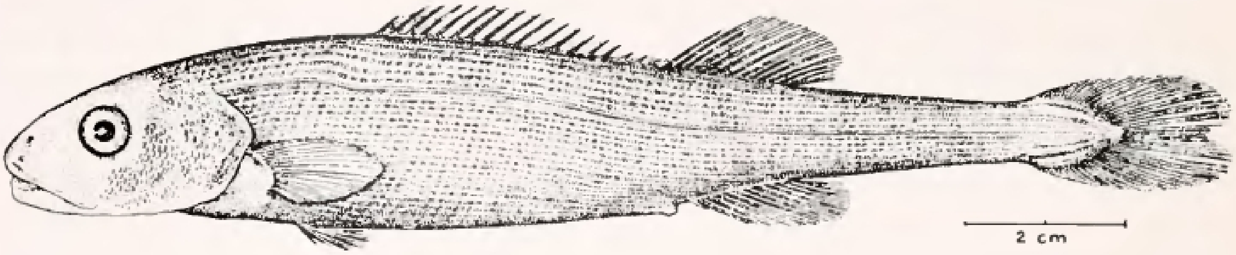

Figure 38. *Tetragonurus cuvieri*, drawing of a 129-mm specimen, from Grey, 1955.

one short spine preceding the rays. Anterior rays the longest, those that follow decreasing slightly in length, 9 to 15 finrays in all. Pectoral fin small, the central rays the longest. Pelvic fins small, inserting behind pectoral fin base and before origin of first dorsal, innermost ray attached to abdomen for its entire length. Caudal fin forked. Scales moderate in size, with heavy longitudinal keels, very adherent, following a geodesic pattern around the body. Very small scales on bases of median fins. Lateral line usually slightly arched anteriorly, descending to run along mid-lateral line of body and ending on peduncle at origin of keels; no tubed scales. Skin thick; subdermal canals cannot be traced. Pores to surface minute. Head 30 to 20 per cent of the standard length. Top of head and snout naked, small pores in naked skin. Scales extending forward over nape almost to level of posterior border of the eye. Eye large, with a series of grooves on the posterior rim. Nostrils toward top of blunt snout, large, well separated, the anterior round, the posterior a slit. Maxillary ending under eye, angle of gape well before eye. Premaxillary not protractile. Lacrimal bone covering most of upper jaw at all times, ventral border of maxillary remaining exposed. Lower jaw almost completely within upper jaw when mouth is closed. Supramaxillary absent. Teeth in upper jaw small, pointed, recurved, spaced. Teeth in lower jaw large, knifelike, close set, with small cusps, deeply embedded in the gum with only the tips showing. Strong recurved teeth present on head of vomer, and in a single series on shaft of vomer and palatines. Small teeth on basibranchials and, usually, profusely scattered on tongue. Tongue high-sided, depressed in center. Opercle and preopercle thin, fleshy, scaled, margins entire in adult, spinulose in the young; opercle with two very weak spines; angle of preopercle slightly rounded, not bulging backward. Cheeks scaled. Gill-rakers broad, fleshy, shorter than the filaments, toothed on inner edge, spaced, 8 to 14 on lower limb of first arch; rudimentary rakers often present under the large pseudobranch. Scapula not visible. Vertebrae 43 to 58. Sclerotic bones well ossified in adult. Stomach a simple sac; intestine long. Pyloric caeca numerous, in a large dendritic mass.

Color in preservative uniform brown, ranging from tan to almost black. Fins the same color as the body. Inside of mouth, gill cavity, and peritoneum dark.

Natural history. Young *Tetragonurus* have been found associated with medusae (Mansueti, 1963). There are also reports (Emery, 1882; Lo Bianco, 1909; Fitch, 1949) of young specimens found within salps, usually *Pyrosoma.* Mansueti (1963) felt that the association of *Tetragonurus* with jellyfishes was a chance occurrence, but, since jellyfish associations are commonly formed by other stromateoids, it is likely that the association is actively sought.

Tetragonurus probably feeds almost exclusively on coelenterates and ctenophores (Risso, 1826; Fitch, 1952). The large slicing teeth of the lower jaw and the peculiar boxlike jaw seem admirably suited for such a diet (Grey, 1955).

Risso (1826) reported that the flesh of *Tetragonurus* was poisonous, attributing this quality to the fish's diet of venomous jellyfishes of the genus *Stephanomie*. His report has been widely spread, but has only recently been reinvestigated. Fitch (1952) analyzed four California specimens and found them to be not poisonous. The possibility remains that *Tetragonurus* is poisonous only during certain seasons, for example at the time of spawning (Petit and Amar, 1946).

In the Atlantic, *Tetragonurus cuvieri* apparently spawns in spring and summer (Grey, 1955). Guiglia (1950) reports mature females of *T. cuvieri* taken throughout the year in the Mediterranean. *T. atlanticus* spawns during the fall in the eastern and northern Atlantic, but in winter and spring in the western Atlantic (Grey, 1955).

Tetragonurus is strictly oceanic (Grey, 1955). Although young specimens occur near the surface with jellyfish, the adults, judging from their somber coloration, probably are members of the meso- or bathypelagic faunas. *Tetragonurus* has been considered a rare fish (Fitch, 1949), but recent surveys in the North Pacific (Larkins, 1964) indicate that it is much more common than is usually thought, bearing out a prediction of Grey (1955).

Species. Tetragonurus has been ably treated by Marion Grey (1955), who recognized three species in the genus. As she has pointed out, each species varies widely, and further division may be justified when more specimens are available. The species are:

T. cuvieri Risso, 1810. Mediterranean Sea, Atlantic, Pacific oceans. D XV–XXI, 10–17. A I 10–15. P 14–21(?). Lateral line scales 97–114. Vertebrae 52–58. (From Grey, 1955.)

**T. atlanticus* Lowe, 1839. Atlantic, Pacific, Indian oceans. D XIV–XVII, 10–13. A I 9–12. P 14–18. Lateral line scales 83–95. Vertebrae 45–51. (From Grey, 1955.) *Ctenodax wilkinsoni* Macleay, 1885, is a synonym.

T. pacificus Abe, 1953. Pacific, Indian oceans. D X–XI, 10–12. A I 10–12. P 15–17. Lateral line scales 73–78. Vertebrae 40(?)–43. (From Grey, 1955.)

Family STROMATEIDAE

Type genus: *Stromateus* Linnaeus, 1758

Stromatées. Cuvier and Valenciennes, 1833:372 (in part, descr.).
Stromateina. Günther, 1860:397 (in part, def.). Gill, 1862:126 (genera listed).
Stromateinae. Gill, 1884:669 (def., gen.). Bühler, 1930:62 (digestive system).
Stromateidae. Jordan and Gilbert, 1882:449 (descr.). Jordan and Evermann, 1896:964 (descr., North America). Jordan, 1923:182 (list, + Pampidae). Berg, 1940:323 (dist.); 1955:248 (dist.).

Diagnosis. Deep-bodied stromateoid fishes with pelvic fins absent in the adults, continuous dorsal fin, toothless palate, four hypural and two or three epural bones in the tail, and well ossified sclerotic bones. The papillae in the pharyngeal sacs not in bands, in both the upper and lower halves of the sac; bases of the papillae stellate.

Description. Body deep, compressed. Single dorsal and anal fins, with none or one to ten flat, bladelike spines and three to five slender, graduated spines preceding the rays. Median fins about the same length, usually falcate; caudal fin deeply forked. Pectoral fin long and pointed. Pelvic fins present only in young *Stromateus*; absent in all others. Scales small, cycloid, extremely deciduous. Lateral line high, following dorsal profile, and extending onto the short peduncle. Opercular and preopercular margins entire. Opercle very thin, with two short, flat, weak spines. Gill membranes usually free from isthmus, but united in *Pampus*. Five or six branchiostegal rays. Mouth terminal to sub-terminal, small, angle of gape rarely reaching below eye. Teeth very small, laterally flattened, with three minute cusps, and uniserial in the jaws. Vomer, palatines, and basibranchials toothless. Supramaxillary absent. Eye fairly small; adipose tissue usually not well developed. Sclerotic bones well ossified. Vertebrae 30 to 48. Caudal skeleton with four hypurals and two epurals, except three epurals in *Stromateus fiatola*. Pharyngeal sacs with papillae in upper and lower halves, not in bands; bases of the papillae stellate, with teeth seated all along a central stalk. Adults usually about a foot in length. Silvery to blue, some with spots.

Distribution. Stromateids live over the continental shelves and in the bays of tropical, subtropical, and temperate waters. They are found on the east and west coasts of North and South America, from the Mediterranean Sea to South Africa, and from the Iranian Gulf to Japan (Fig. 56). None occur near oceanic islands, and none have reached Australia. *Stromateus*, in southern South America and western Africa, is the only genus that has representatives on both sides of an ocean. The genera are allopatric except for a small area of overlap between *Stromateus* and *Peprilus* in South America. All stromateids school, and many are important commercially.

Relationships. The Stromateidae are the current zenith in stromateoid evolution. The reduced number of branchiostegals and elements in the caudal skeleton (Figs. 42, 47), the absence of pelvic fins, the small mouth with cusped teeth, the broad stellate bases of the papillae in the pharyngeal sacs (Figs. 43, 46), and the deepened body are all advanced conditions.

The stromateids were derived from somewhere near the *Seriolella* group of the Centrolophidae, perhaps from a fish very like the deep-bodied *Psenopsis*. In *Stromateus fiatola* the presence of pelvic fins in the young and the three epurals recalls the centrolophid heritage.

The stromateids may have evolved only recently. Though the three genera are distinct, little speciation has occurred, but, in some cases, seems to be in an incipient stage. Almost-sibling species occur on either side of the Isthmus of Panama.

The stromateids are an end-point, and no other groups have been derived from them. But they are by no means an evolutionary deadend. *Pampus*, with its restricted gill-opening, elongate pharyngeal sac, and peculiar spines in some species, is diverging rapidly from the central stromateid bauplan and is widely successful along the coasts of southern Asia.

Key to Stromateid Genera

1 (4). Inter- and subopercles not united to the isthmus. End of maxillary before or at anterior border of eye. Cusps on teeth in lower jaw subequal, the teeth appearing truncate to the naked eye. Spine on end of pelvic bone present or absent. In small specimens (less than 80 mm SL) pelvic fins present or absent. Six branchiostegal rays. 2

2 (3). One to three flat, bladelike spines ahead of median fins. A small spine projecting posteroventrally from end of pelvic bone. Median fins falcate or not. Pelvic fins never present. 30 to 35 vertebrae. .... *Peprilus*, p. 103. Figs. 40, 41

3 (2). No flat, bladelike spines ahead of median fins. No spine at end of pelvic bone. Median fins never falcate. Pelvic fins absent in adult, but present in some small specimens. 40 to 48 vertebrae. .... *Stromateus*, p. 99. Fig. 39

4 (1). Inter- and subopercles broadly united to isthmus. End of maxillary under eye. Central cusp on teeth of lower jaw much larger than the other two cusps, which can hardly be seen without extreme magnification. No spine at end of pelvic bone. Pelvic fins never present. Five branchiostegal rays. .... *Pampus*, p. 108. Figs. 44, 45

Genus *STROMATEUS* Linnaeus, 1758

Figure 39

Stromateus Linnaeus, 1758:248. (Type species: *Stromateus fiatola* Linnaeus, 1758:248, by monotypy. Mediterranean.)

Chrysostromus Lacépède, 1802:697. (Type species: *Chrysostromus fiatoloides* Lacépède, 1802:697, by monotypy. Mediterranean. A synonym of *Stromateus fiatola* Linnaeus, 1758: 248.)

Fiatola Cuvier, 1817:342. (Type species: *Stromateus fiatola* Linnaeus, 1758:248, by monotypy. Mediterranean.)

Seserinus Cuvier, 1817:342. (Type species: "*Seserinus* Rondelet" [*Seserinus rondeleti*] Cuvier, 1817:343, by subsequent designation of Jor-

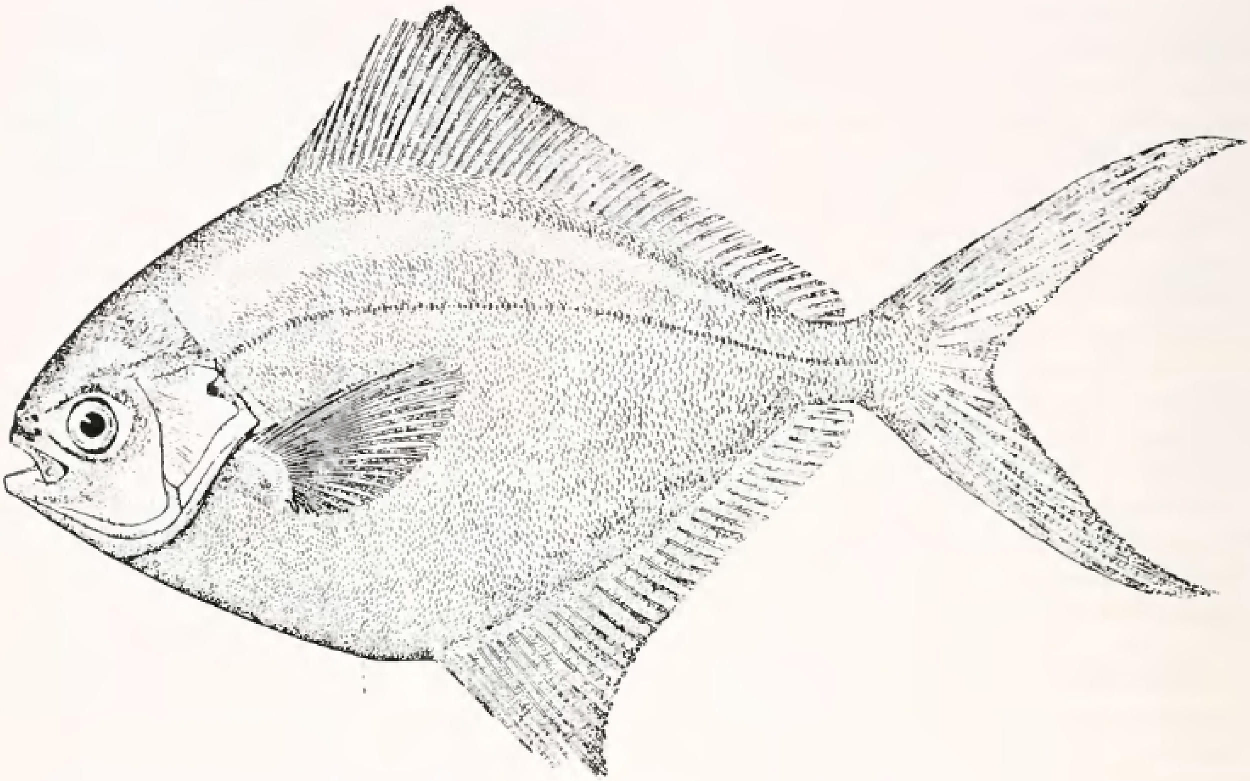

Figure 39. *Stromateus fiatola*, drawing of a 228-mm specimen, from Poll, 1959.

dan, 1923:106. Mediterranean. A synonym of *Stromateus fiatola* Linnaeus, 1758:248.)

Pterorhombus Fowler, 1906:118. (Subgenus. Type species: *Fiatola fasciata* Risso, 1826:289, by original designation. Mediterranean. A synonym of *Stromateus fiatola* Linnaeus, 1758: 248.)

The combination of deep body, small eye, moderate pectoral fin, no bladelike spines ahead of the median fins, no ventral spine on the pelvic bone, spotted body pattern, and (sometimes) pelvic fins in the young distinguishes *Stromateus* from all other stromateoid genera. The name, a masculine noun, is from the Greek *στρῶματευς*, a brightly colored quilt or bedding, probably in reference to the shape and pattern of the fish.

Description. Body deep, maximum depth generally greater than 40 per cent of the standard length, compressed; musculature firm. Peduncle very short, compressed. Dorsal fin continuous, originating over base of the pectoral fins, the anteriormost elements usually very small and buried in the skin, 44 to 53 elements in all. Anal papilla before mid-body, in a deep slit. Anal fin originating slightly before middle of body but behind dorsal origin, the small anteriormost elements buried in the skin, 35 to 47 elements in all. Anterior rays of the median fins produced, two to three times longer than the subequal rays of the posterior two-thirds of the fin, the lobes rounded and not falcate. No bladelike spines preceding median fins. Pectoral fin moderate in length, broad. Pelvic fins present in the young of at least some species, inserting under end of pectoral fin base, the fins lost in adult but with two dark flaps of skin sometimes indicating their former presence. Pelvic bone usually not visible on mid-line and lacking a ventral spine. Caudal fin stiff, deeply forked, the lobes very long. Scales small, cycloid, deciduous, minute scales covering all fins. Simple tubed scales of the lateral line moderately high, following dorsal profile and extending onto peduncle but not to caudal base. Skin moderately thick, subdermal canals not visible, pores to surface seem to be wanting. Head around 25 per cent of the standard length, very deep and broad. Top of head naked, small pores easily seen, naked skin underlain with numerous parallel canals projecting slightly backward over the nape. Eye small, adipose tissue around eye well developed and extending forward surrounding the nostrils. Nostrils moderate in size, the anterior round, the posterior a slit, located nearer to tip of blunt snout than to eye. Mouth broad. Maxillary scarcely reaching anterior border of the eye, angle of gape well before eye. Premaxillary not protractile. Lacrimal bone reduced, scarcely covering top of upper jaw when mouth is closed, end of maxillary exposed. Supramaxillary absent. Jaw teeth minute, uniserial, laterally flattened, with three subequal cusps, close set, covered laterally by a membrane; vomer, palatines, and basibranchials toothless. Gill membranes broadly united across the isthmus, divided from level of the back part of the eye. Opercle and preopercle thin, scaled, margins entire; opercle rounded, with two ill-defined, weak spines; angle of preopercle broadly rounded, projecting backward slightly. Cheek scaled. Gillrakers a little less than half the length of the filaments, diminishing in size anteriorly, not toothed, fairly close-set, about 12 on the lower limb of the first arch; no rudimentary rakers under the small pseudobranch. Six branchiostegal rays, four on the ceratohyal, two on the epihyal. Scapula not visible. Vertebrae slightly variable, usually $16 + 26 = 42$ to $19 + 26 = 45$. Sclerotic bones well ossified. Stomach a simple sac; intestine very long. Pyloric caeca numerous, in a long dendritic mass.

Color in preservative brown or bluish with a silvery or whitish overlay, dark above, lighter below. Back and sides with numerous dark spots. The young may have four or five dark vertical bands. Fins darker or lighter than the body; pectoral in some species blackish. Gill cavity, inside of mouth, and peritoneum light.

Natural history. The young of *Stromateus* commonly associate with medusae (Padoa, 1956), and Lo Bianco (1909) observed them eating jellyfish. Fish up to five inches in length have been reported in association (Smith, 1949a), but the majority probably desert their coelenterate host before reaching this size.

Poll (1959) found the adult common in depths from 12 to 50 meters off the coast of West Africa. I have examined adults taken by the Guinean Trawling Survey in 30 meters of water, and adults from Chile captured with a trammel net. Adult *Stromateus* may rarely descend to deeper water.

Small *Stromateus fiatola* have a vertically barred pattern and small pelvic fins. The bars and the pelvics are lost usually before the fish reaches 100 mm standard length. At this point, the young fish probably moves into the adult habitat. Whether or not the young of South American *Stromateus* have pelvic fins is unknown. Poll (1959) reports a *Stromateus fiatola* 500 mm long weighing 151 grams; this is probably near the maximum size attained.

In the Patagonian region, *Stromateus* moves shoreward to spawn in early summer (Hart, 1946). At this time the fishes form their maximum concentrations. Following spawning, they move offshore during the fall and winter, and become widely dispersed. In addition to inshore and offshore movement, Hart (1946) found evidence that *Stromateus* moves from lower to higher latitudes in the summer, and back in the winter.

Said to be a fish with "delicate flesh and fine flavour" (Gilchrist and von Bonde, 1923:11), *Stromateus* apparently does not receive the attention it deserves. Once described as numerous in the markets at Lima (Cuvier and Valenciennes, 1833), it is today the subject of only small local fisheries in parts of Chile and along the African coast.

Relationships. Stromateus contains the most primitive species of the family Stromateidae. *Stromateus fiatola*, the African species, has three epural elements in the caudal skeleton and, when young, has pelvic fins. These characters indicate the centrolophid heritage of the stromateids. In the South American species of *Stromateus*, there seem to be only two epural elements in the tail, and the young may lack pelvic fins.[1] This situation is typical of the stromateid grade.

Stromateus has a very high number of vertebrae, more than forty, an advanced condition. This high number may be a recently acquired characteristic of the genus. The number itself is variable, and, in a large proportion of cases, fusions of the centra occur in the caudal series. Centra with two or three neural and haemal spines appeared in four of the fourteen specimens radiographed. The variability and high incidence of fusions suggests a genetic instability perhaps correlated with recent acquisition.

Because of its high vertebral count, *Stromateus* cannot be the direct ancestor of either of the other two stromateid genera, both of which have lower counts. Rather, all three must share a common ancestor, a fish most like *Stromateus* but with a vertebral count somewhere near 13 + 17.

Species. Stromateus lives in temperate to tropical waters along the coasts of Mediterranean countries, West Africa, Argentina, and Chile. Though numerous species have been described, there seem to be no more than two, or possibly three, valid ones. Species are widespread along a coastline, but none jump ocean barriers. The species in the genus are:

Stromateus fiatola Linnaeus, 1758. Mediterranean, coast of West Africa south to Capetown, type locality Mediterranean Sea. D 48–51 (total elements). A 35–38 (total elements). P 22–24. Gill-rakers usually 3 + 1 + 11. Vertebrae 18–19 + 24–26. Specimens less than 100 mm SL have pelvic fins and vertical bars on the sides. The fins and the bars are gone in adults. The names of the Mediterranean *Fiatola fasciata* Risso, 1826, and *Seserinus microchirus* Cuvier and Valenciennes, 1833, are synonyms based on juveniles. Other synonyms are *Chrysostromus fiatoloides* Lacépède, 1802, from the Mediterranean and *Stromateus capensis* Pappe, 1866, from South Africa.

Stromateus stellatus Cuvier, 1829. Pacific coast of South America, Chile and rarely north to Lima, type locality coasts of Peru. D 44–53 (total elements). A 39–44 (total elements). P 19–24. Gill-rakers around 4 + 1 + 12. Vertebrae 16 + 26–27. **Stromateus maculatus* Cuvier and Valenciennes, 1833 (= S. *advectitius* Whitley, 1935), a junior synonym, is the name most often used for this fish. *S. *maculatus* is also generally applied to the species of *Stromateus* which occurs along the Atlantic coast of South America. The two forms are very close in appearance but the Chilean form is a slenderer fish with a slightly longer head. The counts of the two overlap almost completely. The Atlantic form seems to breed near the northern limit of its range (Hart, 1946). Nothing is known concerning the breeding habits of the Pacific form, but the spawning area is probably well north of Tierra del Fuego. It seems unlikely that there is any gene exchange between the two populations, and I suspect that future study will show that sufficient difference exists to warrant recognition of both at the species level. The available name for the Atlantic population is:

**Stromateus brasiliensis* Fowler, 1906. Atlantic coast of South America, Tierra del Fuego north to Uruguay, type locality Rio Grande do Sul, Brazil. D 47–53 (total elements). A 44–47 (total elements). P 19–20. Gill-rakers around 3 + 1 + 12. Vertebrae 16–17 + 27–30. The bionomics and potential fishery for this fish are the subject of an excellent discussion by Hart (1946).

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[1] I have seen no small *Stromateus* from South America, but the adults lack the two dark flaps of skin which bespeak the former presence of pelvics in adult African *Stromateus*.

Genus *PEPRILUS* Cuvier, 1829

Figures 40, 41

Rhombus Lacépède, 1800:60. (Type species: *Chaetodon alepidotus* Linnaeus, 1766:460, by monotypy. Charleston, South Carolina. Preoccupied by *Rhombus* Humphrey, 1797, Mollusca.)

Peprilus Cuvier, 1829:213. (Type species: *Sternoptyx gardenii* Bloch and Schneider, 1801: 494, by subsequent designation of Gill, 1862: 126. Charleston, South Carolina. A synonym of *Chaetodon alepidotus* Linnaeus, 1766:460.)

Poronotus Gill, 1861:35. (Type species: *Stromateus triacanthus* Peck, 1804:51, by monotypy. Piscataqua River, New Hampshire.)

Palometa Jordan and Evermann, 1896:966. (Subgenus. Type species: **Stromateus palometa* Jordan and Bollman, 1889:156, by original designation. Bay of Panama, Pacific Ocean.)

Simobrama Fowler, 1944b:2. (Type species: **Seserinus xanthurus* Quoy and Gaimard, 1824:384, by original designation. Rio de Janeiro. A synonym of *Stromateus paru* Linnaeus, 1758: 248.)

The combination of deep body, large eye, long pectoral fin, one to three bladelike spines ahead of the median fins, a ventral spine on the pelvic bone, and no pelvic fins, distinguishes *Peprilus* from all other stromateoid genera. The name, a masculine noun, is from the Greek *πεπρίλος*, one of Hesychian's many *ἰχθῦς ποίος*, unknown fish.

Description. Body deep, maximum depth 35 to 70 per cent of the standard length, highly compressed; musculature firm. Peduncle very short, compressed. Dorsal fin continuous, originating just behind insertion of the pectoral fin; one to three flat, bladelike spines, the first spine pointed on both ends, preceding the 30 to 40 finrays. Anteriormost rays of the median fins produced, the fins often falcate, the rays which follow much shorter, diminishing very slightly in length to the last ray, the shortest. Pectoral fins long, winglike, their bases slightly inclined. No pelvic fins. Pelvic bone visible on midline of body under the end of the pectoral fin base; a small spine on the end of the bone projecting posteroventrally through the skin. Tip of coracoid sometimes projecting slightly underneath the head at about level of margin of the preopercle. Caudal fin stiff, deeply forked, the lobes long and equal. Scales very small, cycloid, thin, very deciduous, extending onto all fins. Simple tubed scales of the lateral line moderately high, following dorsal profile and extending onto peduncle but not to caudal base. A branch of the lateral line extending upward from the head of the hyomandibular in a short, wide, bony tract. Skin very thin; main subdermal canal along intermuscular septum and side branches conspicuous, pores to surface very small. In some species, a row of large conspicuous pores in the back under the first half of the dorsal fin. Head around 25 per cent of the standard length. Top of head naked, pores clearly visible, naked skin underlain with numerous parallel canals projecting backward over the nape. Eye large. Adipose tissue around the eye developed, extending forward and surrounding the nostrils. Nostrils small, the anterior round, the posterior a slit, located near tip of the obtuse snout at level of top of the eye. End of maxillary barely reaching to below eye, angle of gape well before eye. Premaxillary not protractile. Lacrimal bone reduced, scarcely covering top of upper jaw when mouth is closed, end of maxillary exposed. Supramaxillary absent. Jaw teeth minute, uniserial, laterally compressed, with three subequal cusps, close set, covered laterally by a membrane. Vomer, palatines, and basibranchials toothless. Gill membranes united across the isthmus, divided from about level of the forward part of the eye. Opercle and preopercle thin, not scaled, preopercle finely striated, opercle smooth, margins entire; opercle with two ill-defined flat spines; angle of preopercle rounded, not projecting backward. Cheek not scaled. Gill-rakers a little more than half the length of the filaments, with fine teeth on the inner edge, the rakers close set, about 18 on the lower limb of the first arch; no rudimentary rakers under the small pseudobranch. Six branchiostegal rays, four on the ceratohyal, two on the epihyal. Scapula visible. Vertebrae variable, $13 + 17 = 30$ to $12 + 23 =$

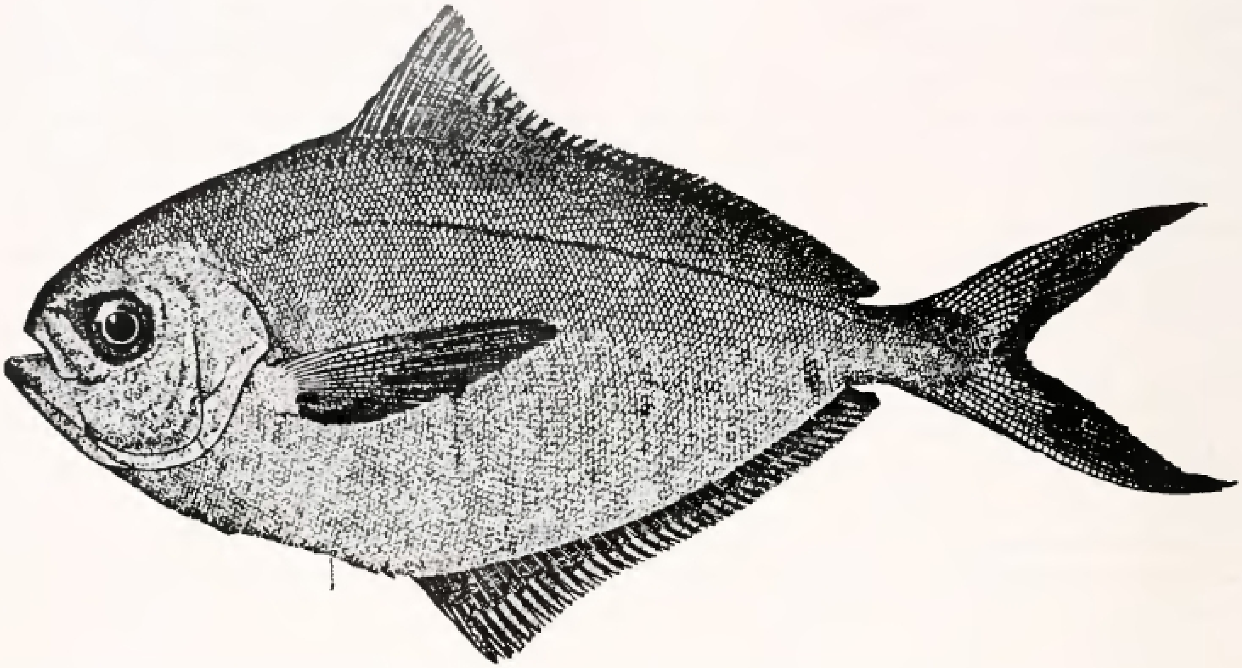

Figure 40. *Peprilus triacanthus*, drawing of a 7.5-inch specimen, courtesy of the Smithsonian Institution.

35. Sclerotic bones well ossified. Stomach a simple sac; intestine very long. Pyloric caeca very numerous, in a dendritic mass.

Color in preservative brownish, often with a silvery overlay, dark above, lighter below. Back and sides sometimes with spots. Median fins darker or lighter than the body; pectoral light. Gill cavity, inside of mouth, and peritoneum light.

Natural history. The species of *Peprilus* are prized for food wherever they occur. The biggest fishery is for *P. triacanthus*, which is found along the east coast of the United States. In some years, more than two million pounds of this species are landed in Massachusetts alone (Bigelow and Schroeder, 1953). Considering its commercial importance, surprisingly little is known of the habits of *Peprilus*. Almost all our knowledge of the natural history of the genus comes from a few general studies on *P. triacanthus*. The discussion here is based largely on the excellent review of Bigelow and Schroeder (1953).

Though young *P. triacanthus* are sometimes found with *Cyanea*, they do not seem to associate with medusae as actively as some other stromateoids. The small fishes are just as often observed swimming independently at the surface or clustered under floating Gulf weed. A much stronger association is formed by *P. alepidotus* with the sea nettle *Chrysaora* in Chesapeake Bay. *P. alepidotus* feeds actively on the medusa (Mansueti, 1963).

Peprilus triacanthus spawn in Massachusetts waters from summer into early fall. Spawning takes place a few miles offshore, but, except at this time, the adults are usually closer to shore in water less than 30 fathoms deep. The eggs are pelagic and, at a temperature of 65°F, hatch in less than two days. During their first summer, the young fish may grow to a length of three or four inches. They probably mature when about two years old at a length of seven inches. A large adult is no more than a foot long.

During the late fall, schools of *Peprilus triacanthus* apparently move offshore where they winter near bottom in about 100 fathoms. Though sometimes occurring as far

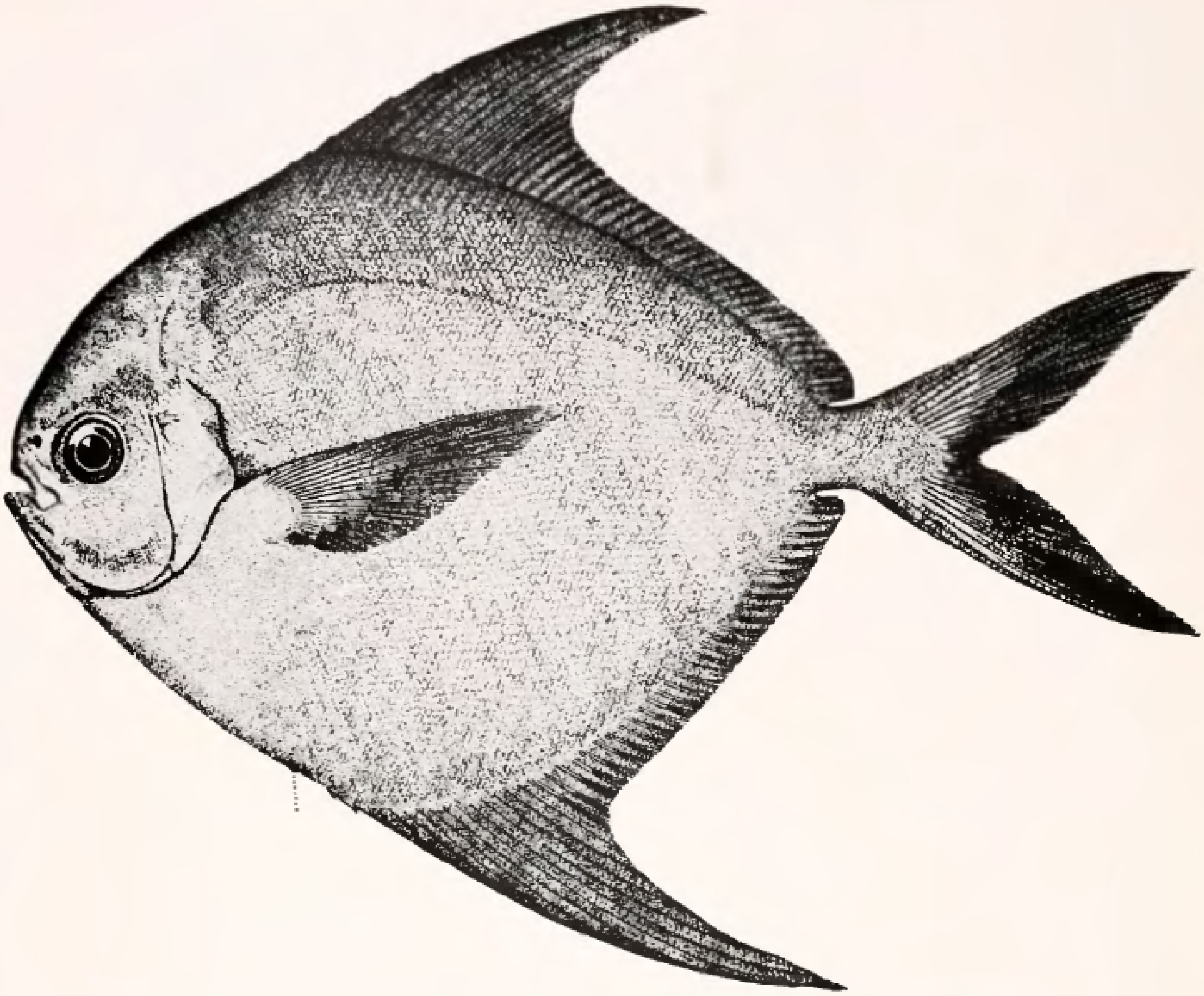

Figure 41. *Peprilus alepidotus*, drawing of a 7.5-inch specimen, courtesy of the Smithsonian Institution.

north as Newfoundland, *P. triacanthus*, like all members of the genus, is basically a warm water fish.

Relationships. Peprilus is more advanced than *Stromateus* in that all species lack pelvic fins and have only two epural elements in the caudal skeleton (Fig. 42). But it is more primitive than *Pampus* in having six instead of five branchiostegal rays and a shorter pharyngeal sac (Fig. 43; cf. Fig. 46). The few spines before the median fins in *Peprilus* are very similar in form to the more numerous spines of some *Pampus*, but the similarity is probably due to common heritage rather than to direct ancestry. It is unlikely that *Pampus* is derived from *Peprilus*. The most primitive species in *Pampus* has no spines before the median fins and shows no trace of the pelvic spine so characteristic of *Peprilus*. *Peprilus* is derived from a fish somewhat like *Stromateus*, but probably with fewer vertebrae.

Species. Peprilus is widespread, with a number of species along both the Atlantic and Pacific coasts of the New World north of the equator. One species is found as far south as Montevideo on the east coast of South America. *Peprilus* has been divided into several nominal genera, but the differences on which these are based—depth of body, fins falcate or not, certain pores well developed or not—are the differences between species, not genera. Osteologi-

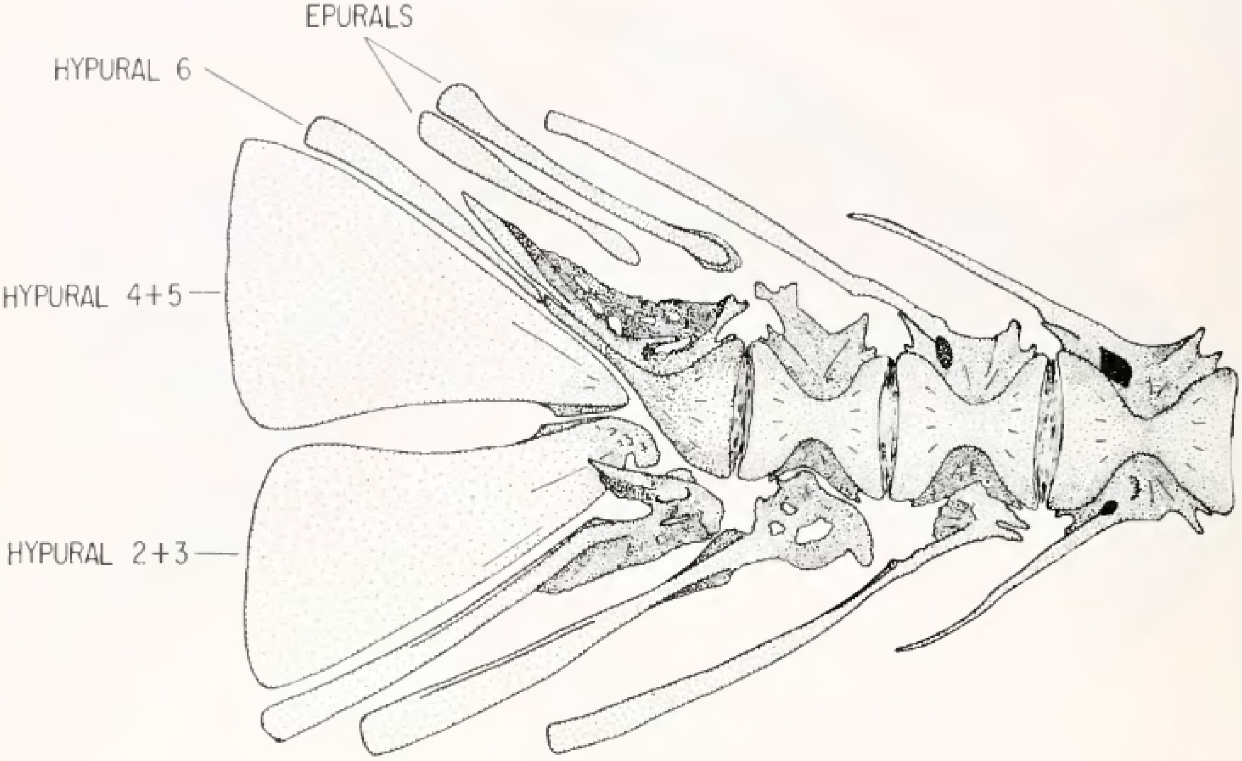

Figure 42. Caudal skeleton of *Peprilus triacanthus*, drawing of a cleared-and-stained preparation from a 36-mm specimen. All elements identified in Figure 1.

cally, all members of the nominal genera are very similar.

The species differ but little from one another. There is some question as to whether or not certain populations are to be regarded as full species or only as subspecies. The marked similarity between species, and therefore the doubt as to the rank to be accorded certain forms, is probably due to the fact that active speciation is occurring now in the genus. More variational studies and increased knowledge of the natural history are needed to resolve these questions.

The species in *Peprilus* are:

Peprilus paru (Linnaeus, 1758) = *Stromateus paru* Linnaeus. West Indies to Uruguay, type locality Jamaica. D III 38–44. A II 35–41. P 20–22. Vertebrae 13 + 17. This species is distinguished from the very closely related *P. alepidotus* (Linnaeus, 1766) by the lower counts and narrower pectoral fin (Hildebrand, MS). Synonyms are: **Seserinus xanthurus* Quoy and Gaimard, 1824, from Brazil; *Rhombus crenulatus* Cuvier and Valenciennes, 1833, from Cayenne; and *Rhombus orbicularis* Guichenot, 1866a, also from Cayenne.

Peprilus alepidotus (Linnaeus, 1766) = *Chaetodon alepidotus* Linnaeus. East coast of North America from Massachusetts to Florida and Gulf of Mexico, type locality Charleston, South Carolina. D III 43–49. A II 39–43. P 21. Vertebrae 13 + 17. This species is considered distinct from *P. paru* by Hildebrand (MS), although both are often lumped under this name. This is the "harvestfish" of the North American fisheries literature. *Stromateus longipinnis* Mitchill, 1815, from New York Bay, is a synonym.

Peprilus triacanthus (Peck, 1804) = *Stromateus triacanthus* Peck. East coast of North America from Newfoundland to Florida, type locality Piscataqua River, New Hampshire. D III 43–46. A II 37–43. P 19–21. Vertebrae around 13 + 19. This spe-

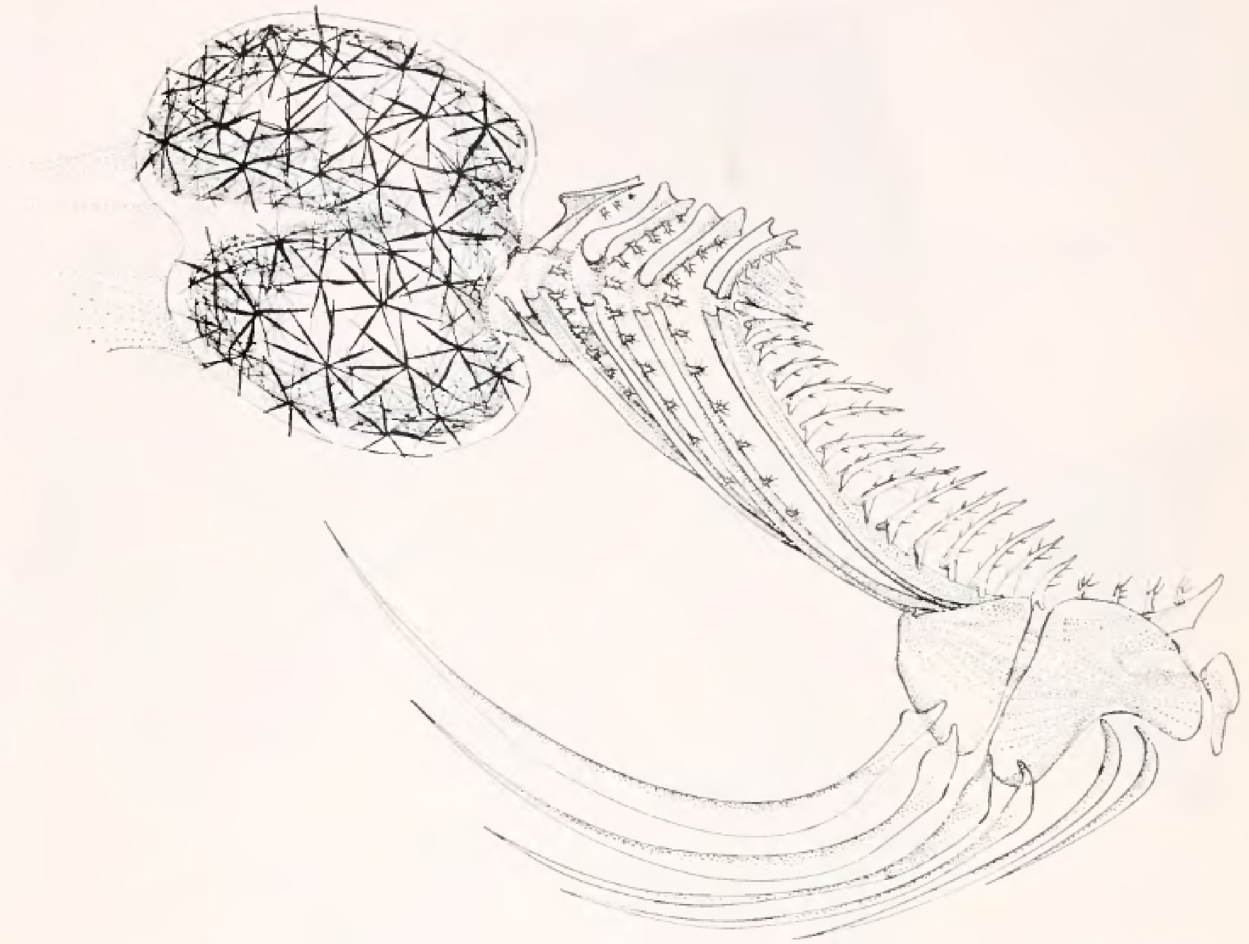

Figure 43. Branchial region of *Peprilus triacanthus*, drawing of a cleared-and-stained preparation from a 120-mm specimen. Elements identified in Figure 2.

cies is very close to *P. burti* Fowler, from which it is distinguished by a slightly higher vertebral count (Collette, 1963). These two forms have only recently diverged. This fish is usually known as *Poronotus triacanthus*, the "butterfish" of North American fisheries literature. *Stromateus cryptosus* Mitchill, 1815, from New York Bay, is a synonym.

Peprilus simillimus (Ayres, 1860) = *Poronotus simillimus* Ayres. West coast of North America, British Columbia to Baja California, type locality San Francisco. D III 45–47. A III 39–44. P 20–22. Vertebrae 13 + 17. This species is a member of the *P. triacanthus–burti* complex.

Peprilus medius (Peters, 1869) = *Stromateus medius* Peters. Known only from Mazatlán, Mexico, Pacific Coast. D III 42. A III 32. (From Fordice, 1884.) Possibly a synonym of *P. simillimus* (Ayres, 1860).

Peprilus palometa (Jordan and Bollman, 1889) = **Stromateus palometa* Jordan and Bollman. Pacific coasts of Panama and Colombia. D III 44–48. A II 43–46. P 22–23. Gill-rakers 5–6 + 1 + 15–16. Vertebrae 13 + 20–21. This deep-bodied fish with falcate median fins is a member of the Atlantic *P. alepidotus–paru* group.

**P. snyderi* Gilbert and Starks, 1904. Known only from Panama Bay. D III 41–47. A III 41–42. P 22–23. Gill-rakers 4 + 1 + 14. Vertebrae 13 + 23. This rarely seen species is distinguished from *P. palometa* (Jordan and Bollman, 1889) in having more vertebrae, a longer snout, and very short

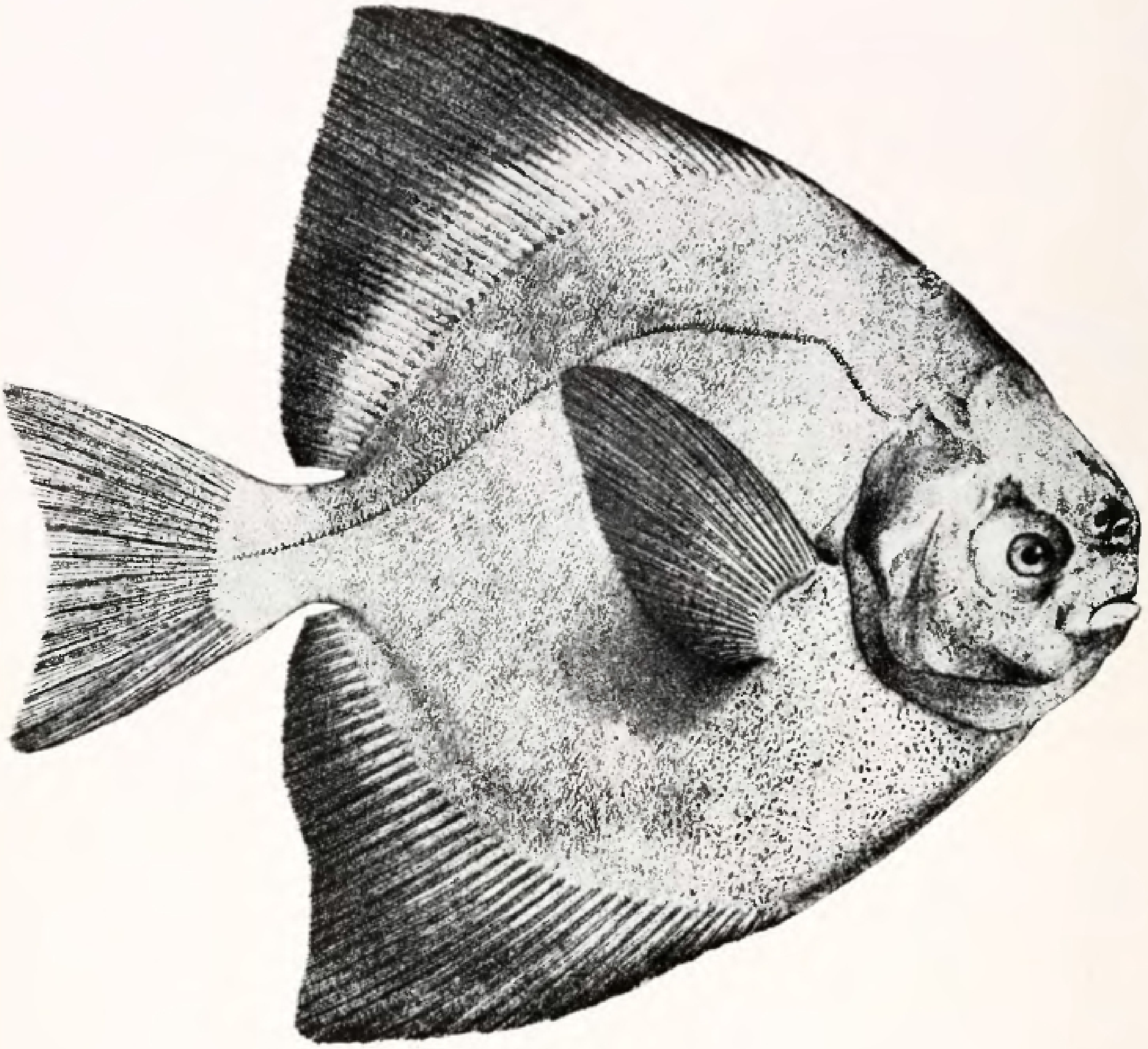

Figure 44. *Pampus chinensis*, a species lacking spines before the median fins, drawing of a 4-inch specimen, from Day, 1875.

lobes on the median fins. *P. snyderi* approaches *Stromateus* in the increased number of vertebrae and in the very reduced spines preceding the rays in the median fins. It may be very like the stromateid ancestral to *Peprilus* and *Stromateus*. Investigations of its systematic position, geographic distribution, and natural history should be very instructive.

Peprilus burti Fowler, 1944b. Gulf of Mexico, type locality Breton Island, Louisiana. D III 43–45. A III 40–41. P 20–21. (From Fowler, 1944b.) Vertebrae around 13 + 17 (Collette, 1963). This species is very close to *P. triacanthus* (Peck, 1804). Caldwell (1961) and Collette (1963) differ in their interpretation of its systematic status.

Genus *PAMPUS* Bonaparte, 1837

Figures 44, 45

Pampus Bonaparte, 1837:48. (Subgenus. Type species: *Stromateus candidus* Cuvier and Valenciennes, 1833:391, by subsequent designation of Jordan, 1923:187. Malabar Coast.

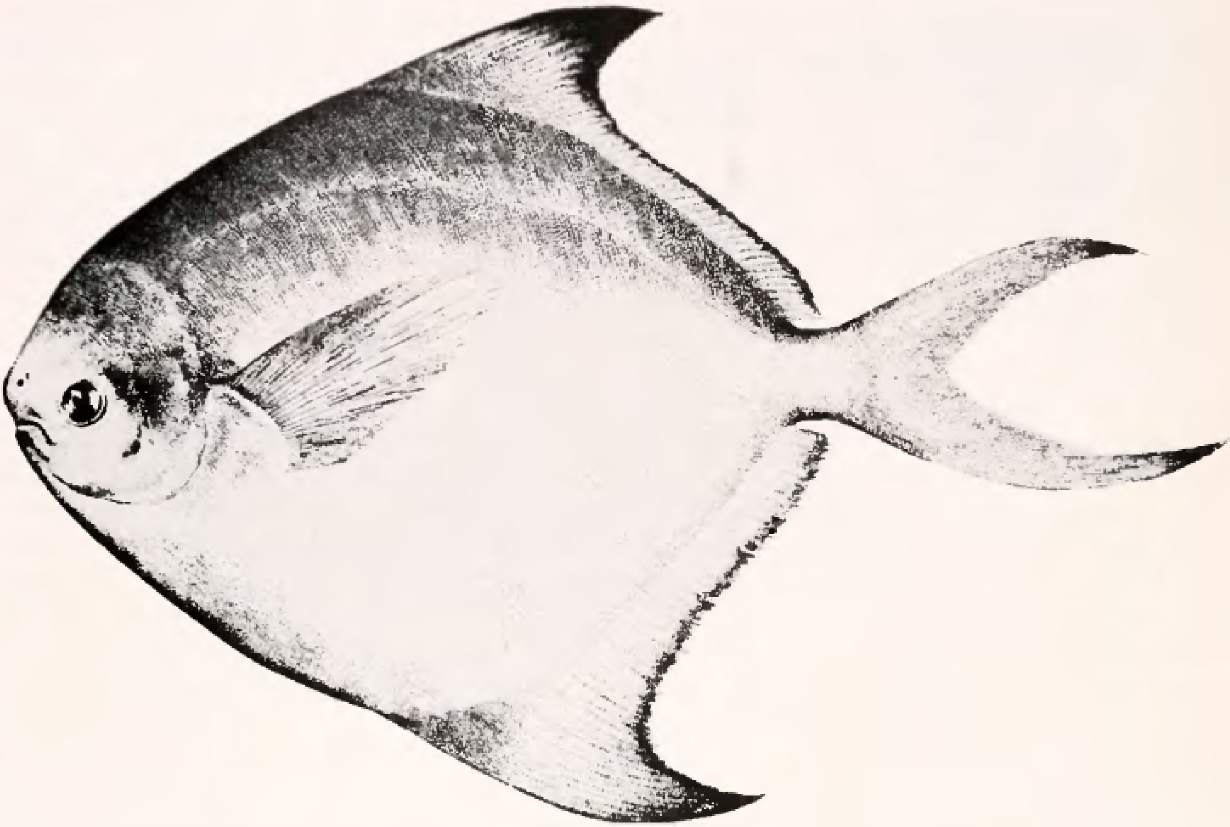

Figure 45. *Pampus argenteus*, a species with spines before the median fins, drawing of a 10.5-inch specimen, from Jordan and Metz, 1913.

A synonym of *Stromateus argenteus* Euphrasen, 1788:53.)

Stromateoides Bleeker, 1851:368. (Type species: *Stromateus cinereus* Bloch, 1793:90, by subsequent designation of Gill, 1862:126. A synonym of *Stromateus argenteus* Euphrasen, 1788:53.)

Chondroplites Gill, 1862:126. (Type species: *Stromateus atous* Cuvier and Valenciennes, 1833:389, by original designation. After Russell's "atoo-koia" (1803: plate 21), Vizagapatam. A synonym of *Stromateus chinensis* Euphrasen, 1788:54.)

The combination of deep body, no pelvic fins, fixed maxillary, and gill membranes broadly united to the isthmus distinguishes *Pampus* from all other stromateoid genera. The name, a masculine noun, is from the vernacular of the 19th century East Indian Spanish and Portuguese colonials, who generally used the term "pampus" (ultimately from "pampano") for any silvery, compressed fish.

Description. Body very deep, maximum depth greater than 60 per cent of the standard length, highly compressed; musculature firm. Peduncle very short, compressed. A continuous dorsal fin; both median fins preceded by either none or five to ten flat, bladelike spines, pointed on both ends, protruding but slightly and resembling the ends of free interneurals. In forms with bladelike spines, dorsal fin originating slightly behind end of pectoral fin base, the first spine generally over or slightly before the pectoral insertion; in forms lacking spines, dorsal fin originating over the pectoral fin base. Anal papilla well before midbody, in a slit. Anal fin originating at or before middle of body and only slightly behind origin of the soft dorsal. Anteriormost rays of the median fins produced, the fins often falcate, rays which follow shorter; in forms with bladelike spines, rays of the posterior two-thirds of the fin short and subequal, the anal fin lobe often extremely produced; in forms lacking spines, rays of the posterior two-thirds of the fin decreasing in length evenly to the last ray, the shortest. Pectoral fin long, winglike, the base of the fin inclined about 45°. No pelvic fins. Pelvic bone not visible on midline and lacking a ventral spine. Tip of coracoid often projecting slightly underneath head at about level of margin of preopercle. Caudal fin stiff, deeply forked, in forms with bladelike spines the ventral lobe often extremely produced. Scales very small, cycloid, thin, deciduous, extending onto bases of all fins. Simple tubed scales of the lateral line fairly high, following dorsal profile, and extending onto peduncle. Skin thin; main subdermal canal along intermuscular septum and side branches usually quite apparent, pores to surface seem wanting. Head around 25 per cent of the standard length, very deep and broad. Top of head naked, subdermal canals visible under naked skin but pores not visible, naked skin underlain with numerous parallel canals projecting backwards over the nape and along first part of lateral line. Eye small. Adipose tissue around eye developed and extending forward around the nostrils. Nostrils large, the anterior round, the posterior a long slit, located near tip of the inflated snout at level of the top of the eye, nasal capsules greatly expanded. Mouth subterminal, curved downward, small, maxillary scarcely reaching to below eye and angle of gape before eye. Premaxillary not protractile. Maxillary immobile, covered with skin and united to cheek. Lacrimal bone very much reduced. Supramaxillary absent. Jaw teeth minute, uniserial, flattened, with a large rounded central cusp and two shorter auxiliary cusps, close set, covered laterally by a membrane. Vomer, palatines, and basibranchials toothless. Gill membranes broadly united to the isthmus. Gill opening a straight slit, covered with a flap of skin. Gill-rakers small, about one-quarter the length of the filaments, not toothed, widely spaced. Pseudobranch absent. Five branchiostegal rays, three on the ceratohyal, two on the epihyal. Scapula not prominent. Vertebrae variable in species with bladelike spines, $14 + 20 = 34$ to $16 + 25 = 41$; in species without bladelike spines, vertebrae $14 + 19 = 33$. Dermal skeleton soft and spongy, but sclerotic bones well ossified; skeleton in general fibrous. Stomach a simple sac; intestine very long. Pyloric caeca numerous, in a small dendritic mass.

Color in life very silvery with a bluish cast on the back. Color in preservative brown or bluish with a silvery or whitish overlay. Median fins and caudal yellowish with dark borders. Head a little darker than the body, with fine speckling. Gill membranes and inside of mouth dark. Peritoneum silvery with black speckles.

Natural history. Pampus is the most sought after of all the stromateoid fishes. Throughout the Orient, it commands a good price wherever it appears. In India, where it is known as "pomfret," the 1962 landings totaled 25.7 thousand metric tons, more than four per cent of the total marine catch (FAO 1964). However, despite its commercial importance, virtually nothing is known of the life history of *Pampus.*

The young occur in shallow water along the coasts, and may even ascend estuaries (Day, 1875). The small mouths with cutting teeth and the long pharyngeal sacs suggest that soft-bodied coelenterates may figure largely in the diet. Most stomachs examined seemed to contain the shredded remains of these animals, but bits of fish were also found. Chopra (1960) found that a sudden appearance of numerous ctenophores and medusae in the waters off Bombay was accompanied by a marked increase in the local catch of *Pampus.*

Relationships. Pampus is the most advanced stromateid genus. The advanced characters are the reduction in the number of branchiostegal rays to five, the lengthening of the pharyngeal sac (Fig. 46), the restriction of the gill opening, the loss of the pseudobranch, and the development, in

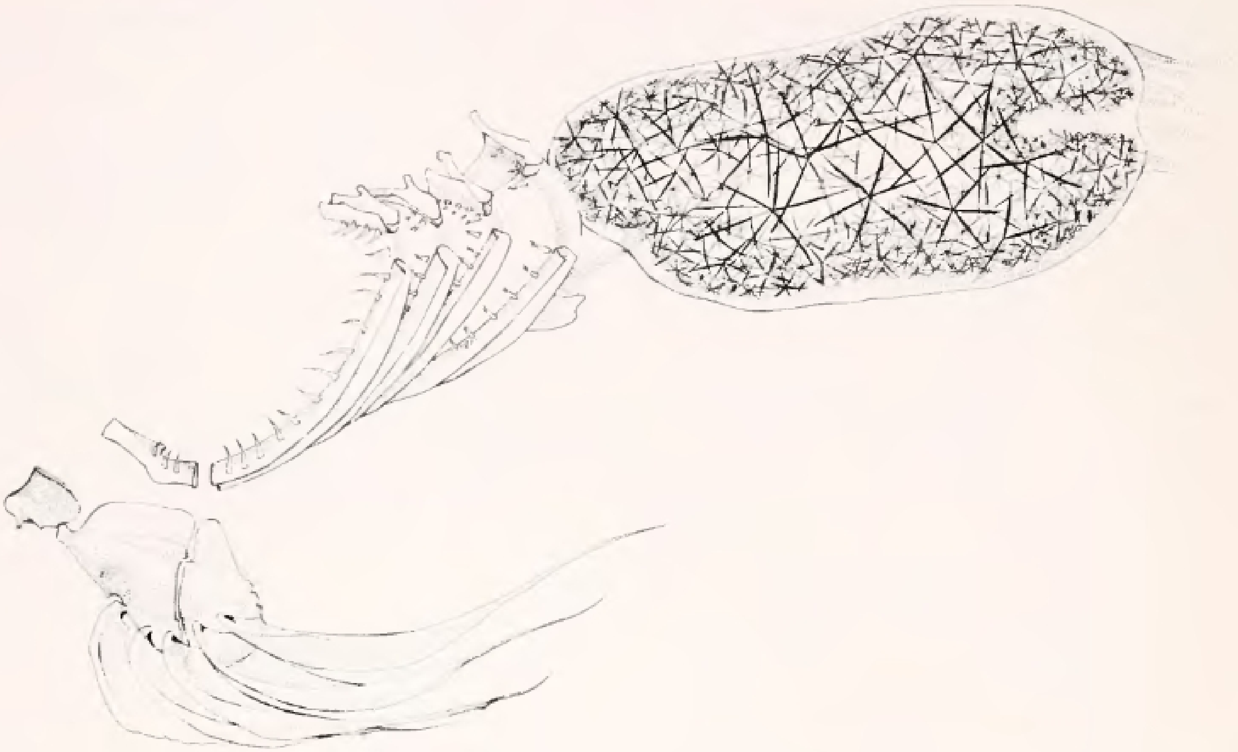

Figure 46. Branchial region of *Pampus echinogaster*, drawing of a cleared-and-stained preparation from a 180-mm specimen, ABE 1743. Elements identified in Figure 2.

some species, of flat, bladelike spines ahead of the median fins. The genus is derived from a fish very like *Stromateus*, but with fewer vertebrae. The most primitive species in *Pampus* has 14 + 19 vertebrae, but the more advanced may have as many as 16 + 25. All members of the genus have the typical stromateid caudal skeleton (Fig. 47).

Species. Pampus is widely distributed in tropical waters over the continental shelves from the Iranian Gulf to Japan. There are reports of specimens from Hawaii (Fowler, 1938) and from the Adriatic (Sòljan, 1948). No subsequent records have appeared from either place. The two localities are so far out of the established range of the genus that the records can only have been based on specimens brought from elsewhere.

Gill (1884) divided the genus *Stromateoides* (= *Pampus*) into two groups, which he apparently regarded as subgenera. The group *Stromateoides* had falcate fins and prominent dorsal and anal spines; the other group, *Chondroplites*, had neither. This dichotomy does exist in *Pampus*, but more work is needed to decide whether or not the distinction merits subgeneric recognition.

Numerous species have been described in the genus. The majority are probably synonyms. Published descriptions provide for the most part no clear-cut means of distinguishing species. At the present state of knowledge, only three can be recognized:

Pampus chinensis (Euphrasen, 1788) = *Stromateus chinensis* Euphrasen. India to China, type locality "Castellum Chinense Bocca Tigris." D 43–50 (total elements). A 39–42 (total elements). P 24–27. Vertebrae 14 + 19. This species lacks the peculiar flat spines before the median fins which are found in the other two species. The median fins are not falcate. The finrays gradually diminish in length posteriorly (Fig. 44). *P. chinensis*, the type for

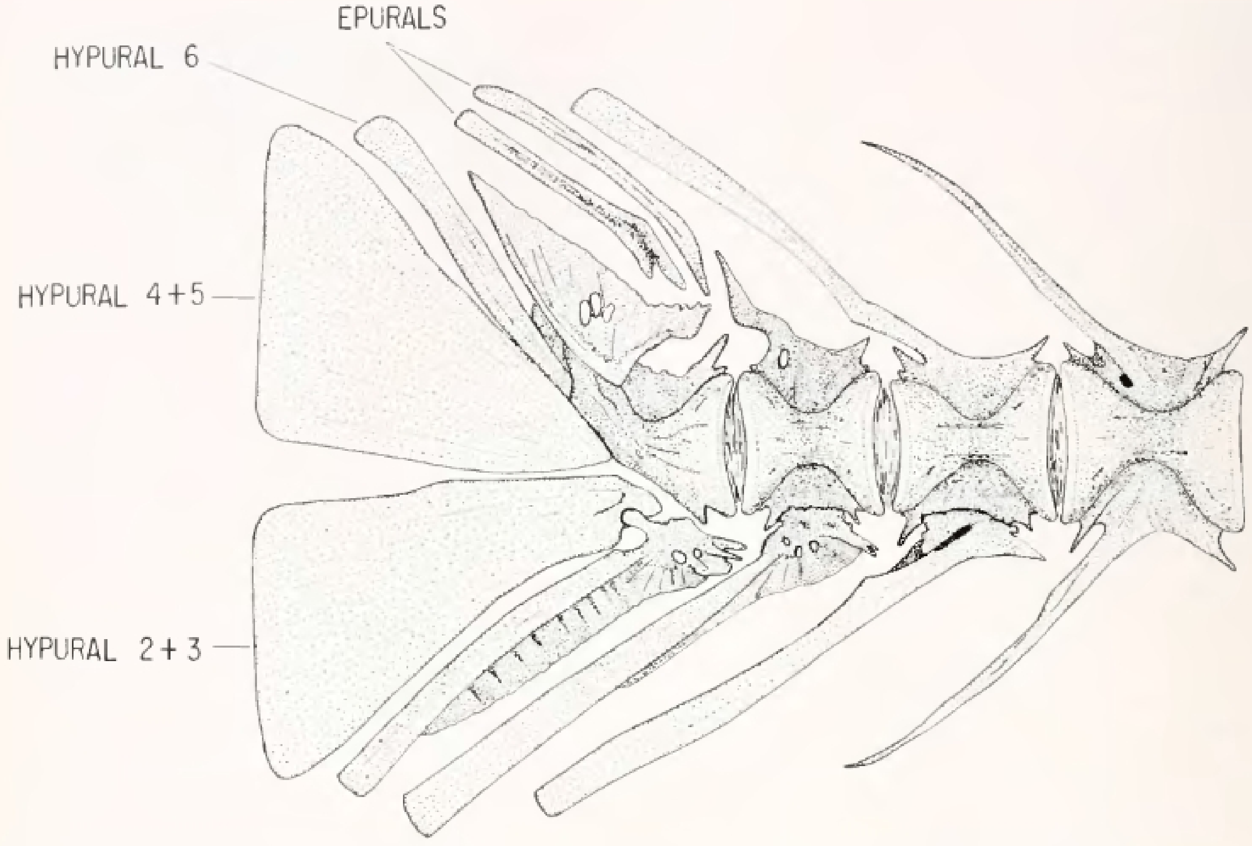

Figure 47. Caudal skeleton of *Pampus argenteus*, drawing of a cleared-and-stained preparation from a 48-mm specimen, ABE 1937. All elements identified in Figure 1.

Gill's (1884) genus *Chondroplites*, is certainly the most primitive species in *Pampus*. Synonyms are: *Stromateus albus* Cuvier and Valenciennes, 1833, from Pondichéry; *Stromateus atous* Cuvier and Valenciennes, 1833, from Vizagapatam; and *Stromateoides atokoia* Bleeker, 1852, from Malaysia. The trivial name is commonly written incorrectly *sinensis*.

Pampus argenteus (Euphrasen, 1788) = *Stromateus argenteus* Euphrasen. Iranian Gulf to Japan, type locality "Castellum Chinense Bocca Tigris." D V–X 38–43. A V–VII 34–43. P 24–27. Vertebrae 14–16 + 20–25. Falcate median fins, preceded by flat bicuspid spines, are characteristic of this species (Fig. 45). The species is apparently very wide ranging. Further study will no doubt show it to be composed of numerous subspecies or even species. This fish is the "pomfret" of Eastern fisheries literature, and is important commercially in India, China, and Japan. Probable synonyms are: *Stromateus cinereus* Bloch, 1793; *Stromateus candidus* Cuvier and Valenciennes, 1833, from Pondichéry; *Stromateus securifer* Cuvier and Valenciennes, 1833, from Bombay; *Stromateus griseus* Cuvier and Valenciennes, 1833, from Pondichéry; *Stromateus punctatissimus* Temminck and Schlegel, 1850, from Japan; and *Pampus simoprosopus* Fowler, 1934b, from Siam.

Pampus echinogaster (Basilewsky, 1855) = *Stromateus echinogaster* Basilewsky. China, Korea, and Japan, type locality China. D VIII–X 42–49. A V–VII 42–47. P 24–25. Vertebrae 14–15 + 24–26. This species has more median finrays than *P. argenteus*. Abe and Kosakai (1964) report that *P. echinogaster* has fewer, thicker pyloric caeca than *P. argenteus*, and 3–6 + 12–15 gill-rakers as opposed to 2–3 + 8–10 in *P. argenteus*. *Pampus lighti* Evermann and Shaw, 1927, from Nanking is a probable synonym.

EVOLUTIONARY TRENDS IN THE STROMATEOIDEI

Gosline (1959) and Liem (1963) have recently stressed the need for an understanding of functional morphology in connection with phylogenetic studies. Natural selection acts on efficiencies and abilities, and evolutionary change results. If function is understood, or at least taken cognizance of, an attempt can be made to evaluate observed differences in terms of efficiences and abilities. Within this framework, evolutionary trends can be discussed. Anatomy alone is insufficient; the way of life must also be taken into account.

The functional significance of many characters, however, is not known. It is hard to understand, for example, why selection should favor a fish with 15 principal branched rays in the caudal fin or with 25 vertebrae, yet these numbers have appeared in many independent phyletic lines. Studies of characters of this sort are, nonetheless, of much importance. The argument that the overall trends observed are real is made stronger when these characters change in step with characters for which the function is at least partially understood.

The trends in the evolution of the stromateoid fishes are discussed below, treating separately, as much as possible, groups of characters which can be considered anatomical units, i.e., caudal skeleton, branchial region, etc. Drawing on what little is known of the way of life of stromateoids, functional significance can be attached to changes in the teeth and jaws, the pharyngeal sacs, and the caudal skeleton. But the meaning of the changes in the size and shape of the body, the fin pattern, the branchial region, and the number of vertebrae cannot be easily interpreted. By and large, the discusion under each of these is necessarily brief and loaded with conjecture. Though each unit is treated separately, it must be remembered that they have evolved together. The organism responds as a whole to the environment, and the products of natural selection are all interdependent.

Attention should be drawn to the distinction between characters typical of a taxon and those typical of the grade of a taxon. In the first case, the characters are found in all members of the taxon. In essence, they are a part of the definition of that taxon. Grade refers to the "average" evolutionary status of the taxon *vis-a-vis* other taxa. The characters typical of a grade need not be found in all members of the taxon. In fact, because different parts of the animal respond to the environment at differing evolutionary rates, it is unlikely that these characters will be found in all. The use of grades provides a convenient way of discussing evolutionary trends without constantly itemizing the exceptions to the general picture. Thus, while 25 vertebrae characterize the centrolophid grade, not all members of the family Centrolophidae have 25 vertebrae. Most do have 25 but some have 26 and others have near 60.

Before proceeding to the discussion, let us briefly recall the more salient features of each of the five stromateoid families. The characters of the individual genera are presented in Table 2.

The Centrolophidae are one to four feet in length with moderately deep to elongate bodies. All have pelvic fins. Their mouths and the teeth in their jaws are fairly large. There are no teeth on the palate. The papillae in the round pharyngeal sacs have irregularly shaped bases. There are seven branchiostegal rays, a pseudobranch, and 25, 26, 29, 30, or 50 to 60 vertebrae. The caudal skeleton has six hypural and usually three epural elements. There are six genera: *Hyperoglyphe*, *Schedophilus*, *Centrolophus*, *Icichthys*, *Seriolella*, and *Psenopsis*.

The Nomeidae are six inches to over two feet in length with deep to elongate bodies. All have pelvic fins. Their mouths and the teeth in their jaws are small. The palatines and the vomer bear teeth. The papillae in

TABLE 2. CHARACTERS OF THE STROMATEOID GENERA. + DENOTES PRESENCE; — ABSENCE.

	Body Shape	Maximum Length	Pelvic Fins	Form of Teeth	Palatal Dentition	Branchiostegal Rays	Vertebrae	Epurals + Hypurals
Hyperoglyphe	moderate	4 feet	+	simple	—	7	25	3 + 6
Schedophilus	deep	3 feet	+	simple	—	7	25, 26, 29, 30	3 + 6
Centrolophus	elongate	4 feet	+	simple	—	7	25	3 + 6
Icichthys	elongate	3 feet	+	simple	—	7	50 to 60	2 + 6
Seriolella	moderate to elongate	3 feet	+	simple	—	7	25	3 + 6
Psenopsis	deep	1 foot	+	simple	—	7	25	3 + 6
Stromateus	deep	1 foot	— in adult	cusped	—	6	42–48	3 + 4
Peprilus	deep	1 foot	—	cusped	—	6	30–33	2 + 4
Pampus	very deep	18 inches	—	cusped	—	5	33–41	2 + 4
Cubiceps	elongate	3 feet	+	simple	+	6	30–33	3 + 4
Nomeus	elongate	1 foot	+	simple	+	6	41	3 + 4
Psenes	moderate to deep	1 foot	+	simple or cusped	+	6	30–42	3 + 4
Ariomma	deep to elongate	3 feet most <1 foot	+	simple or cusped	—	6	30–33	3 + 2
Tetragonurus	very elongate	2 feet	+	simple and cusped	+	5–6	43–58	2 + 4

the round pharyngeal sacs have stellate bases. There are six branchiostegal rays, a pseudobranch, and 30 to 38, 41 or 42 vertebrae. The caudal skeleton has four hypural and three epural elements. There are three genera: *Cubiceps*, *Nomeus*, and *Psenes*.

Most species of the Ariommidae are less than a foot long, although a few species attain more than twice that length. Their bodies are either deep or elongate. All have pelvic fins. Their mouths and the teeth in their jaws are very small. There are no teeth on the palate. The papillae in the elongate pharyngeal sacs have round bases. There are six branchiostegal rays, a small pseudobranch, and 30 to 33 vertebrae. The caudal skeleton has two hypural and three epural elements. There is one genus: *Ariomma*.

The Tetragonuridae are less than two feet long with very elongate bodies. All have small pelvic fins. Their mouths are fairly large. In the upper jaw, their teeth are small and recurved; in the lower jaw, they are large and knifelike. The palatines and the vomer bear teeth. The papillae in the very elongate pharyngeal sacs are much reduced and have small round bases. There are five or six branchiostegal rays, a pseudobranch, and 43 to 58 vertebrae. The caudal skeleton has four hypural and two epural elements. There is one genus: *Tetragonurus*.

The Stromateidae are usually no more than a foot long with deep bodies. None have pelvic fins when adult. Their mouths and the teeth in their jaws are very small. There are no teeth on the palate. The papillae in the round-to-elongate pharyngeal sacs have stellate bases. There are five or six branchiostegal rays, either a small pseudobranch or none at all, and 30 to 48 vertebrae. The caudal skeleton has four hypural and usually two epural elements. There are three genera: *Stromateus*, *Peprilus*, and *Pampus*.

There are two main lineages in the stromateoids (p. 51). One is composed of the Centrolophidae and their derivative, the Stromateidae. The other, a looser assemblage, is composed of the Nomeidae and their two derivatives, the Ariommidae and the Tetragonuridae (Fig. 7). The Centrolophidae and the Nomeidae are the basal stocks. Of these two, the Centrolophidae are in most respects the most primitive. Familial and generic relationships, to be touched upon only briefly here, have been discussed in the individual accounts of family and genus.

Figure 48 summarizes some of the major evolutionary trends in the stromateoid fishes. Each group is treated more or less as a grade in the diagram. The characters shown are relative size and shape of the body, fin pattern, presence or absence of palatal dentition, number of branchiostegal rays, vertebrae, epural plus hypural elements in the tail, and the shape of the papillae in the pharyngeal sacs. These are discussed in detail in the following accounts. The width of the arrow leading to each grade is proportional to the number of genera in that family.

Body (Fig. 48). The largest stromateoids are members of primitive centrolophid genera. McCulloch (1914) reports a 1,072-mm *Hyperoglyphe porosa* weighing 41 pounds from the Great Australian Bight, and I have seen an 1,195-mm *Centrolophus niger* taken south of New England on a long-line. The maximum depth in most centrolophids is within 25 to 30 per cent of the standard length and never exceeds 50 per cent. In the nomeids and in the ariommids, there are a few species whose maximum length approaches a meter but most are smaller. The maximum depth in these families is from about 25 to 40 per cent of the standard length. A large tetragonurid is 600 mm long (Fitch, 1951). These highly modified fishes are very slender, with the maximum depth usually less than 20 per cent of the standard length. The stromateids rarely exceed 450 mm in length, and mature when less than 200 mm long. These fishes are very deep bodied, the maximum depth ranging from 35 to over 70 per cent of the standard length.

The course of evolution in the form of the body has been one of diminution in size and of increase in depth. These two evolutionary tendencies are also displayed in other teleostean groups (Myers, 1958; Liem, 1963).

Fins (Fig. 48). Only one major change has occurred in the fin pattern of stromateoids—the loss of the pelvic fins at the stromateid grade. The presence of pelvics in young *Stromateus fiatola* and their subsequent loss in the adult are important clues in understanding the phylogeny of stromateids. There is a difference between the basic fin patterns of the two stromateoid lineages. Members of the nomeid line have two dorsal fins; members of the centrolophid line usually have but one.

The thoracic pelvic fins of perciform fishes are used in braking and turning (Harris, 1938). In deep-bodied fishes, however, the effectiveness of the fins for these purposes is probably greatly decreased due to the change in the hydrodynamic profile of the fish. In this situation, selective pressure may favor loss of the fins. This has apparently been the case in stromateids, and is also observed in *Parastromateus*, *Monodactylus*, *Psettus*, and a number of other unrelated deep-bodied teleosts.

In the great majority of stromateoids, the anterior rays of the median fins are no more than two or three times the length of the posterior rays. In the stromateids, however, the median fins have become falcate and the anterior rays are very much produced. In *Stromateus* this tendency is but little pronounced. The deeper-bodied species in *Peprilus* have very falcate fins. The anterior finrays of the anal fin in these species are

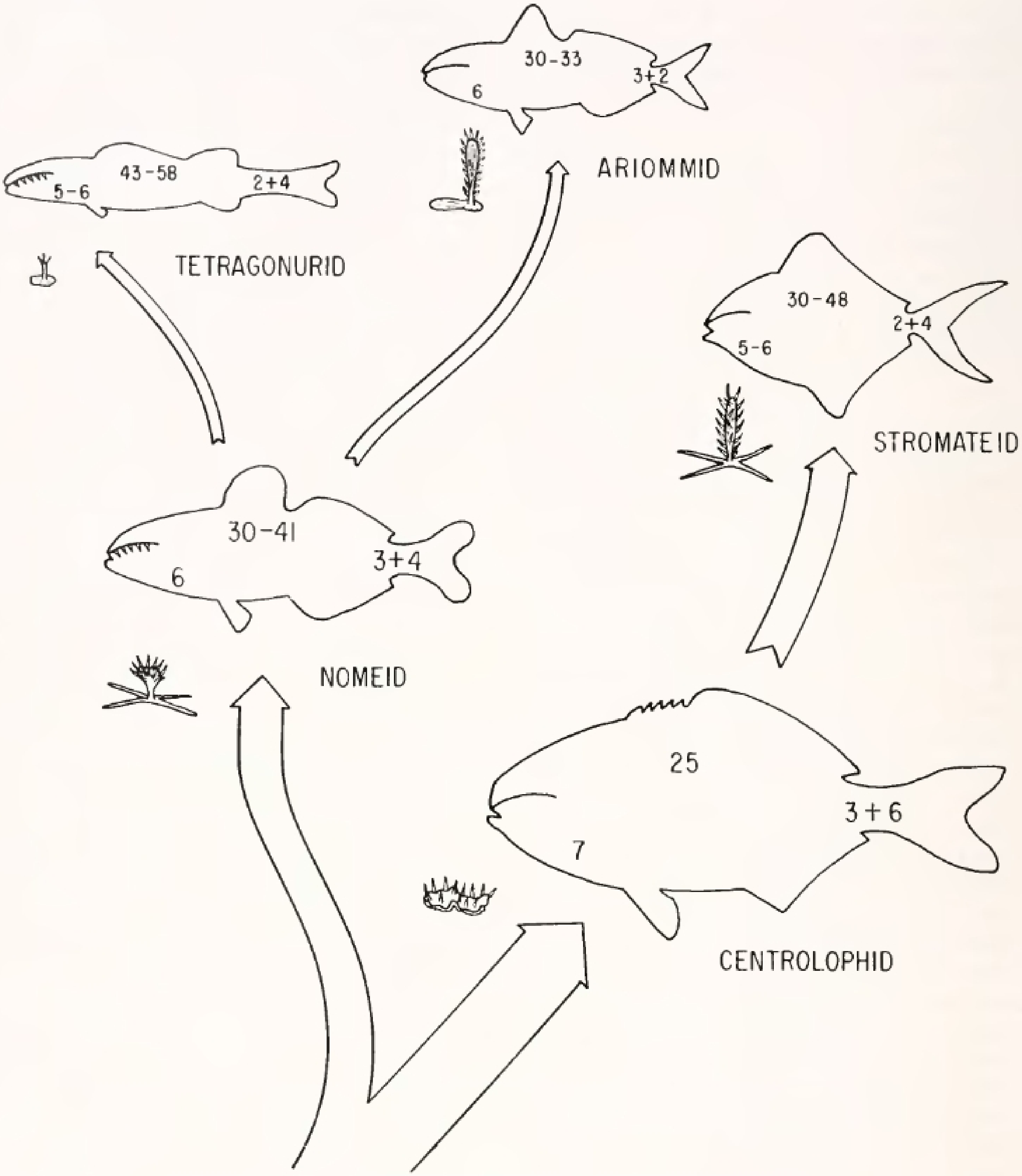

Figure 48. Evolutionary trends in the Stromateoidei, showing relative size and shape, fin pattern, and (within the outline from left to right) presence or absence of palatal dentition, and numbers of branchiostegals, vertebrae, and epurals + hypurals. Inset shows a papilla. Width of arrows proportional to number of genera in the family. See text.

seven or eight times longer than the posterior rays. In *Pampus* both the anterior rays of the anal fin and of the lower caudal lobe are produced, and those in the anal fin may be ten to 20 times longer than the posterior finrays. Lacking observations on living *Pampus*, it is difficult to know what advantage these elongate fins confer.

Teeth and jaws (Fig. 48). In most centrolophids the angle of the gape may be below the eye but in all other stromateoids the angle of the gape is before the eye. The ariommids and stromateids have the smallest mouths of all. In these two families even the end of the maxillary is before the eye. Centrolophids, with the exception of *Psenopsis*, have a small supramaxillary bone, but this is gone in all other stromateoids.

The presence of teeth on the palate is usually considered primitive (Liem, 1963). The palatine and vomerine teeth in the nomeids indicate that this group branched off early from the ancestral stock. Both the centrolophids, in most respects the most primitive of stromateoids, and their derivative, the stromateids, lack these teeth. Palatal dentition is well developed in the tetragonurids, which are derived from fish ancestral to the nomeids. The ariommids, which are probably derived directly from a nomeid, have lost these teeth.

In the majority of primitive centrolophids and in many nomeids, the jaw teeth are relatively large, strong, spaced, and often slightly recurved. The advanced centrolophids, stromateids, and ariommids have much smaller, close-set, straight teeth. The teeth of all stromateids and of some ariommids are laterally flattened and bear minute cusps. Tetragonurids and some species in the nomeid genus *Psenes* have two sorts of teeth in the jaws. Those in the upper jaw are conical, spaced, and recurved; those in the lower jaw are long, knifelike, very close set, and often bear very minute cusps.

The structure of the teeth and jaws is certainly a function of the diet. In stromateoids, which possess a masticatory organ in the pharyngeal sacs, the jaw teeth are primarily for catching and holding prey.

The diet of most centrolophids and nomeids is fairly diverse and often includes rather large animals. The strong, conical, slightly recurved teeth are ably suited to the catching and holding of fairly vigorous prey. The stromateids feed rather extensively on jellyfishes. Their smaller jaws and flattened, cusped teeth are more suited to slicing the tissues of coelenterates. With such animals, there is little need for catching and holding. Nonetheless, the tetragonurids, existing almost entirely on salps and coelenterates, have conical, recurved teeth in the upper jaw and on the palate which must hold the prey firmly while the long, knifelike teeth of the lower jaw slice off mouthfuls.

In the course of evolution, the jaws of stromateoids have become shorter and the supramaxillary bone is lost. The conical teeth have become flattened, cusped, smaller, and more closely set. In the nomeid lineage, the palatine dentition is lost. Changes in the dentition by and large reflect increasing specialization in the food habits.

Pharyngeal sacs (Figs. 49, 50). The sacs of centrolophids are higher than they are long, and the papillae are arranged in ten or more elongate patches (Fig. 49A). The bases of the papillae (Fig. 50A) are irregular in shape, with the teeth seated all over the inner face; the base is often humped up to fit over a ridge of muscle in the sac. In the nomeids, the sac is not so high in respect to its length, and the papillae are in about five longitudinal patches (Fig. 49B). The papillae are very different from those of the centrolophids. The bases (Fig. 50B) are stellate, and the teeth are concentrated near the end of a stalk. The sac in stromateids (Fig. 49C) is at least as long as it is high; in *Pampus* (Fig. 46) it is much longer. The papillae are in only two ill-defined patches in the top and bottom halves of the sac. As in the nomeids, the bases (Fig. 50C) are stellate, but they are in general larger, and the teeth are seated all along the long central stalk instead of only near the end. The sacs in both the ariommids (Fig. 49D) and the tetragonurids are longer than high, markedly so in the latter (Fig. 36). The large papillae of ariommids (Fig. 50D) have round bases, and the small teeth are seated all along the central stalk. The papillae are

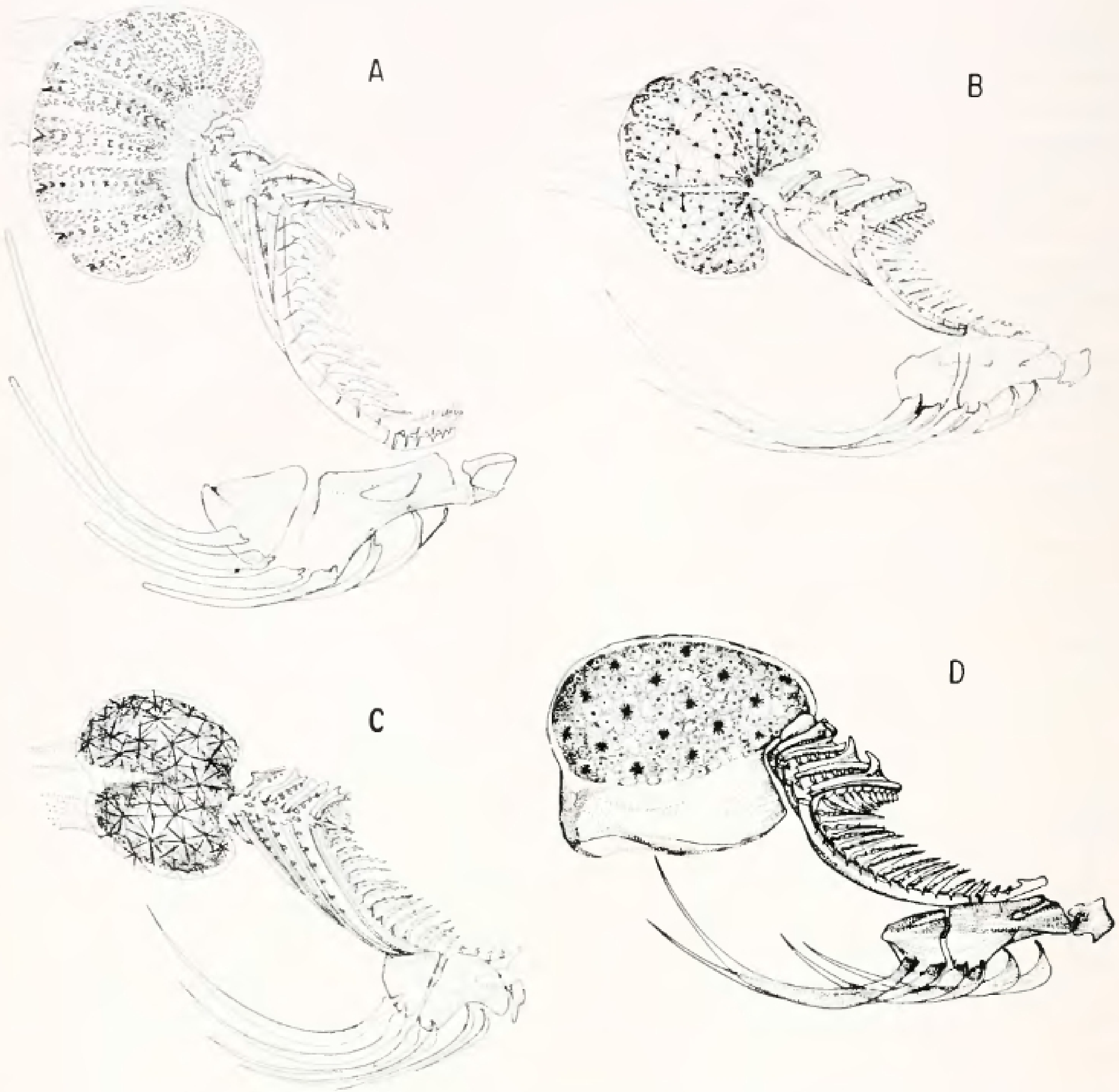

Figure 49. Comparison of branchial regions in four stromateoid families. A. Centrolophidae, *Hyperoglyphe*, from Figure 9. B. Nomeidae, *Nomeus*, from Figure 25. C. Stromateidae, *Peprilus*, from Figure 43. D. Ariommidae, *Ariomma*, from Figure 31. See text.

in a single patch, in the upper half of the sac only. In tetragonurids, the small papillae are widely separated and are not in bands. They are rounded, and there are a few weak teeth on the end of a short stalk.

The nomeids and the stromateids do not share a direct common ancestor. The nomeids are derived from a pre-centrolophid form and the stromateids are derived from an advanced centrolophid. Nonetheless, there is a great similarity in the stellate papillae found in both families (Fig. 50B, C), but this similarity is due to parallelism.

The centrolophid fishes are unspecialized in their diets. They feed on other fishes, on squids, on crustaceans, on jellyfishes and, sometimes but certainly not customarily, on garbage. The large sacs are capable of admitting fairly large objects. The crude papillae do shred the prey to some extent,

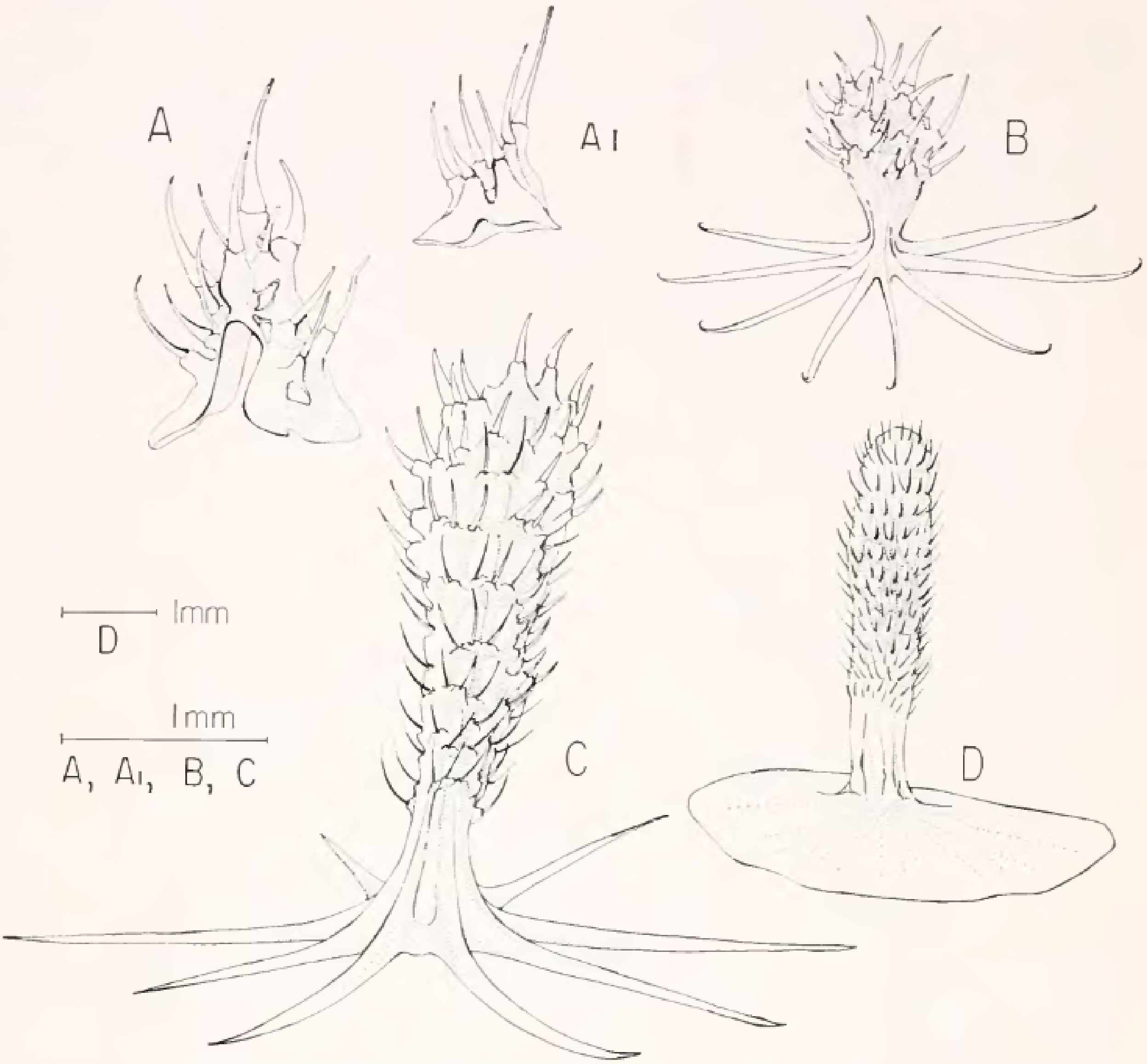

Figure 50. Comparison of papillae in the pharyngeal sacs of four stromateoid families. A. Centrolophidae, *Hyperoglyphe*, from preparation shown in Figure 9, large papilla. A_1. Same, small papilla. B. Nomeidae, *Nomeus*, from preparation shown in Figure 25. C. Stromateidae, *Peprilus*, from preparation shown in Figure 43. D. Ariommidae, *Ariomma*, from preparation shown in Figure 31. See text.

but never so much as to render stomach contents completely unrecognizable.

Little is known of the feeding habits of nomeids. Fish and jellyfish remains have been found in their stomachs. The fairly small sacs and the papillae with their stellate bases firmly seated in the muscular wall of the sac combine to make a good shredding organ, and stomach contents are often difficult to identify.

Stromateids may feed very largely on small crustaceans and medusae. The relatively smaller and more elongate sacs, the papillae with greatly extended bases, and the teeth ranged all along the central stalk of the papillae make a very efficient shredding organ, ably suited to rendering the rubbery tissues of medusae. The shredded stomach contents of stromateids are almost impossible to identify.

Too little is known of the natural history of ariommids to be able to understand the structure of the peculiar pharyngeal sacs found in this group. In almost every specimen examined, the sacs were filled with mud and silt. Is it possible they perform some sort of filtering function?

Tetragonurids may live largely on jellyfishes. The sacs of these fishes are very elongate, as might be expected, but the papillae are very reduced and are probably not very efficient shredders. The upper pharyngeal bones, however, are studded with teeth and extend very far backward into the sacs (Fig. 46). The pharyngeal bones are capable of considerable back-and-forth motion (Grey, 1955) and, in tetragonurids, may perform the shredding action for which the papillae do not seem suited.

The main changes that have occurred in the pharyngeal sacs of stromateoids have been elongation of the sac, reduction in the number of bands of papillae, and increase in complexity of the papillae. These changes are correlated with a change from more or less omnivorous feeding habits to increasing utilization of jellyfishes for food.

Branchial region (Figs. 48, 49). Seven, blunt-ended branchiostegals and a large ceratohyal fenestra are found at the centrolophid grade (Fig. 49A). The advanced centrolophids *Seriolella* and *Psenopsis* have pointed branchiostegals, and the first one is reduced in size (Figs. 20, 23). In nomeids (Fig. 49B) and ariommids (Fig. 49D) there are six tapering branchiostegals, and the ceratohyal fenestra is much smaller, or, in some species, closed. At the stromateid grade (Fig. 49C) there are six tapered branchiostegals and the ceratohyal fenestra is closed. The stromateid genus *Pampus*, perhaps the most advanced of stromateoids, has but five branchiostegal rays. Within the tetragonurids, the number of branchiostegals is either six or five.

A pseudobranch is present in all stromateoids with the exception of *Pampus*. Its loss may be correlated with the unification of the gill-covers to the isthmus. In most stromateoids, the pseudobranch is very well developed and the gill-covers are cleft well forward. In the stromateid genera *Stromateus* and *Peprilus* the pseudobranch is small and the gill-covers are united across, but not to, the isthmus. Finally, in *Pampus* the pseudobranch is gone and the gill-covers have become broadly united to the isthmus.

In the hyal series of stromateoids, two changes have occurred. The branchiostegal rays have become more slender and one ray is lost, and the ceratohyal fenestra becomes closed. The pseudobranch, well developed in most stromateoids, is lost in *Pampus*.

Axial skeleton (Fig. 48). Most centrolophids have 10 + 15 vertebrae, the well-known basic perciform number. The exceptions are in some *Schedophilus* with 10 + 16, 12 + 17, or 10 + 20, and *Icichthys* with a total of 50 to 60. In the nomeids both numbers have increased; there are 13 to 15 precaudal, and 17 to 23, 26, or 27 caudal vertebrae. The stromateids have 12 to 18 precaudal, and 19 to 27 caudal vertebrae, and within any one species the number may be quite variable. Ariommids, derived from a nomeid stock, usually have 12 or 13 + 17 or 18 vertebrae. The tetragonurids, also derived from the nomeids, have continued the increase, to a total of 43 to 58 vertebrae.

It is difficult to understand the selective pressures responsible for an increase in vertebral number. In *Nomeus*, however, the situation is reasonably clear. This genus has 41 vertebrae and is elongate in form. The high number of vertebrae allows the fish to move in a very sinuous manner, and to turn in a very small radius. The pelvic fins are also much enlarged and aid in the turning. This ability enables the fish to avoid more easily the stinging tentacles of the *Physalia* under which it lives.

In general, as the number of vertebrae has increased, the relative length of each individual vertebra has decreased. Fishes with an increased number of vertebrae have more neural and haemal spines than fishes with fewer vertebrae, and these are closer together. Hence there is a stronger frame

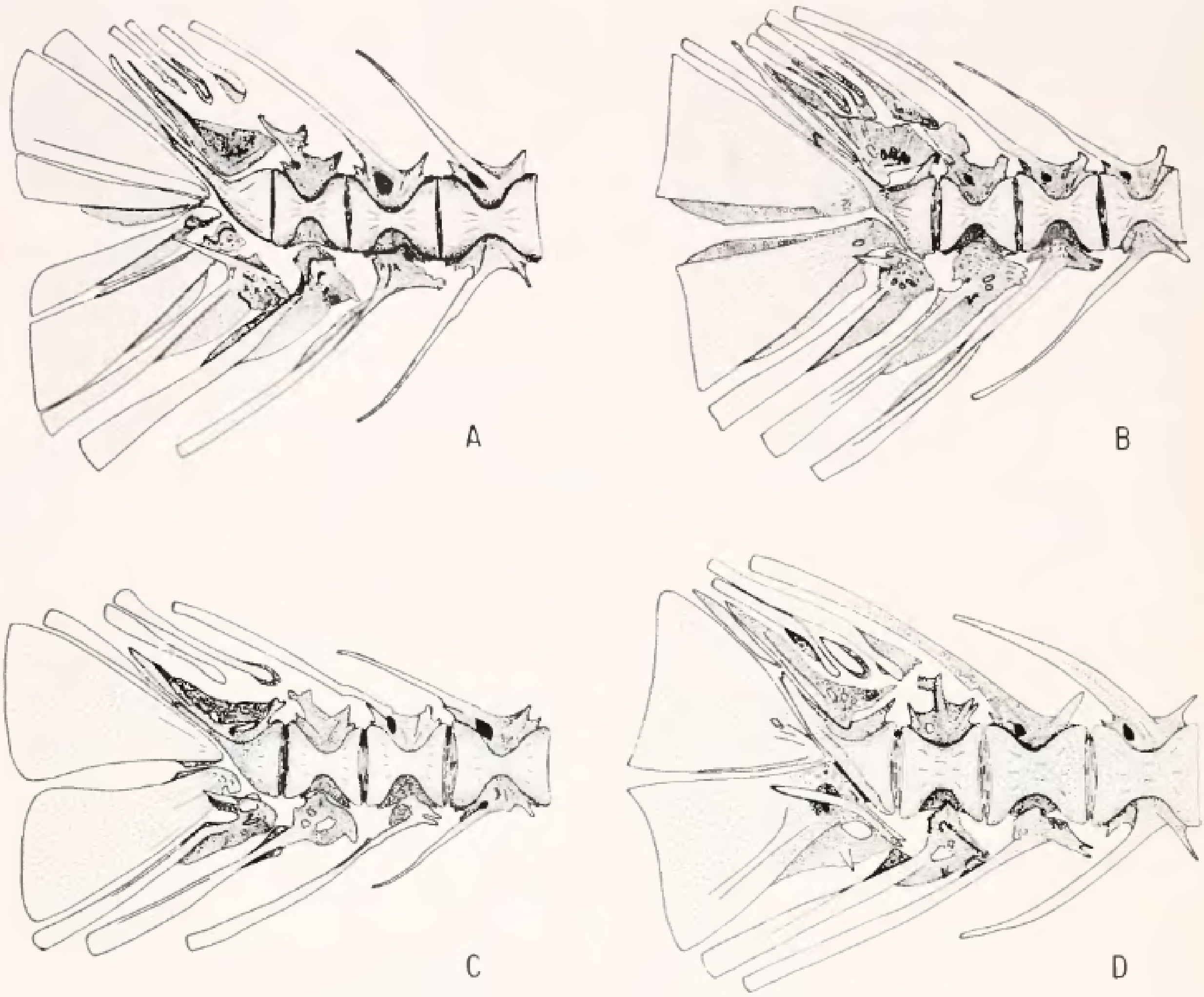

Figure 51. Comparison of caudal skeletons of four stromateoid families. A. Centrolophidae, *Hyperoglyphe*, from Figure 10. B. Nomeidae, *Nomeus*, from Figure 24. C. Stromateidae, *Peprilus*, from Figure 42. D. Ariommidae, *Ariomma*, from Figure 33. See text.

for attachment of the muscles. This probably has permitted, or even encouraged, the evolution of the deep, firm body characteristic of the stromateid grade.

With the increase in vertebral number, the number of median finrays increases as well. This, of course, might be expected, but need not necessarily follow. The ariommids and the tetragonurids, both with increased numbers of vertebrae, have very decreased numbers of median finrays. In *Psenes* and in the stromateids, the increased number of anal finrays has resulted in a forward swing of the first interhaemal so that it forms an abrupt angle with the haemal spine of the first precaudal vertebra. This tends to support and protect the belly of the fish. In the stromateids, the enlargement and extension of the pelvic bones, which bear no fins, and of the postcleithrum almost complete this trend towards support and, possibly, protection.

There has been a general tendency towards increase in the number of vertebrae in the evolution of the stromateoids. The number of caudal vertebrae has tended to increase the most, but the number of precaudal vertebrae has been affected as well. Secondary increase in the number of vertebrae from a basic number near 10 + 15 is of common occurrence in teleosts (Gregory, 1951; Liem, 1963). In many stromateoids, there has been a concomitant increase in the number of median finrays.

Caudal skeleton (Figs. 48, 51). The generalized perciform type of caudal skeleton with six hypurals and three epurals is typical of the centrolophid grade (Fig. 51A). With the fusion of hypurals 2 + 3 and 3 + 4, the number is reduced to four in the nomeids (Fig. 51B), stromateids (Fig. 51C), and tetragonurids. Three epurals are present in nomeids, but one of these is lost at the stromateid grade (Fig. 51C). In the ariommids (Fig. 51D), the fusion of hypurals 1 + 2 + 3 and 4 + 5 + 6 forms two solid blocks. In both the ariommids and some stromateids there is a tendency towards further fusion of hypural elements with the urostylar vertebrae. The ariommids have three epurals but the second one is very reduced in size, and is probably on its way to becoming lost. The tetragonurids have two epurals. Fusion of the uroneurals, both with each other and with the urostylar vertebrae, has occurred in several stromateoid genera.

Most of the centrolophid fishes spend at least the first part of their lives hovering quietly under floating objects. These fishes are able to hang almost motionless with a slight fanning of the pectorals and strong rotary motion of the caudal fin. This rotary motion is possible because of the numerous elements in the caudal skeleton. In the advanced centrolophids—fast-swimming, schooling fishes such as *Seriolella violacea*—partial fusions in the hypural series result in a more rigid tail.

Many of the nomeids are hovering fishes. At this grade, fusions in the hypural series tend to make the tail fairly stiff. This may be counteracted by the long, well-developed autogenous haemal spines, which may be moved laterally to produce a rotary motion in the fin. The long pectoral fins of nomeids, too, may aid their hovering. Observations on living fishes are, however, lacking, and are sorely needed.

The consolidated tail of stromateids allows for little rotary motion. These schooling fishes probably do not hover as much as nomeids or centrolophids but may swim fairly constantly. Specimens of *Peprilus triacanthus* observed in the Woods Hole Aquarium never remained still, but moved slowly forward, bouncing up and down with beats of their long, broad pectoral fins.

There are no observations of living ariommids or tetragonurids. From the structure of their caudal skeleton and fin, it can be assumed that the former at least are very strong, fast swimmers. Living near the bottom, they may not need to hover, but may cruise over the sea floor buoyed up by their well-developed air bladder.

The evolution of the caudal skeleton in stromateoids is marked by a reduction in the number of elements. In the hypural series, this reduction is accomplished by a series of fusions; in the epural series, an element is lost. The tendency toward consolidation and reduction of elements, ultimately resulting in a fused hypural plate, is a general phenomenon found in numerous perciform lineages (Gosline, 1961a). The changes in the stromateoid tail coincide approximately with a change from hovering to swimming fairly constantly in schools.

DISTRIBUTION OF THE STROMATEOIDEI

Distributional data for stromateoid fishes are at best scanty. Nonetheless, all available data tend to support the conclusions based on anatomical data, that is, that the centrolophids arose first, followed by the nomeids, tetragonurids, and, most recently, the stromateids and ariommids. Because of the scantiness of the data, the map figures accompanying this section must be considered approximate only. In general, the distributions have been extrapolated from a few records. Although I am fairly sure of the general picture presented, fine details of the distribution of stromateoids are lacking.

Centrolophidae. The major features of the centrolophid distribution are discontinuity, bipolarity, endemism, and sympatry of genera. The first three are found in the

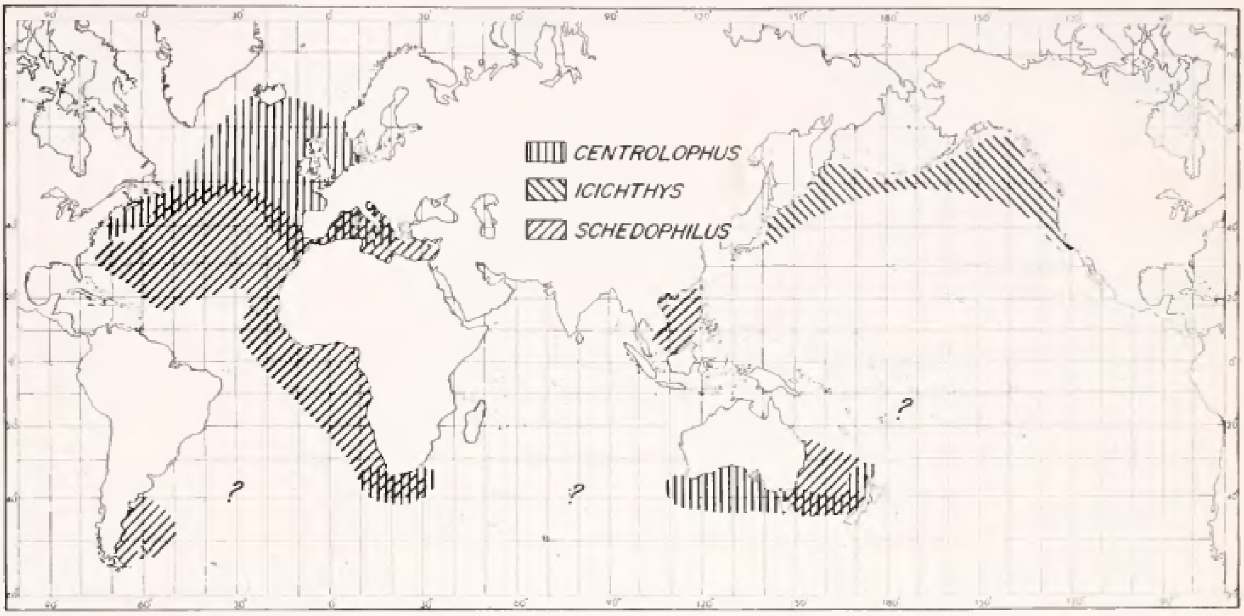

Figure 52. Distribution of the soft-spined Centrolophidae.

more primitive members of the family, the soft-spined centrolophids (Fig. 52). *Schedophilus* is found mainly in the Atlantic Ocean. The presence of two isolated populations, in the China seas and in the environs of the Tasman Sea, indicates that the former range of the genus was once much wider. The distribution of the two Pacific area populations of *Schedophilus* and the distribution of *Centrolophus* are bipolar, again indicative of a shrinking range. *Icichthys*, formerly considered an endemic element of the North Pacific fauna, has recently been found off New Zealand (Haedrich, in press), and is thus bipolar. *Icichthys* and *Centrolophus* probably share a common ancestor; the characteristics of each genus may well have developed in the isolation provided by an ancestral relict distribution. In the hard-spined centrolophids (Fig. 53), *Hyperoglyphe*, like *Schedophilus*, is bipolar in the Pacific but widespread in the Atlantic. The most primitive species in this genus, *H. antarctica*, is found only south of 30° S. *Seriolella*, a relatively advanced genus, is widespread in the higher latitudes of the Southern Hemisphere, where it is no doubt endemic. The most recently evolved centrolophid genus, *Psenopsis*, may be spreading out from the waters of the East Indian region. By and large, centrolophid species are oceanic or found near the edge of the continental shelf. Some species of the soft-spined centrolophids may even be meso- or bathypelagic. The advanced genera *Seriolella* and *Psenopsis*, however, commonly occur in shallow water, and some species may even enter estuaries. Some overlap with at least one other genus occurs within the ranges of all centrolophid genera. Four of the six genera occur in Australia and New Zealand.

Nomeidae. In the distribution of the nomeids (Fig. 54) there are no relicts, no bipolar species, and no regional endemism. For the most part, the three genera seem broadly sympatric, but records are too few to discuss the limits of each genus with precision. In the North Atlantic, however, *Nomeus* is found in the western parts, but has never been reported from Madeira, where its companion *Physalia* is common. *Cubiceps*, though it occurs in the western Atlantic, is much more common in the eastern portions and the Mediterranean. Most nomeid species are oceanic; a few species in *Psenes* seem to be mesopelagic. In general confined to more tropical waters, a

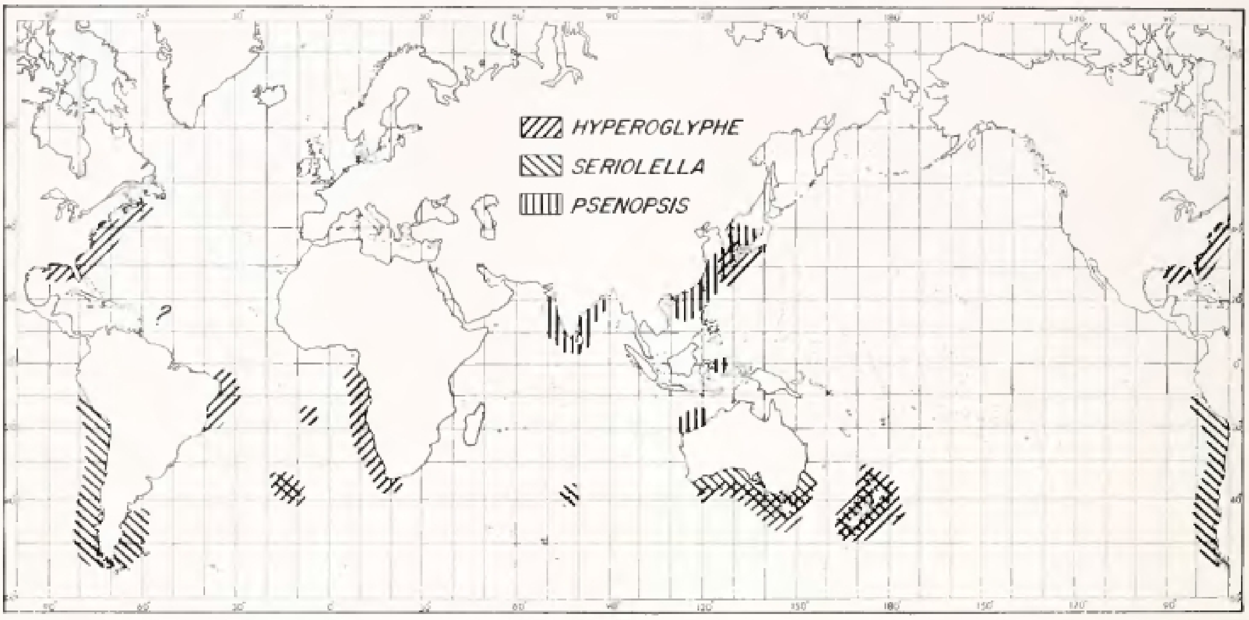

Figure 53. Distribution of the hard-spined Centrolophidae.

number of species, such as *Nomeus gronovii* and *Psenes cyanophrys*, are found in all oceans. All genera are found in Australia and New Zealand.

Tetragonuridae. The distribution of the tetragonurids is very poorly known. In general it seems to approximate the distribution of the nomeids (Fig. 54).

Ariommidae. The family Ariommidae, a nomeid derivative, is found mainly in tropical waters (Fig. 55). One deep-bodied species occurs off South Africa. All members of the single genus *Ariomma* seem to be engybenthic in deep water over continental shelves or near islands. The deep-bodied and elongate forms of *Ariomma* occur together in the New World, but tend to be allopatric elsewhere. Apparently there are no representatives on the west coast of Central America, although the genus is widespread throughout the Gulf of Mexico and the Caribbean, and elongate species occur in Hawaii. The latter are undoubtedly derived from Japanese forms. The most advanced species in the genus, *A. indica*, is a deep bodied silvery species with cusped teeth, found from the Gulf of Iran throughout the East Indian region to the East China Sea. No ariommids occur in Australia or New Zealand.

Stromateidae. The stromateid distribution is characterized by continuity, widespread species, restriction to continental shelves, a trans-Isthmian genus in the New World, and allopatry of genera. The distributions of each of the three genera (Fig. 56) are more or less continuous. In *Stromateus*, one species is found from the Mediterranean to South Africa. *Stromateus* is the only genus that has managed to cross an ocean. This has been accomplished across the shortest possible gap, from Africa to South America, and in the direction of the prevailing winds and currents. The advanced *Stromateus* of the east and west coasts of southern South America are very little differentiated from one another, and may be speciating at the present time. The genus *Peprilus*, apparently derived from *Stromateus* through a species such as the west coast *P. snyderi*, has spread on both coasts of North America and southward along the east coast of South America to Uruguay, where it occurs sympatrically with *Stromateus*. This is the only place where two stromateid genera are found to-

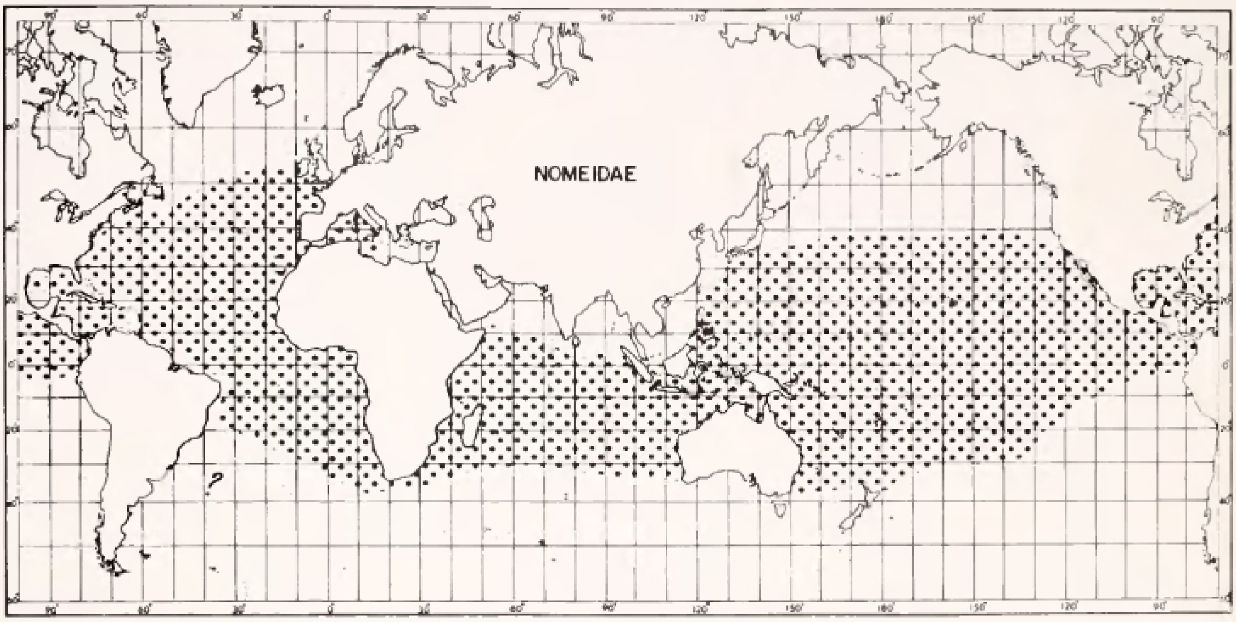

Figure 54. Distribution of the Nomeidae: *Cubiceps, Nomeus,* and *Psenes.*

gether. The most advanced stromateid genus, *Pampus*, occurs from the Gulf of Iran to Japan. Both an advanced species, *P. argenteus*, and a more primitive species, *P. chinensis*, occur through most of the East Indian region. No stromateids have crossed Wallace's line into Australia or New Zealand.

Discussion. The two most recently evolved families are the ariommids and the stromateids. In the ariommids, a single genus is widespread. Containing two incipient genera, one elongate and one deep-bodied, *Ariomma* has apparently had insufficient time for characteristics worthy of generic division to develop. Three genera have evolved in the stromateids, but in general each genus is restricted to a separate continental area. *Peprilus* has spread in a classical circular pattern, from Pacific South America across the Isthmus of Panama and south to Uruguay, to re-encounter the ancestral *Stromateus* stock. This small region in the western South Atlantic is the only area where stromateid genera occur sympatrically. Speciation is currently active in both families.

The ariommids and the stromateids, in contrast to the other stromateoid families, are restricted to near land. The ariommids live in deep water over the shelves and in the vicinity of Hawaii. The stromateids may prefer quite shallow water, and occur in large schools in wide embayments. Because of this relationship with the land, it is possible to examine and possibly date the emergence of the two families in the light of past tectonic activity.

The present stromateid distribution throughout Asia (but not the Red Sea), the Mediterranean, West Africa, and the New World is strongly suggestive of an ancestral Tethyan distribution. The stromateid ancestor could have been a member of the warm water shelf fauna which extended uninterrupted across this region in Tertiary times. In the Upper Eocene or Oligocene, the emergence of land in the Near East divided this fauna in two. The ancestral stromateid isolated in the East gave rise to *Pampus*; the form in the West was the central *Stromateus* stock. In the Pacific Panamanian region, separated from the southern stock of *Stromateus* by long coastlines unsuitable for stromateids, *Peprilus* evolved. Found today in both oceans, this genus must have been established be-

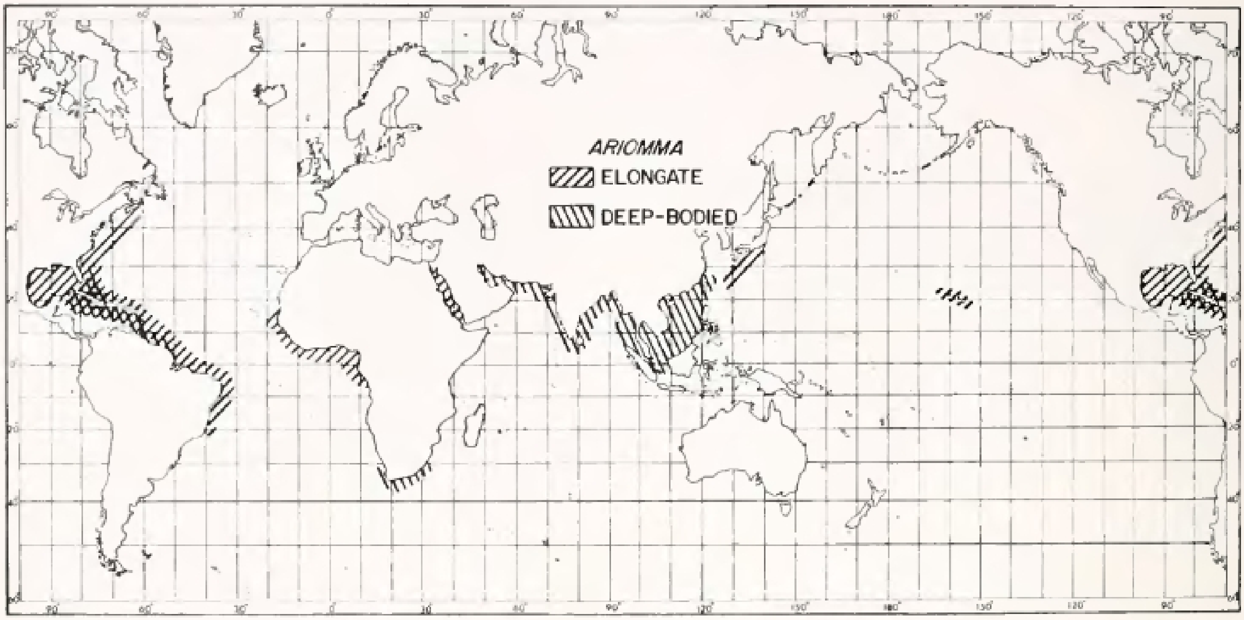

Figure 55. Distribution of the Ariommidae.

fore the emergence of the Isthmus of Panama in the lower Pliocene.

The ariommids are not so tightly bound to the coasts as the stromateids. Oceanic dispersal may be facilitated by pelagic juveniles, a few of which have been taken at Bermuda and in the tropical Central Atlantic. Widespread in the Gulf of Mexico and the Caribbean, no ariommids occur on the west coast of the New World. This suggests at least a late Pliocene dispersal. This fact, plus the remarkable homogeneity of the group and the structure of the pharyngeal sacs and the fused hypural fan, are strong evidence for considering the ariommids the most recently evolved stromateoid fishes.

The remaining stromateoid families, the centrolophids, nomeids, and tetragonurids, are by and large all oceanic. Changes in the configuration of the land would not have affected these fishes as they did the ariommids and stromateids. Since the major ocean basins have probably been a stable feature since well before the Cretaceous, the period of the great flowering of the teleosts, it is unlikely that tectonic activity has been an important isolating mechanism in the evolution of these groups.

The centrolophid distribution bears all the earmarks of an older group. Disjunct distributions, including bipolarity, are characteristic of an old group which has passed its peak. Another indication of the age of the centrolophids is their diversity. There are six genera in the family, and the species inhabit a wide range of environments. In Australia and New Zealand, where no stromateids occur, the advanced centrolophid genus *Seriolella* lives in shallow waters near the coast, the typical stromateid habitat. Numerous ebbs and flows have occurred in the distribution of the centrolophids, for numerous genera are found together. Lacking fossils, it is impossible to date the emergence of the centrolophids. Nonetheless, they certainly antedate the stromateids which had their beginnings in the mid-Tertiary. The centrolophids, then, probably arose in the early Tertiary, or perhaps even in the late Cretaceous.

The nomeids probably arose concurrently with, or perhaps a little after, the centrolophids. The genera occur together throughout the range of the family. Little specific differentiation seems to have developed, although the apparent commonness of circumtropical species in this group may only

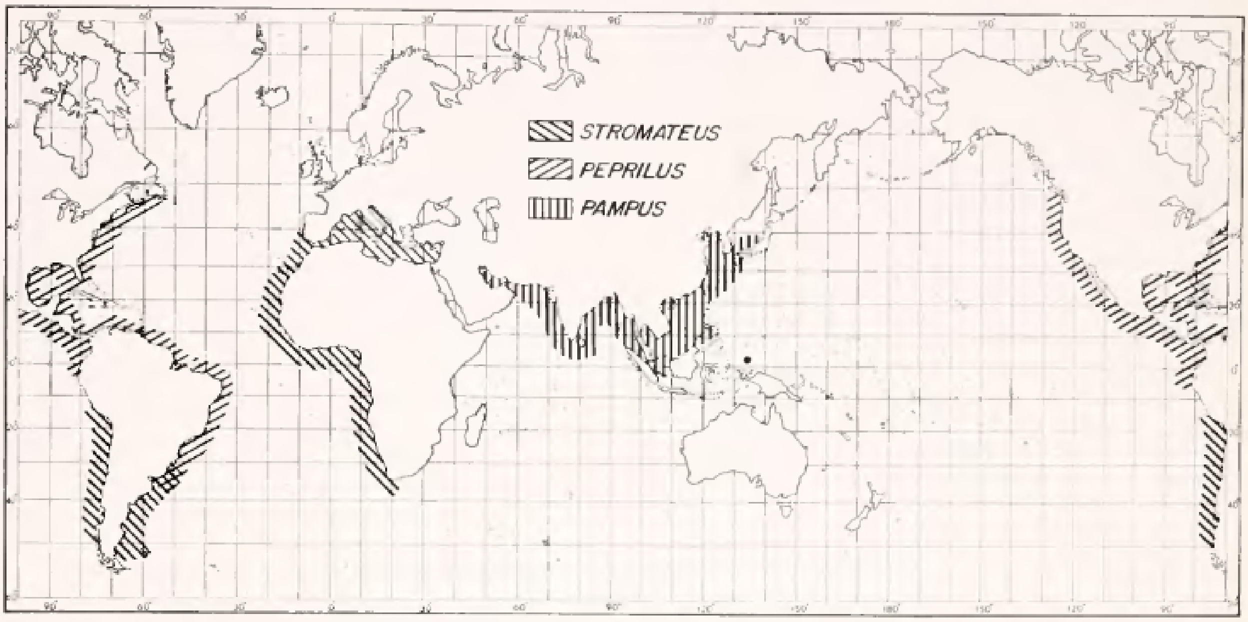

Figure 56. Distribution of the Stromateidae.

reflect the premium placed on a particular phenotype in the rigorous oceanic environment.

The great divergence from the nomeid condition of a derived family, the tetragonurids, suggests that they branched off at an early stage. The tetragonurids have become very specialized, and may be an evolutionary dead-end. There are apparently only three species in the single genus.

Two general features of the stromateoid distributions are of interest. The first is the tendency for the more primitive taxa to be found in higher latitudes. Included in this group are: *Centrolophus*, *Icichthys*, *Hyperoglyphe antarctica*, *Stromateus* in the New World, and, perhaps, the giant nomeid *Cubiceps capensis*. The Ariommidae and Stromateidae, both advanced, have not reached the Australian region. The second feature is that the most advanced or most recently evolved taxa have their centers of distribution in the East Indian region. Examples are the centrolophid genus *Psenopsis*, the stromateid genus *Pampus*, and the ariommid *Ariomma indica*.

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SUMMARY

Known to the ancients, and investigated by such able ichthyologists as Günther, Gill, and Regan, the development of the stromateoid classification has a long history. Only recently, however, has sufficient material become available to clarify the confusion surrounding the systematics of these fishes.

The perciform suborder Stromateoidei is diagnosed by the possession of toothed pharyngeal sacs and small uniserial teeth in the jaws. Comparative study of the nature of the pelvic and dorsal fins, the tooth pattern, the number of vertebrae and branchiostegal rays, and, in particular, the structure of the caudal skeleton and the pharyngeal sacs suggests a separation of the suborder into five families and fourteen genera. These are: Centrolophidae—*Hyperoglyphe*, *Schedophilus*, *Centrolophus*, *Icichthys*, *Seriolella*, *Psenopsis*; Nomeidae—

Cubiceps, *Nomeus*, *Psenes*; Ariommidae (fam. nov.)—*Ariomma*; Tetragonuridae—*Tetragonurus*; and Stromateidae—*Stromateus*, *Peprilus*, *Pampus*. The Centrolophidae are the most primitive in the suborder, and have given rise directly to the Stromateidae. The Nomeidae have evolved parallel to the centrolophid–stromateid line, and have given rise to the Tetragonuridae and the Ariommidae.

Within the suborder, evolutionary trends from the generalized to the highly evolved condition are marked. The maximum size attained becomes smaller, and, in the stromateids, the relative depth of the body increases. The pelvic fins are lost. The mouth becomes smaller, the jaw teeth become cusped, and the palatine dentition may be lost. The pharyngeal sacs become more elongate and the structure of the papillae within them becomes more complex. The number of branchiostegal rays is reduced from seven to five. The pseudobranch is lost. The vertebrae increase in number from a basic 25. The number of elements in the caudal skeleton is reduced through losses and fusions.

The major features of the centrolophid distribution are discontinuity, bipolarity, endemism, and sympatry of genera. Four of the six genera occur in Australia and New Zealand. The three nomeid genera are broadly sympatric in temperate and tropical oceans, and there are no relicts, no bipolarity, and no regional endemism. The tetragonurid distribution is very poorly known, but is similar to that of the nomeids. The ariommids are found in deep water over the edge of the continental shelves from the east coast of the New World to Japan, and near Hawaii. The stromateid distribution is characterized by discontinuity, widespread species, restriction to continental shelves, and allopatry of genera. None occur in Australia and New Zealand. The distributional data support the conclusions based on comparative morphology.

The relationships and natural history of the stromateoid taxa are discussed. Synonymies, keys, and, under each genus, lists of nominal species are included.

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