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Percoidei: Development and Relationships

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AS the largest and most diverse of the perciform suborders, the Percoidei exemplifies the inadequacies that characterize perciform classification. Regan (1913b) defined the Percoidei "by the absence of the special peculiarities which characterize the other suborders of the Percomorphi [=Perciformes]," and seventy years of research in systematic ichthyology have failed to produce a more meaningful definition. In the absence of even a single shared specialization uniting the percoids, the monophyly of this great assemblage of fishes is doubtful. In spite of our inability to adequately define the Percoidei, or because of it, half of the approximately 145 families of perciform fishes are usually referred to this suborder. Greenwood et al. (1966) listed 71 percoid families in their "highly tentative" familial classification of the Perciformes, and Nelson (1976) stated that the Percoidei contains 72 families, 595 genera and about 3,935 species.

Percoids are best represented in the nearshore marine environment and form a significant component of the reef-associated fish fauna of tropical and subtropical seas. A few groups are primarily epipelagic or mesopelagic. Association with brackish water occurs in many nearshore marine families, some of which have one or more exclusively freshwater members, but only four families are primarily restricted to freshwaters, the north temperate Percidae and Centrarchidae, the south temperate Percichthyidae (with one brackish water species) and the tropical Nandidae.

In a practical sense, the suborder Percoidei serves the Perciformes in much the same capacity as the Serranidae once served the Percoidei itself, as a convenient repository for those "generalized" perciform families that cannot obviously be placed elsewhere. I have treated the percoids in a similar sense here, one of practicality and convenience. I do not intend to imply or formulate hypotheses about the monophyly of the Percoidei or to consider their intrarelationships as a whole. My major objectives are to provide some preliminary documentation of the variability of a number of character complexes among adults and larvae of those fishes we now call percoids, to suggest what I believe to be promising avenues of future research and to offer some specific examples illustrating the utility of larval morphology in elucidating percoid phylogeny.

CLASSIFICATION

As here defined (Table 119) the Percoidei includes 80 families and 12 *incertae sedis* genera, making it by far the largest and most diverse suborder of teleostean fishes. The overall limits of the suborder are only slightly modified from Greenwood et al. (1966). The Pomacentridae, Embiotocidae and Cichlidae are excluded because of their recent placement in the Labroidei by Kaufman and Liem (1982). The suborder Acanthuroidea is treated separately in this volume, but a recent hypothesis (Mok and Shen, 1983), with which I concur, based on additional evidence, suggests a close relationship between acanthuroids and the Scatophagidae. The affinities of the questionably monophyletic Nandidae remain unresolved (Lauder and Liem, 1983), and although the nandids are provisionally included in my list

of percoid families, they were not considered in the larval and adult tables. The genus *Elassoma*, formerly a member of the family Centrarchidae, is excluded from the Percoidei, for reasons discussed below. The monophyly of the suborder Trachinoidei, as defined by Greenwood et al. (1966) is suspect, and the affinities of families such as the Mugiloididae, Percophidae, Chiasmodontidae and others may lie with the percoids. However, these families are treated elsewhere in this volume, and of the "trachinoids," only the Opistognathidae are here included as percoids.

Although the overall limits of the Percoidei are similarly perceived in my classification and that of Greenwood et al. (1966), substantive discrepancies result from differences in concepts of family limits. For example, my Serranidae (Johnson, 1983) includes the Pseudogrammidae and Grammistidae of Greenwood et al. (1966), *Leptobrama* is treated as a monotypic family separate from the Pempherididae (Tominaga, 1965), epigonids are treated as a separate family, etc. The high percentage of monotypic families that has historically characterized percoid classification is a disturbing but unavoidable problem that can only be remedied with a better understanding of percoid intrarelationships. In my classification (Table 119), 26 of the 80 families are monotypic and 12 genera, which lack family names, are retained *incertae sedis*. Families and *incertae sedis* genera are arranged alphabetically for easy reference and to avoid any inference of affinity based on sequence. The classification of Springer (1982) was followed for most families treated by him and otherwise that of Nelson (1976). Below, I discuss differences between my classification and that of Springer (1982) or that of Nelson (1976), and present some new information about familial relationships. Early life history information contributed substantially to some of these modifications.

Acropomatidae and *Symphysanodon*.—The "oceanic percichthyids" of Gosline (1966) do not share the defining characteristics of the Percichthyidae (see below), and are treated here as a separate family, including the following genera—*Acropoma*, *Apogonops*, *Doederleinia* (= *Rhomboserranus*), *Malakichthys*, *Neoscombrops*, *Synagrops* and *Verilus*. I know of no synapomorphy that unites the acropomatids, and further work will be necessary to test their monophyly. Larvae of four genera are known. Those of *Acropoma* (Fig. 254C), *Doederleinia* (Fig. 254D) and *Malakichthys* are quite similar, but those of *Synagrops* (Fig. 254B) differ in pigmentation, body form, and the presence of more extensive head spination. Although the larvae of *Symphysanodon* (Fig. 254A) are unique in their possession of horn-like frontal spines, they are otherwise remarkably similar to those of *Synagrops* (Fig. 254B), suggesting that these two genera may be closely related.

Callanthiidae and Grammatidae.—Springer (1982) noted that "there is little evidence to unite" the five genera he included in the family Grammatidae. I concur with this and treat two of these genera, *Callanthias* and *Grammatonotus* as a distinct family, the Callanthiidae (currently under revision in collaboration

with W. D. Anderson). Callanthiids share a flat nasal organ without laminae, a lateral line that runs along the base of the dorsal fin, ending near its terminus or continuing along the dorsolateral margin of the caudal peduncle, and a midlateral row of modified scales that bear a series of pits and/or grooves. The larvae of these two genera appear dissimilar (Fig. 255E, F), but specimens of *Grammatonotus* smaller than 13 mm are unknown. *Stigmatonotus* (based on a small, now lost specimen) was reported to have three opercular spines, and probably represents a larval or juvenile anthiine serranid. The family Grammatidae, as considered here, contains only *Gramma* and *Lipogramma*.

Carangidae. Coryphaenidae, Echeneididae, Rachycentridae and Nematistiidae.—See discussion on utility of larval morphology.

Coracinidae, Drepanidae and Ephippididae.—The family Ephippididae, as defined here, contains the following genera: *Chaetodipterus*, *Ephippus*, *Parapsettus*, *Platax*, *Proteracanthus*, *Rhinoprenes* and *Tripterodon*. Ephippidids exhibit considerable diversity in several features that are more commonly conservative among percoids, such as scale morphology and the structure and arrangement of median fin supports and predorsal bones. Nonetheless, monophyly of the family is supported by shared specializations of the gill arches that include reduction or absence of the basihyal, absence of the interarcual cartilage, a relatively large first pharynogobranchial and, most notably, a peculiar comblike series of large blunt rakers loosely associated with the anterior margin of the broadened first epibranchial. Springer (1982; pers. comm.), following some previous authors (Jordan, 1923; Golvan, 1965) included *Parapsettus* in the Scorpididae. *Rhinoprenes* was previously treated as a monotypic family, possibly related to the Scatophagidae (Munro, 1967), and *Proteracanthus* as a girellid (Norman, 1966). Although *Drepane* may be related to the ephippidids, it does not share the branchial specializations described above, and lacking further evidence of a direct relationship, I treat it separately. Based on other features of the gill arches a close relationship between *Drepane* and *Coracinus* seems likely. In both genera the basihyal is embedded in thick connective tissue and is tightly bound along the anteroventrally sloping median junction of the hypohyals. In addition, an unusual moveable articulation between the hypohyals and the anterior ceratohyal allows for dorsoventral rotation of the ceratohyal. Pending further investigation of the possible affinities of these two genera, I retain them as monotypic families. Larval morphology could provide important information in resolving the relationships among the five ephippidid genera, *Drepane* and *Coracinus*, but to date, only the larvae of *Chaetodipterus* have been described (Fig. 256G).

Elassoma.—In an extensive comparison of the acoustico-lateralis system of the Centrarchidae, Branson and Moore (1962) placed the pygmy sunfishes, genus *Elassoma*, in a separate family, based on over 20 "major characteristics." These include numerous reductions in the laterosensory system (e.g., absence of a lateral-line canal on the body, absence of all infraorbitals except the lacrimal, absence of the mandibular and angular lateralis canals, etc.), presence of numerous free neuromasts of a distinctive form, rudimentary olfactory organ, gill membranes broadly united across the isthmus, rounded caudal fin, and cycloid scales. To these, I add the following reductive features of *Elassoma*, not shared by the Centrarchidae: basisphenoid absent; endopterygoid absent; ectopterygoid absent or fused to

TABLE 119. LIST OF THE FAMILIES AND *INCERTAE SEDIS* GENERA OF THE SUBORDER PERCOIDEI. * Families with a single genus.

Acanthoclinidae	Emmelichthyidae	Nematistiidae*
Acropomatidae	Enoplosidae*	Nemipteridae
Ambassidae	Ephippididae	<i>Neoscorpis</i>
Aplodactylidae	Epigonidae	Opistognathidae
Apogonidae	Gerreidae	Oplegnathidae*
Arripididae*	Giganthiidae*	Ostracoberycidae*
Banjosidae*	Girellidae	Parascorpididae*
Bathylupeiidae*	Glaucosomatidae*	Pempherididae
Bramidae	Grammatidae	Pentacerotidae
Caesionidae	Haemulidae	Percichthyidae
<i>Caesiocorpsis</i>	<i>Hapalogenys</i>	Percidae
Callanthiidae	<i>Hemilutjanus</i>	Plesiopidae
Carangidae	<i>Howella</i>	Pomacanthidae
Caristiidae*	Inermidae	Pomatomidae*
Centrarchidae	Kuhliidae*	<i>Polyprion</i>
Centrarchidae	Kyphosidae	Priacanthidae
Centrogenysidae*	Lactariidae*	Pseudochromidae
Centropomidae	<i>Lateolabrax</i>	Rachycentridae*
Cepolidae	Latrididae	Scatophagidae
Chaetodontidae	Leiognathidae	Sciaenidae
Cheilodactylidae	Leptobramidae*	Scombropidae*
Chironemidae	Lethrinidae	Scorpididae
Cirrhitidae	Lobotidae*	Serranidae
Congrogadidae	Lutjanidae	Sillaginidae
Coracinidae*	Malacanthidae	<i>Simperca</i>
Coryphaenidae*	Menidae*	Sparidae
<i>Datnioides</i>	Microcanthidae	<i>Stereolepis</i>
Dinolestidae*	Monodactylidae*	<i>Symphysanodon</i>
<i>Dinoperca</i>	Moronidae	Teraponidae
Drepanidae*	Mullidae	Toxotidae*
Echeneididae	Nandidae	

palatine; palatine with a single notch-like articulation with ethmoid cartilage; predorsals usually absent, a single bone present in some (vs. 3–7 in centrarchids); branchiostegals 5 (vs. 6–7); principal caudal rays 6–7 + 7–8 (vs. 9 + 8); hypurals 1–2 and 3–4–5 fused.

Branson and Moore (1962) concluded that "either the elassomids diverged from the centrarchid stock early in the history of the group or they have entirely different affinities." Subsequent classifications (Greenwood et al., 1966; Nelson, 1976) have continued to treat *Elassoma* as a subfamily of the Centrarchidae, presumably accepting the conclusion of Eaton (1953, 1956) that *Elassoma* is a neotenus centrarchid, with most of its distinctive features having arisen through paedomorphosis. Weitzman and Fink (1983) attributed similar reductions in the laterosensory system of small characids to paedomorphosis and suggested that these characters may be quite labile. These and other osteological reductions similar to those of *Elassoma* are found in other small fishes such as gobioids (Springer, 1983) and cyprinodontoids (Parenti, 1981), but I know of no such extreme examples among small percoids.

That the reductive specializations of *Elassoma* actually represent character states of earlier developmental stages of centrarchids has never been clearly demonstrated or even adequately investigated, and comparative studies of the osteological development of these fishes would be necessary to answer this question. However, a crucial point, that seems to have been overlooked, is the absence of any other evidence suggesting a close relationship between *Elassoma* and the Centrarchidae. Although I know of no morphological specialization that defines the family, all centrarchids exhibit a similar mode of nest-build-

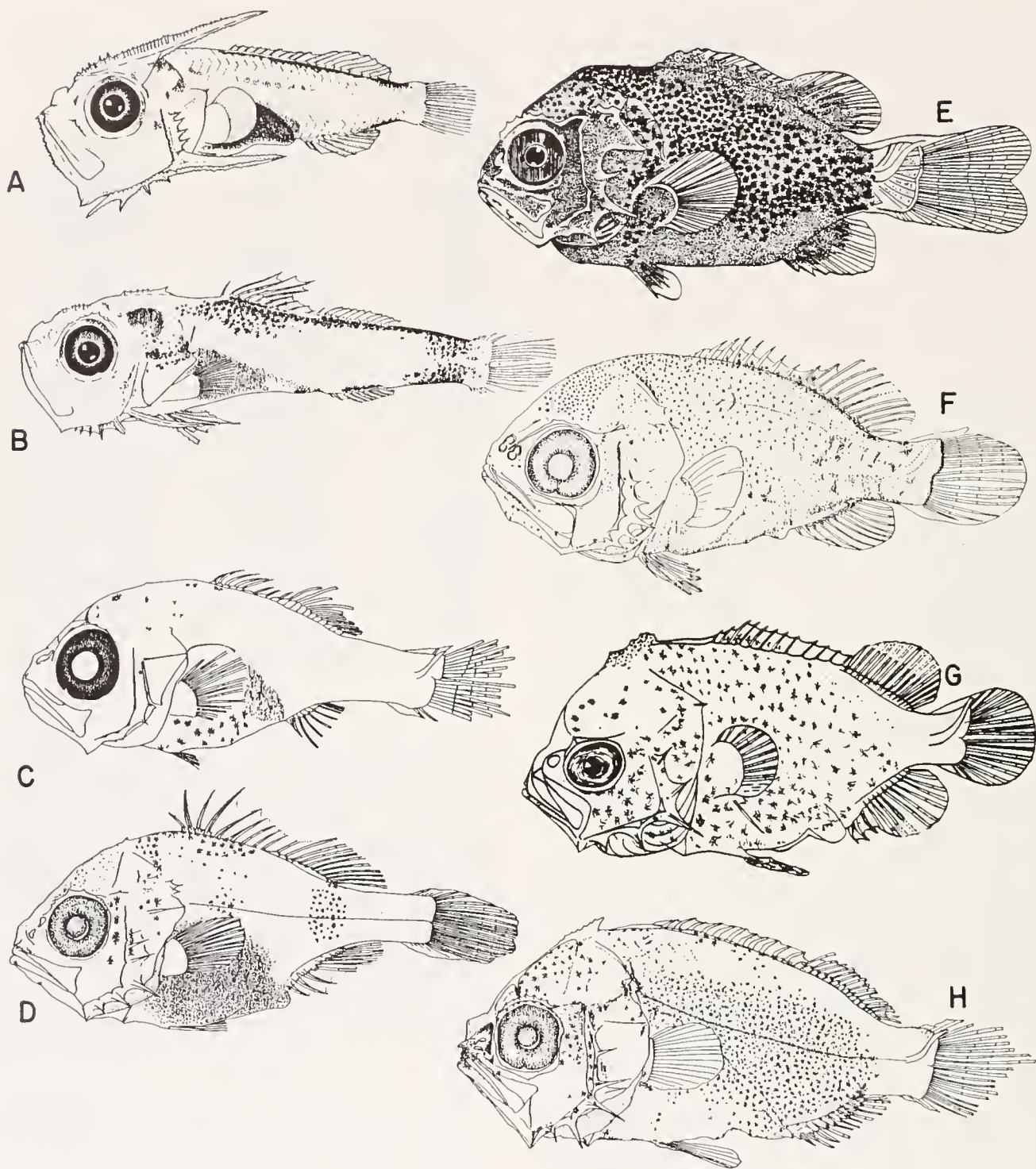


Fig. 254. (A) *Symphysanodon* sp., 5.1 mm SL; (B) Acropomatidae—*Synagrops* sp., 8.5 mm SL; (C) Acropomatidae—*Acropoma japonicum*, 6.0 mm SL, from Y. Konishi (unpubl.); (D) Acropomatidae—*Doederleinia beryeoides*, 8.0 mm SL, from Okiyama (1982b); (E) *Polyprion americanus*, 12.2 mm TL, from Sparta (1939a); (F) *Stereolepis doederleini*, 7.2 mm SL, from Okiyama (1982b); (G) Lobotidae—*Lobotes surinamensis*, 6.0 mm TL, from Uchida et al. (1958); (H) *Hapalogenys* sp., 7.3 mm SL, from Okiyama (1982b).

ing and parental-care behavior, and this behavioral "synapomorphy" is not shared by *Elassoma* (Breder and Rosen, 1966; M. F. Mettee, pers. comm.). Consequently, though *Elassoma* may be a product of pedomorphosis, I see no reason to limit

the search for its origins to the Centrarchidae. Quite the contrary, I believe the affinities of *Elassoma* will be shown to lie outside the Percoidei and, perhaps, outside the Perciformes.

My preliminary findings indicate that *Elassoma* possesses a

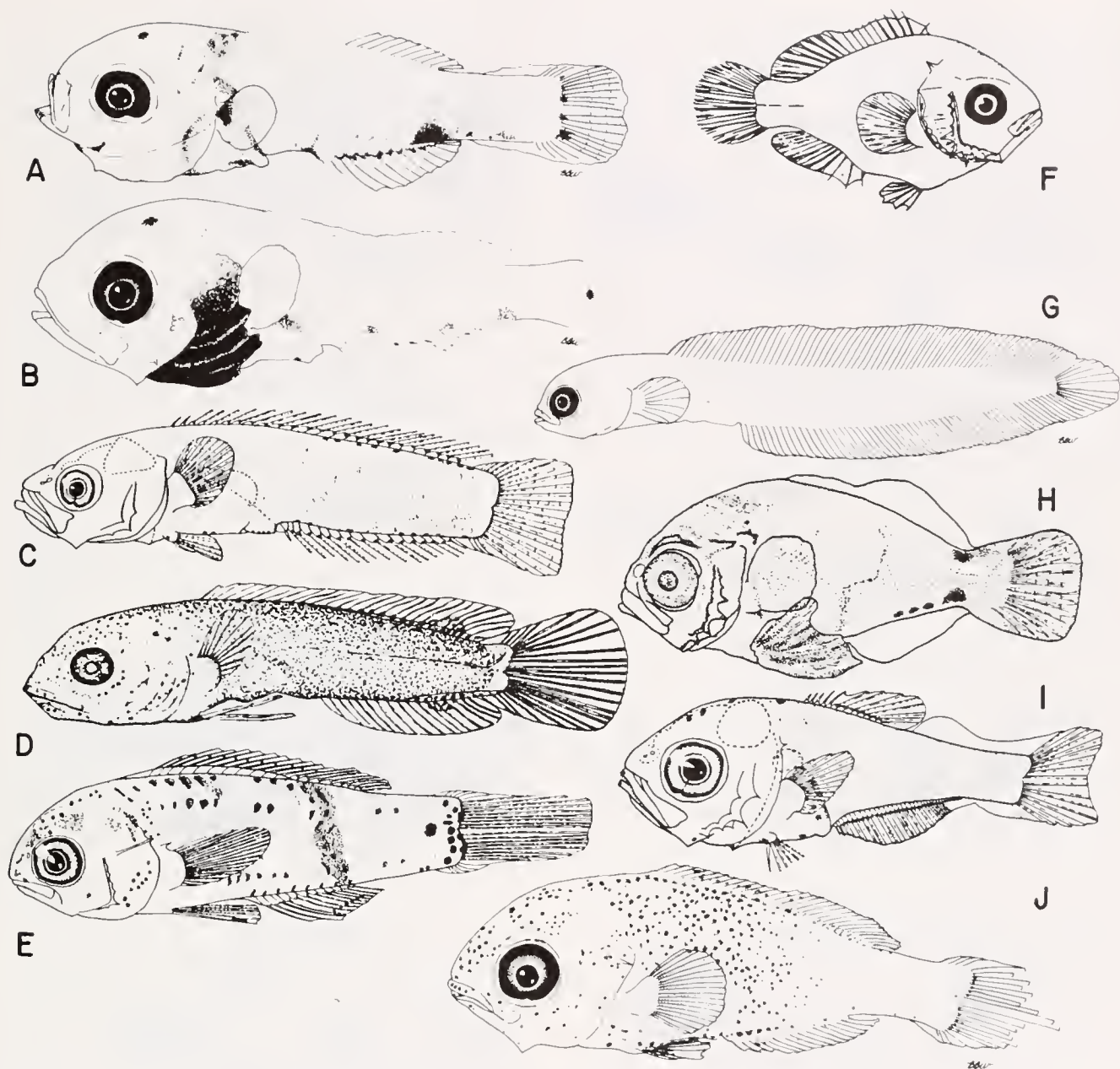


Fig. 255. (A) Ambassidae—*Velambassis jacksonensis*, 5.5 mm SL; (B) Opistognathidae—*Opistognathus* sp., 6 mm SL; (C) Pseudochromidae, 8.1 mm SL, from Leis and Rennis (1983); (D) Acanthoclinidae—*Acanthoclinus trilineatus*, 10.0 mm, from Crossland (1982); (E) Callanthiidae—*Grammatonotus laysanus*, 13.7 mm SL, from Leis and Rennis (1983); (F) Callanthiidae—*Callanthias peloritanus*, 8 mm TL, from Fage (1918); (G) Congrogadidae—*Congrogadus subducens*, 11.8 mm SL; (H) Monodactylidae—*Monodactylus sebae*, 5.2 mm SL, from Akatsu et al. (1977); (I) Pempheridae—*Pempheris* sp., 5.5 mm SL, from Leis and Rennis (1983); (J) Oplegnathidae—*Oplegnathus fasciatus*, 7.5 mm SL.

number of salient features (not mentioned above) that cast doubt on its affinities with the Percoidae. The second preural centrum bears a full neural spine, and there are no autogenous haemal spines. Strong parapophyses begin on the first centrum, and pleural ribs may begin on the first, second or third vertebra. The first neural arch is fused to its respective centrum. The pelvic fin is inserted well behind the pectoral fin base and the pelvic girdle does not contact the cleithra. The first pharyngobranchial and interarcual cartilage are absent and what is apparently the uncinat process of the first epibranchial articulates

directly with the second pharyngobranchial. The fourth pharyngobranchial, usually cartilaginous in percoids, is absent. The proximal base of the medial half of the uppermost pectoral ray does not extend laterally to form a process for articulation with the scapular condyle (also true of at least some cyprinodontoids and gobioids). Finally, the ossified portion of the ethmoid consists of two, closely applied, disc-like bones, a condition listed as one of the defining characteristics of the Atherinomorpha by Rosen (1964) and Rosen and Parenti (1981). (They did not discuss the distribution of this character among other groups,

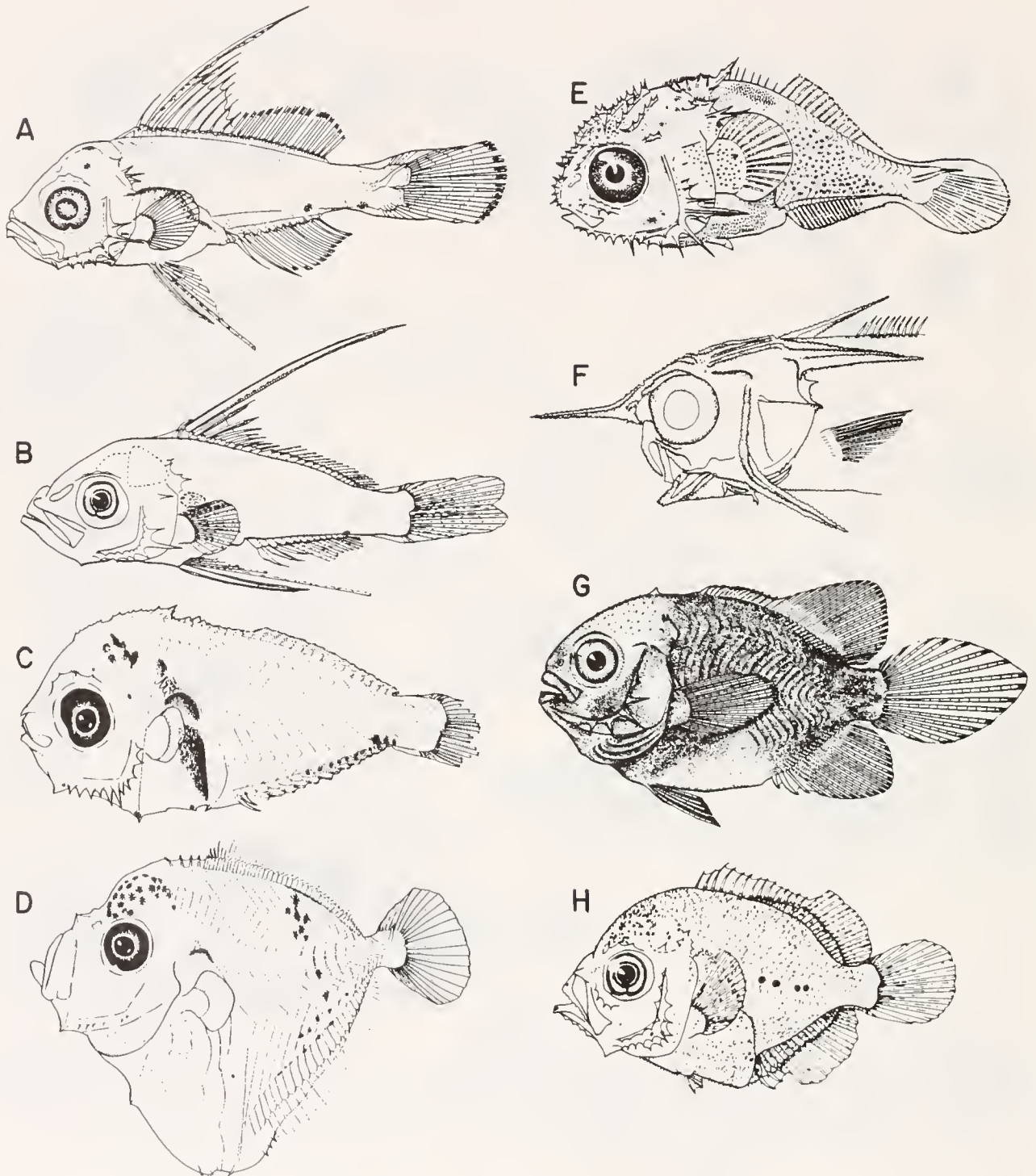


Fig. 256. (A) Lutjanidae—*Lutjanus campechanus*, 7.3 mm SL, from Collins et al. (1980); (B) Caesionidae—*Caesio* sp. or *Gymnocaesio* sp., 7.8 mm SL, from Leis and Rennis (1983); (C) Leiognathidae—unidentified, 4.8 mm SL; (D) Menidae—*Mene maculata*, 4.6 mm SL; (E) Malacanthidae—*Caulolatilus princeps*, 6.0 mm SL, from Moser (1981); (F) Malacanthidae—*Hoplolatilus fronticinctus* (head only), 15 mm SL, from Dooley (1978); (G) Ehippididae—*Chaetodipterus faber*, 9 mm, from Hildebrand and Cable (1938); (H) Pomacanthidae—*Centropyge* sp., 4.4 mm SL, from Leis and Rennis (1983).

but I have observed a similar condition in the gobiid *Dormitator*.)

Elassoma seems to exhibit a confusing mosaic of character states variously shared with atherinomorphs, cyprinodontoids, percopsiforms, perciforms, and gobioids. Resolution of the evolutionary affinities of this genus could be important to our understanding of acanthomorph interrelationships, and I intend to examine this problem more fully.

Epigonidae.—Fraser (1972a) treated *Epigonus*, *Florenciella* and *Rosenblattia* as a subfamily (Epigoninae) of the Apogonidae, but I find no evidence to suggest that these genera are closely related to other apogonids. They are primitive with respect to apogonids in possessing two pairs of uroneurals and a procurrent spur (Johnson, 1975), but specialized in several features listed below. Moreover, the two anal spines of epigonines and apogonids, usually cited as evidence of their close relationship, are not homologous (see discussion on median fins). The Epigonidae are here recognized as a distinct family, including *Brinkmanella*, *Sphyraenops* and Fraser's epigonines. These five genera share the following specializations: rostral cartilage greatly enlarged, ascending processes of premaxillaries reduced or absent; premaxillary articular cartilages enlarged; endopterygoids large, metapterygoids notably reduced; infraorbitals more than six. The larvae of *Sphyraenops* (Fig. 257A) resemble those of *Epigonus* (Fig. 257B) but differ in possessing well-developed head spination.

Girellidae, Kyphosidae, Microcanthidae, Neoscorpis, Parascorpididae and Scorpionidae.—Springer (1982; pers. comm.), following Jordan (1923) and Golvan (1965), included microcanthids, *Neoscorpis*, *Parascorpis* and scorpionids in the family Scorpionidae, but no convincing evidence for uniting them has been presented, and they are treated separately here. The Scorpionidae is here restricted to *Scorpis*, *Medialuna*, *Labracoglossa* and *Bathystethus*. The latter two genera were treated as a separate family, Labracoglossidae, by Springer. Scorpionids share similar meristic and osteological features (not derived) and comparable scale morphology. An unusual small slip of muscle extends from the basioccipital to the first vertebra in *Scorpis* and *Labracoglossa*, but its presence has not been confirmed in the other two genera. The larvae of *Scorpis* and *Bathystethus* are undescribed but those of *Labracoglossa* (Fig. 258A) and *Medialuna* (Fig. 258B) share a similar body form, generalized head spination, late fin development and pigment pattern with larvae of the Girellidae (Fig. 258C). Girellids are specialized in several osteological features with respect to the Scorpionidae (see Table 120) and have a unique adductor mandibulae in which A_2 inserts on the lateral surface of the dentary (Johnson and Fritzsche, in prep.). The distinctive larval form shared by scorpionids and girellids suggests that they may be sister groups. Convincing evidence supporting a close relationship between the Scorpionidae and the Microcanthidae (*Microcanthus*, *Atypichthys* and *Neatypus*) or the Kyphosidae (*Kyphosus*, *Sectator* and *Hermosilla*) is lacking. Furthermore, the larvae of the latter two families (Figs. 259G, J) do not possess the salient features of scorpionid or girellid larvae, but more closely resemble those of the Teraponidae (Fig. 259H). The larvae of *Neoscorpis* and *Parascorpis* are unknown, and available anatomical information is insufficient to clarify the systematic position of these two genera.

Malacanthidae.—See discussion on utility of larval morphology.

Moronidae (*Morone* and *Dicentrarchus*), *Lateolabrax* and *Siniperca*.—Gosline (1966) included the Moronidae (using the name *Roccus*), *Lateolabrax* and *Siniperca* (= *Coreoperca*) in his "estuarine and freshwater percichthyids." I treat these separately, because I lack evidence of their affinities with the Percichthyidae, with one another, or with any other percoid group. It is interesting to note that the Moronidae share one of the two synapomorphies of the Centropomidae described by Greenwood (1976)—the lateral line extends almost to the posterior margin of the caudal fin. In addition, moronids have an auxiliary row of lateral line scales on the caudal fin above and below the main row, as does the centropomid *Lates*. Although both of these conditions occur elsewhere in generalized percoids (e.g., *Neoscorpis*, some species of *Lutjanus*, and the percoid subfamily Luciopericinae) and may actually be primitive for the Percoidei (Springer, 1983), the possibility of a moronid-centropomid relationship seems plausible and should probably be investigated further. Unfortunately, as is typical of most fresh or brackish water spawners, the larvae of these groups (Fig. 260) exhibit relatively direct development and consequently offer little phylogenetic information.

Percichthyidae.—The Percichthyidae of Gosline (1966) represents a polyphyletic assemblage defined on the basis of shared primitive features. I am unable to find synapomorphies that support recognition of the assemblage as a monophyletic group. I restrict the Percichthyidae to the following genera, which occur only in freshwaters of Australia and South America: *Percalates* (brackish water), *Plectroplites*, *Macquaria*, *Maccullochella*, *Percichthys*, *Percilia*, *Bostockia*, *Gadopsis*, *Nannoperca*, *Edelia*, and *Nannatherina*. The monophyly of the family is supported by a series of nested synapomorphies, only a few of which are mentioned here. The scales of most of these genera are similar and unlike those of the excluded genera in having the posterior field filled with simple, only slightly amputated (see McCully, 1970), needle-like ctenii (those of *Bostockia*, *Gadopsis* and *Nannatherina* are secondarily cycloid). The three most generalized genera, *Percalates*, *Plectroplites*, and *Macquaria* are very similar biochemically [MacDonald (1978) synonymized them on this basis], and the latter two share two morphological specializations with *Maccullochella*, *Percichthys*, *Percilia*, *Bostockia* and *Gadopsis*: enlarged sensory pores on the dentary and a separate inner division of adductor mandibulae section A_1 . The three most derived genera, *Nannoperca*, *Edelia* and *Nannatherina* (heretofore treated as kuhliids) share with *Bostockia* a similar vertebral number (29–33), a distinctive asymmetrical nasal rosette, and a number of reductive specializations (absences of the subocular shelf, procurrent spur, and supracleithral sensory canal, reduced numbers of procurrent caudal rays, dorsal spines, branchiostegals and trisegmental pterygiophores, and an interrupted or absent lateral line). Systematic placement of the enigmatic *Gadopsis* has proved problematic, even in recent years. It has generally been treated as a monotypic family and variously assigned to the Percoidei (Greenwood et al., 1966), Ophidiioidei (Gosline, 1968), Perciformes with proposed affinities to the Trachinoidei and Blennioidei (Rosen and Patterson, 1969) or a separate order Gadopsiformes (Scott, 1962). The percoid affinities of *Gadopsis* are manifest in the anatomy of the dorsal gill arches, caudal skeleton and median fin supports. Its affinities with the Percichthyidae are indicated by a number of features shared with some percichthyid genera, including the configuration of the adductor mandibulae noted above. *Gadopsis* shares

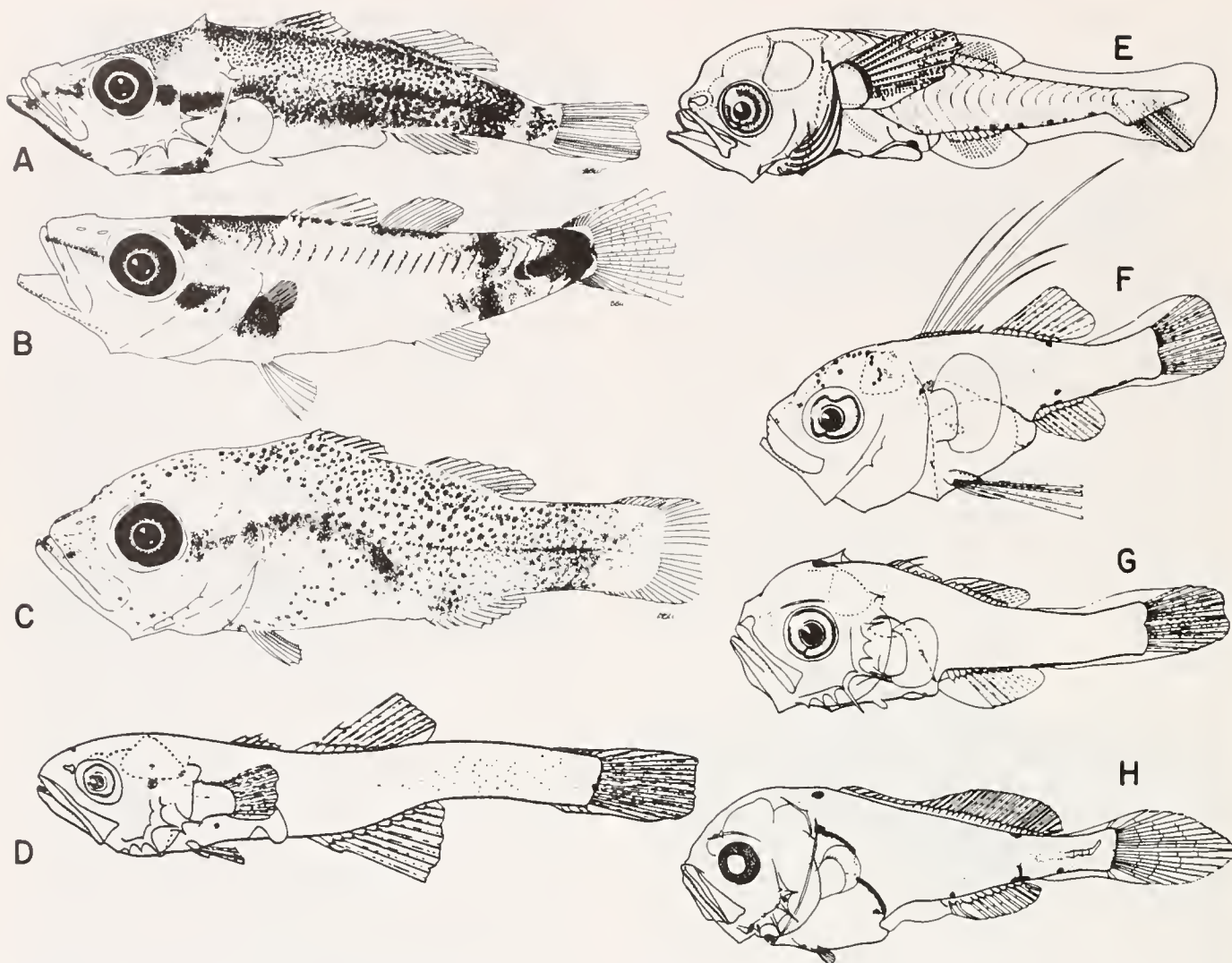


Fig. 257. (A) Epigonidae—*Sphyracnops bairdianus*, 6.8 mm SL; (B) Epigonidae—*Epigonus* sp., 14.0 mm SL; (C) *Howella* sp., 6.0 mm SL; (D) Apogonidae—*Pseudamia* sp. or *Pseudamiops* sp., 8.7 mm SL, from Leis and Rennis (1983); (E) Apogonidae—*Foa brachygramma*, 4.2 mm SL, from Miller et al. (1979); (F) Apogonidae—unidentified, 4.2 mm SL, from Leis and Rennis (1983); (G) Apogonidae—unidentified, 5.0 mm SL, from Leis and Rennis (1983); (H) Sciaenidae—*Stelifer lanceolatus*, 6.2 mm SL, from Powles (1980).

the asymmetrical nasal rosette of *Bostockia*, *Nannoperca*, *Edelia* and *Nannatherina* and all reductive specializations of those genera noted above, except the reduced lateral line and branchiostegal number. Specializations shared with *Bostockia* alone include a tubular anterior nostril placed near the margin of the lip and absences of the basisphenoid, medial tabular, and third epural. Based on this evidence, *Gadopsis* appears to be most closely related to *Bostockia*, however it bears a strong superficial resemblance to *Macullochella* and shares the premaxillary frenum of that genus.

ADULT MORPHOLOGY

The scope of morphological diversity exhibited within the Percoidei surpasses that of all other perciform suborders. Although many percoids have a generalized bass-like or perch-like physiognomy, extremes of adult body form range from deep

bodied, compressed or "slabsided" fishes, such as the ehippidids, chaetodontids and menids to extremely elongate forms like the cepolids and the eel-like congrogadids. Add to this the exceptional variability in fin conformation, ornamentation of head bones, squamation, jaw configuration, and internal osteological features, and the suborder Percoidei presents an impressive heterogeneous array of forms. Lack of progress in elucidating percoid phylogeny is largely attributable to this somewhat overwhelming diversity and the ostensible convergence (particularly in reductive traits) that seems to have characterized percoid evolution. To date, no familial phylogeny, cladistic or otherwise, has been proposed for the suborder. The limits and monophyly of many of the component families are not clearly defined and the affinities of numerous genera remain unresolved. Superficial knowledge of basic percoid anatomy and an inadequate understanding of character distribution and vari-

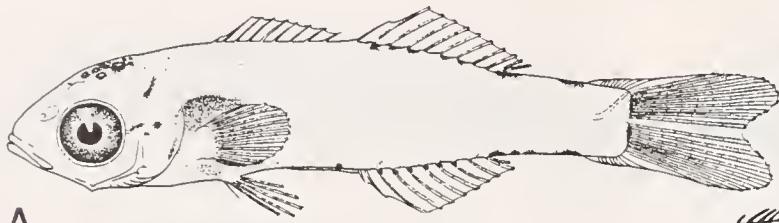


Fig. 258. (A) Scorpididae—*Labracoglossa argentiventris*, 9.9 mm SL; (B) Scorpididae—*Medialuna californiensis*, 10.1 mm SL; (C) Girellidae—*Girella nigricans*, 10.9 mm SL; (D) Leptobramidae—*Leptobrama mulleri*, 7.2 mm SL; (E) Cheilodactylidae—*Palunolepis brachydactylus*, 8.3 mm SL; (F) Cirrhitidae—*Amblycirrhitus pinos*, 13.2 mm SL; (G) Pomatomidae—*Pomatomus saltatrix*, 7.3 mm TL, from Pearson (1941); (H) Nemipteridae—unidentified, 5.1 mm SL, from Leis and Rennis (1983); (I) Sparidae—*Acanthopagrus cuvieri*, 8 mm SL, from Hussain et al. (1981); (J) Centracanthidae—*Pterosmaris axillaris*, 7.7 mm SL, from Brownell (1979).

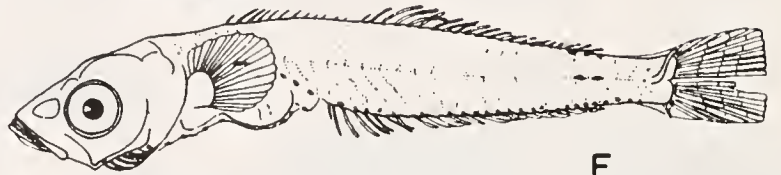
ability, basic to cladistic outgroup comparison, have seemingly inhibited, or at least hindered, meaningful comparative studies within the Percoidae.

Because the group is so large, these problems will necessarily continue to plague studies of percoid relationships. Outgroup comparisons based on a single family are speculative without evidence for a sister group relationship, and broader surveys of each character are frequently impractical if not impossible. One

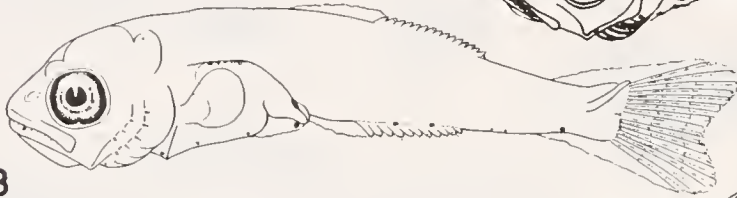
approach that can gradually alleviate this problem is the cumulative tabulation of characters and character states. Comparative tables document the distribution of morphological features throughout the suborder and the variability of these features within families, and they accordingly offer the most complete foundation for outgroup comparison. Furthermore, they provide information about the plasticity of various complexes, allow identification of characters most frequently subject to con-



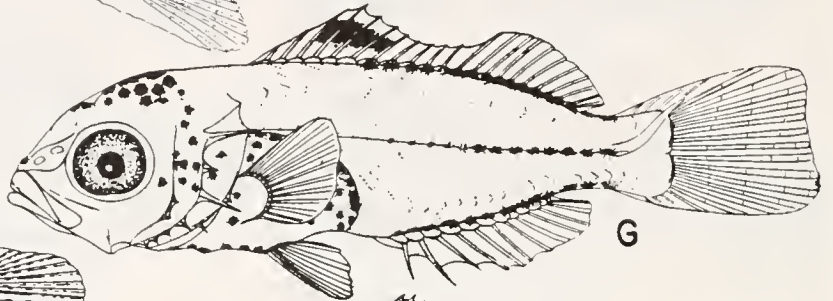
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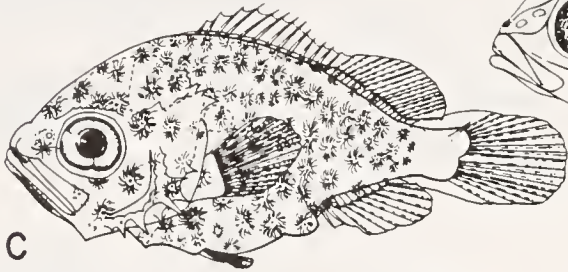
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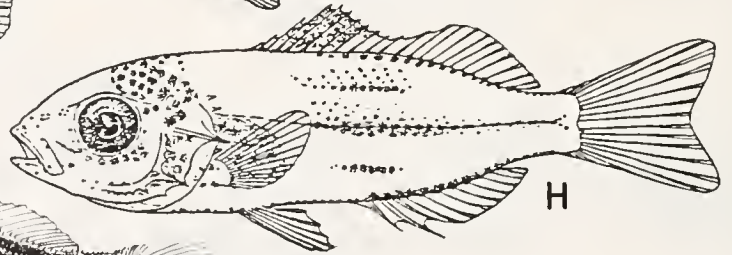
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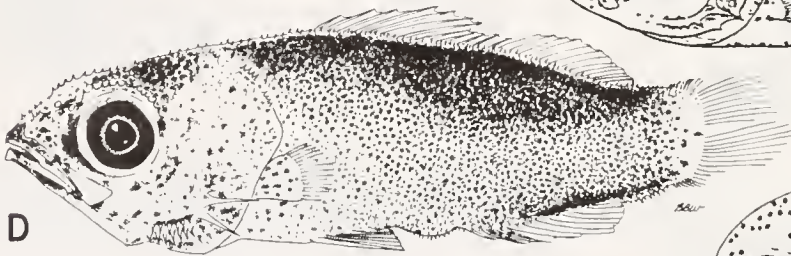
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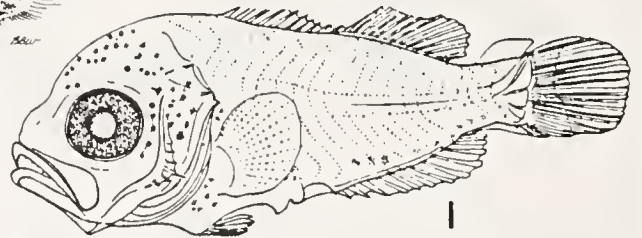
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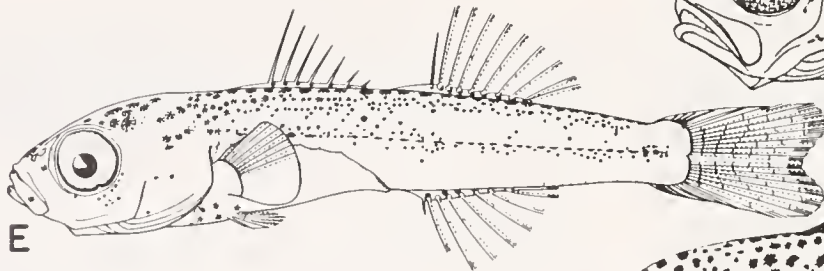
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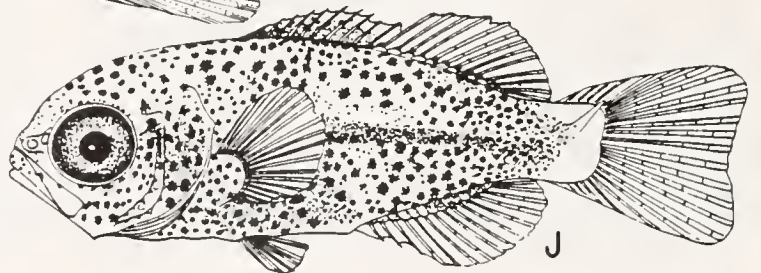
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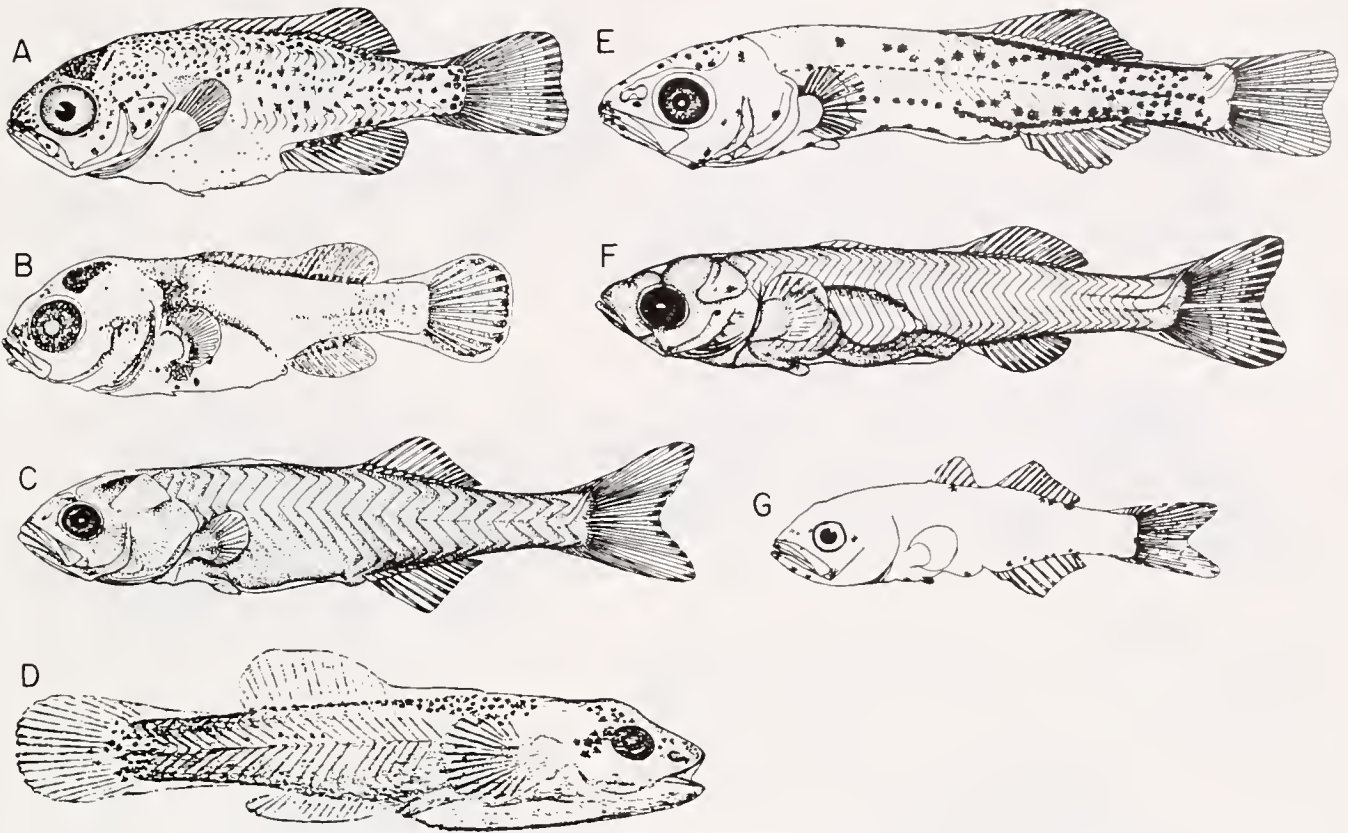


Fig. 260. (A) Centrarchidae—*Ambloplites rupestris*, 10.5 mm TL, from Fish (1932); (B) *Siniperca* (= *Coreoperca*) *kawamebari*, 9.0 mm TL, from Imai and Nakahara (1957); (C) Percidae—*Perca flavescens*, 14.2 mm TL, from Mansueti (1964); (D) Percichthyidae—*Maccullochella macquariensis*, size unknown, from Dakin and Kesteven (1938); (E) *Lateolabrax japonicus*, 13.7 mm TL, from Mito (1957b); (F) Moronidae—*Morone americana*, 13.2 mm TL, from Mansueti (1964); (G) Centropomidae—*Centropomus undecimalis*, 6.3 mm SL, from Lau and Shaffland (1982).

vergence and convincingly document the uniqueness of derived features. With this in mind, I have compiled information about selected morphological features of adults (Table 120) and larvae (Table 121) for each percoid family or *incertae sedis* genus. This information was compiled from the literature (particularly the meristic data) and from my own examination of cleared and stained specimens and radiographs. Data for a few groups were compiled by experts working on those groups. For many families, I examined at least one representative of each genus, but obviously this was not always possible and only in a few of the smaller families were all species examined. As a consequence, this data will not reflect the full range of variability for every family but should represent a reasonably close approximation. Most features considered in Table 120 are discussed below.

Fins.—The primitive perciform complement of one spine and five rays (I, 5) in the pelvic fin is the most consistent feature of

percoid fins. A single spine is always present and fewer than five soft rays are found only in the Acanthoclinidae (I, 2), Congrogadidae (I, 2–4 or absent), Plesiopidae (I, 4), Pseudochromidae (I, 3–5) and the percichthyid *Gadopsis* (I, 1).

The primitive and most common number of principal caudal fin rays (branched rays + 2) is 9 + 8. Where reductions occur (in 18 families) they usually involve one fewer principal ray dorsally and/or ventrally and are frequently consistent within families, e.g., 8 + 7 in Cheilodactylidae, Chironemidae, Cirrhitidae, Latrididae and Mullidae, and 8 + 8 in Acanthoclinidae, Priacanthidae, and Scatophagidae. The most extreme reduction (4–6 branched + 4–8 branched) is seen in the Congrogadidae. The only apparent increases, 10 + 9 found in some grammatids and plesiopids, do not result from an increased number of rays articulating with the hypurals, but from branching of the outermost hypural-associated rays. Numbers of procurrent or secondary caudal rays dorsally and ventrally

Fig. 259. (A) Gerreidae—*Eucinostomus* sp., 8.7 mm SL; (B) Haemulidae—*Xenistius californiensis*, 6.5 mm SL; (C) Haemulidae—*Pseudopristipoma nigra*, 5.8 mm SL, from Leis and Rennis (1983); (D) Haemulidae—*Conodon nobilis*, 9.8 mm SL; (E) Mullidae, 8.2 mm SL, from Miller et al. (1979); (F) Sillaginidae—*Sillago sihama*, 9.0 mm TL, from Uchida et al. (1958); (G) Microcanthidae—*Microcanthus strigatus*, 7.1 mm TL, from Uchida et al. (1958); (H) Teraponidae—*Therapon theraps*, 9.5 mm, from Zvjagina (1965b); (I) Emmelichthyidae—*Erythrocles schlegeli*, 6.9 mm TL, from Nakahara (1962); (J) Kyphosidae—*Kyphosus cinerascens*, 9.8 mm TL, from Uchida et al. (1958).

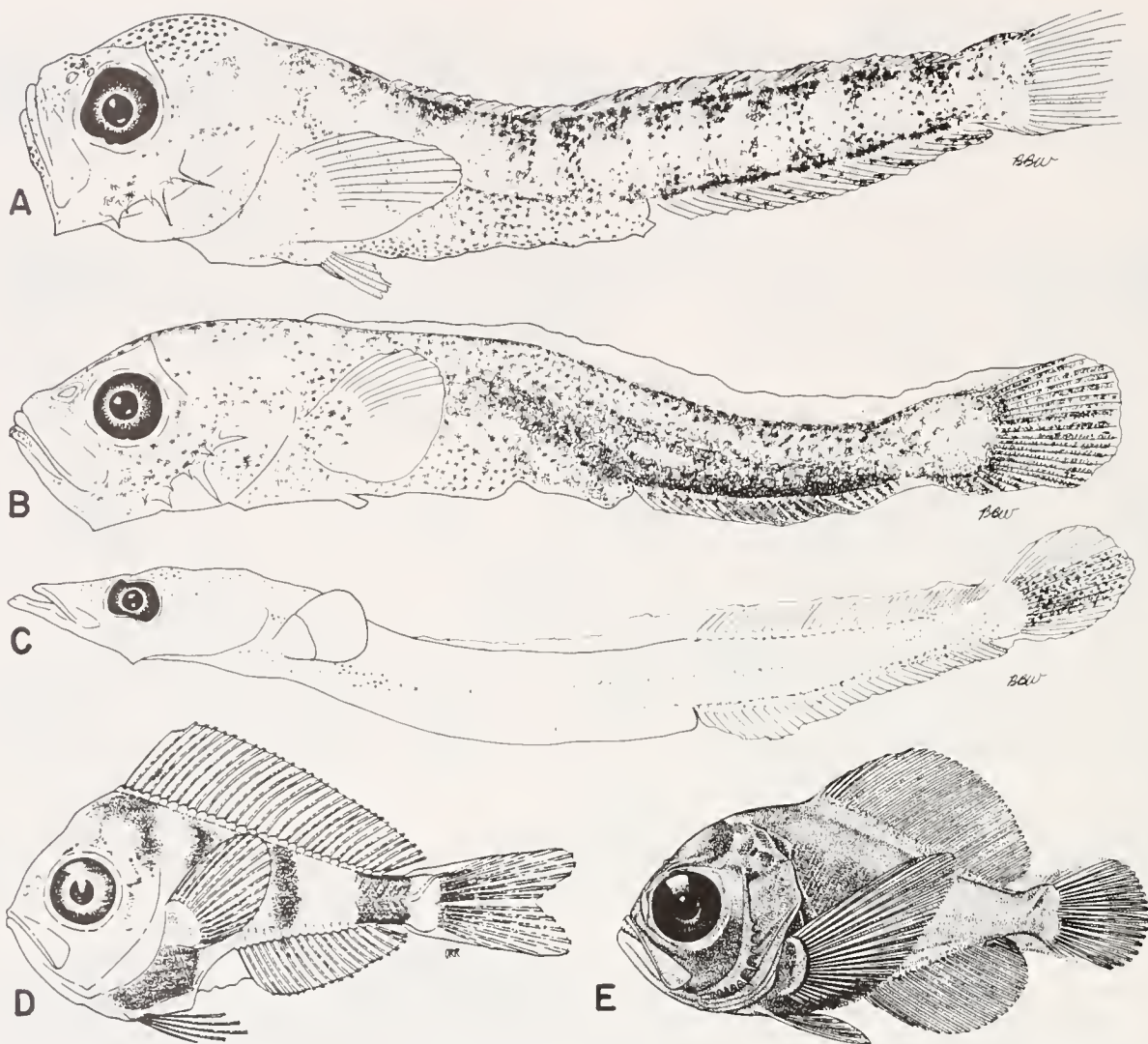


Fig. 261. (A) Coryphaenidae—*Coryphaena hippurus*, 8.5 mm SL; (B) Rachycentridae—*Rachycentron canadum*, 9.0 mm SL; (C) Echeneididae—*Echeneis* sp., 8.8 mm SL; (D) Caristiidae—*Caristiopus* sp., 10.1 mm SL; (E) Bramidae—*Brama dussumieri*, 6.5 mm SL, from Mead (1972).

range from 0 in the Congrogadidae to 19 in the Sillaginidae, the most common numbers being 8–14.

One of the most variable aspects of percoid physiognomy is the form and composition of the dorsal fin. Even the most consistent feature, the presence of spines, does not characterize all percoids. Absence of dorsal spines in six percoid families appears to have originated by at least two different mechanisms. In *Bathyclupea*, it is obvious that the spines have been lost because the spinous pterygiophores are still present and the soft rays occupy a position posterior to them. In *Coryphaena*, how-

ever, Potthoff (1980) showed that although the anteriormost 3–4 pterygiophores bear soft rays, they are of the type that normally support spines. This suggests that the absence of spines in *Coryphaena* is the result of transformation, rather than loss, of pre-existing elements. Absence of spines in the Bramidae, Caristiidae, some cepolids and some congrogadids is also probably the result of transformation.

Spines are present anteriorly in the dorsal fin of all other percoids, ranging from I in some malacanthids and pseudochromids to XXI in some acanthoclinids. Dorsal soft rays range

Fig. 262. (A) Chaetodontidae—unidentified, 10 mm, from Burgess (1978); (B) Chaetodontidae—*Forcipiger longirostris*, 17 mm TL, from Kendall and Goldsborough (1911); (C) Chaetodontidae—*Chelmon* sp. or *Coradion* sp., 6.5 mm SL, from Leis and Rennis (1983); (D) Scatophagidae—*Scatophagus argus*, 10 mm SL from Weber and de Beaufort (1936); (E) Scombroptidae—*Scombroptus boops*, 6.2 mm SL, from Uchida et al. (1958); (F) Lethrinidae—*Lethrinus nematacanthus*, 6.1 mm SL, from K. Mori (unpubl.); (G) Cepolidae—*Acanthocephala* sp., 9.7 mm SL, from Okiyama (1982b); (H) Priacanthidae—unidentified, 4.6 mm SL, from Leis and Rennis (1983); (I) Priacanthidae—*Priacanthus* sp., 10.9 mm SL, from Leis and Rennis (1983); (J) Pentacerotidae—*Pseudopentaceros richardsoni*, 15 mm SL.

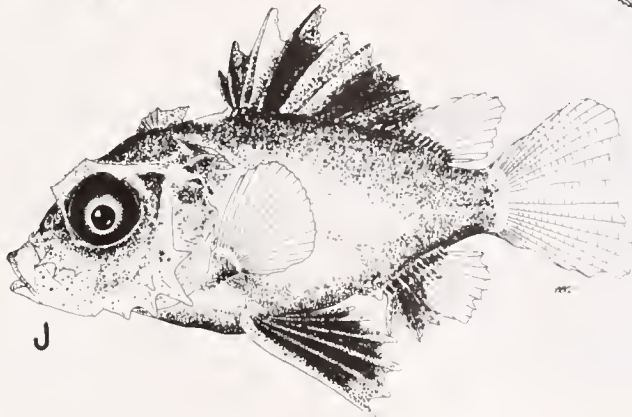
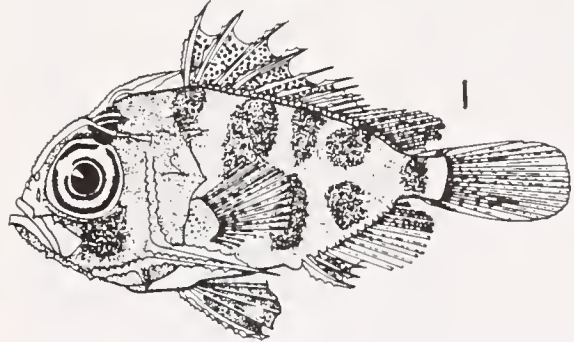
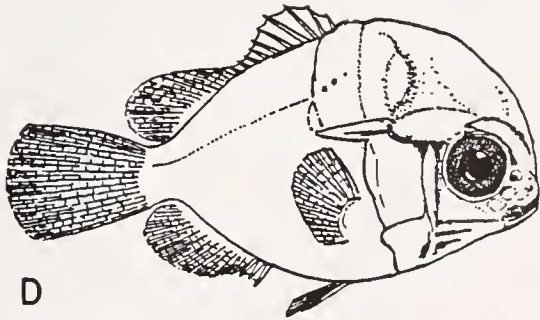
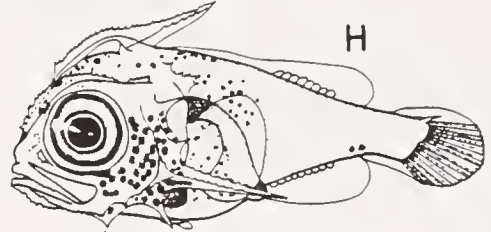
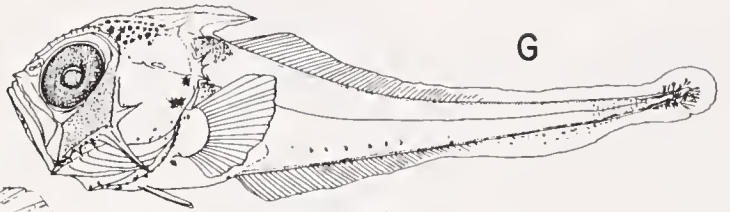
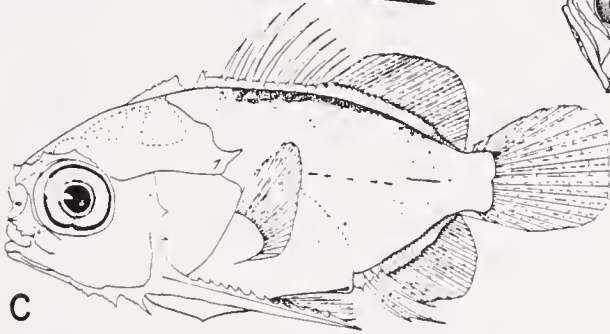
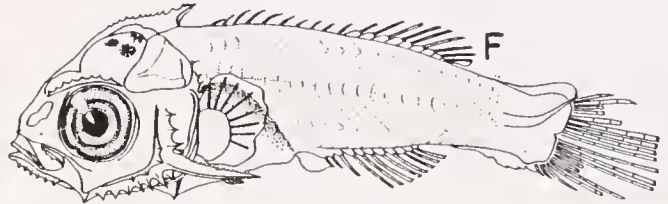
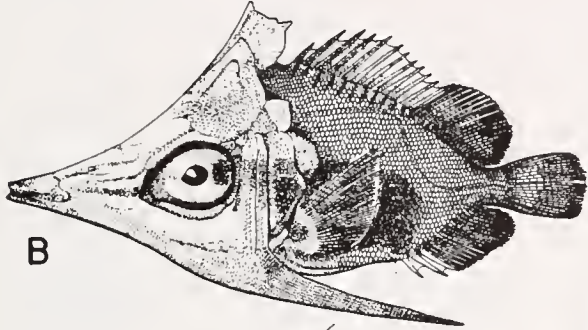
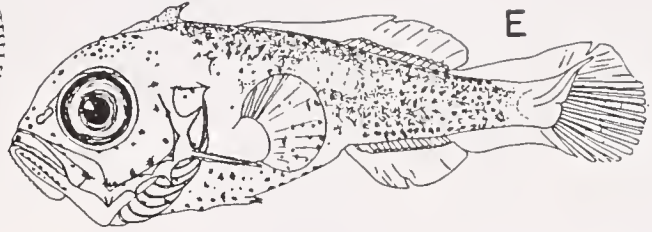
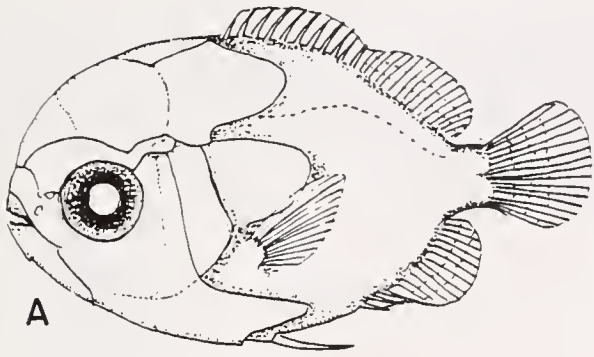


TABLE 120. SELECTED MORPHOLOGICAL FEATURES OF ADULT PERCOIDEI. Abbreviations and definitions: SS—supernumerary (non-serial) spines (or soft rays) on first anal pterygiophore (see Johnson, 1980); D—dorsal fin; A—anal fin; Triseg. pteryg.—pterygiophores with proximal, medial and distal radials separate; Stay—separate bony element posterior to ultimate pterygiophore in D and A; Predorsal formulae—based on Ahlstrom et al. (1976); P—pterygiophore with no supernumerary spines or soft rays; H—hypurals; E—epurals; U—uroneurals; Ah—autogenous haemal spines; pH—parhypural; UR—urostyle; Proc spur—procurent spur (see Johnson, 1975); PU3 cart—radial cartilage anterior to neural and haemal spines of third preural centrum; BR—branchiostegals; IAC—interarcual cartilage; Cy—cycloid; Ct—ctenoid, ctenii free from posterior margin; Ct'—ctenoid, ctenii continuous with posterior margin; and br—branched caudal fin rays. With the exception of (SS), parentheses enclose features known to characterize only some members of a group.

	Vertebrae	Dorsal fin		TriSEG. PTERYG. D Stay A	Pelvic fin	Predorsal formulae	CAUDAL FIN Principal	
		Anal fin (SS)					Procurent	
Acanthoclinidae	10 + 18 11 + 17 11 + 18 12 + 18 13 + 16	XVII-XXI, 3-4 VIII-XI, 4 (1-2)		0 0 +	1, 2	0/0/1/1+1/	8+8 3-4+3-4	
Acropomatidae	10 + 15	VII-X-I, 8-10 or IX-X, 10 II-III, 7-9 (2)		1-6 1-4 +	1, 5	/0+0/0+2/1+1/ 0/0/0+2/1/ 0/0/0+2/1+1/	9+8 9-13+9-13	
Ambassidae	10 + 14	VII-I, 8-11 III, 7-10 (2)		0 0 -	1, 5	0/0/0+1/1/ 0/0/1+1/1/	9+8 7-11+7-10	
Aplodactylidae	15 + 20 16 + 19	XIV-XXI, 16-21 III, 6-9 (2)		0 0 +	1, 5	0/0+0/2+1/1/ 0/0+0/2/1+1/	8-9+7 12-14+12-13	
Apogonidae	10 + 14 10 + 15	VI-VIII-I, 8-14 II, 8-18 (1)		3-11 3-8 +	1, 5	various: 0/0/0+2 or 1/ to ///2 or 1/	9+8 6-10+5-10	
Arripidae	10 + 15	IX, 13-19 III, 9-10 (2)		5 1 +	1, 5	0/0/0+2/1+1/	9+8 7+6	
Banjosidae	11 + 14	X, 12 III, 7		9 5 +	1, 5	0/0+2/1/1/	9+8 6+5	
Bathyclupeidae	9 + 22 10 + 21	9 I, 26-27 (0)		0 0 +	1, 5	0/0/0//P+P/P/P/P/P/P/1/	9+8 9+8	
Bramidae								
Braminae	T:36-47	30-38 21-30 (2-3)		0 0 +	1, 5	0/0/0/P/P/1+1/ 0/0/0/P/1/	9+8 7-8+7-8	
Pteraclinae	T:45-54	46-57 39-50 (?)		1-2 1-2 +	1, 5	1+1+1+1, etc./1/1/	9+8 5+5	
Caesionidae	10 + 14	IX-XV, 9-21 III, 9-13 (2)		2-4 2-4 +	1, 5	0/0/0+2/1+1/ /0+0/2/1+1/	9+8 7-10+5-10	
<i>Caesiocorpis</i>	10 + 15	XI, 20-21 III, 18-20 (2)		6-8 6-8 +	1, 5	0/0+0/2/1	9+8 9-11+8-10	
Callanthidae	10 + 14	X-XI, 8-12 III, 9-12 (2)		1 1 +	1, 5	0/0/2/1+1/	8-9+7-8 5-9+5-9	
Carangidae	10 + 14 10 + 15 10 + 16 10 + 17 11 + 13 11 + 14	IV-VIII-I, 17-44 1-II-I, 15-39 (1-2)		0-3 0-2 -	1, 5	see section on Carangidae	9+8 8-14+8-12	
Caristiidae	T: 35-40	32-40 18-21 (1)		0 0 ?	1, 5	1+1+1+1+1+1/1/1/ 1+1+1+1/1/1/	9+8 7-8+7-8	
Centracanthidae	10 + 14	XI-XIII, 9-11 III, 9 (2)		1-4 1-4 +	1, 5	0/0+0/2+1/1/ 0/0/0+2/1/	9+8 9-10+8-10	
Centrarchidae	11-14 + 15-19 T: 28-32	V-XIII, 9-16 II-VIII, 8-19 (2-3)		3-6 3-6 +	1, 5	3-7 predorsals 1-3 sup. spines	9+8 5-10+5-9	
Centrogenysidae	11 + 14	XIII-XIV, 9-11 III, 5 (2)		0 0 +	1, 5	0/0+2/1/1/	7+7 5+5	

TABLE 120. EXTENDED.

CAUDAL SKELETON H/E/U/Ah H Fusions	Proc spur PU3 cart.	BR	IAC	Scales
3/3/0/0 pH-1-2; 3-4-UR	-- +	6	+	Ct or Cy
5/3/2/2 —	++ +	7	+	Ct or Cy
3/2/1/1 1-2; 3-4	-- +	6	+	Cy
5/3/1/2 —	-- ?	6	?	Cy
2-5/2-3/0-1/0-2 various	-- +	7	+	Ct or Cy
5/3/2/2 —	+ +	7	+	Ct
5/3/2/2 —	++ ?	7	+	Ct
5/3/2/2 —	++ +	7	+	Cy
5/3/2/2 —	+ +	7	+	Ct'
5/3/2/2 —	+ +	7-8	+	Ct'
3 or 5/3/2/2 (1-2; 3-4)	-- ?	7	+	Ct
5/3/2/2 —	++ ?	7	+	Ct
3/2-3/1/1 1-2; 3-4	-- +	6	+	Ct
2-3/2-3/1-2/2 1-2; 3-4-(5)	-- —	7-9	+	Cy
5/3/?/2 —	-- ?	7	+	Cy
3/3/2/2 1-2; 3-4	-- ?	6	+	Ct
5/3/1-2/2 —	-- +	6-7	+	Ct
4/3/1/2 1-2	-- ?	7	+	Ct

from as few as 3 in some acanthoclinids to 89 in some cepolids. Within families, the range of dorsal fin ray counts may be relatively restricted as in the Lutjanidae (X-XII, 10-17) or quite broad, as in the Sciaenidae (VII-XV-1, 17-46).

In most percoids the spinous and soft portions of the dorsal fin are continuous, but gradual shortening of the posteriormost spines results in a variously developed cleft or apparent separation. Where this cleft is present, the ultimate spine is notably longer than the penultimate and is considered to form the first element of the soft dorsal portion of the fin. Some groups (e.g., Pseudochromidae, Grammatidae, Plesiopidae, Priacanthidae, Cepolidae) do not develop this cleft. Others, such as the Acropomatidae, Ambassidae, Apogonidae, Emmelichthyidae, Enoplosidae and Epigonidae have such a well-developed cleft that the spinous and soft portions of the fin appear completely separate. Pterygiophores usually continue beneath the resultant gap and may even bear minute spines. The Mullidae and Echeneididae are exceptional in having no pterygiophores below this gap. Extreme separation of the spinous and soft dorsal fins occurs only in the Echeneididae, where the spinous dorsal fin has been modified as an attachment disc and has moved far forward to cover the flattened cranium.

The anal fin of percoids is less variable in form and composition than the dorsal fin. The most common, and apparently primitive condition is three anal spines. The first anal pterygiophore is larger than the succeeding pterygiophore and bears the first two spines in supernumerary (non-serial) association and the third in serial association (see Johnson, 1980). Scatophagids and some chaetodontids and pomacanthids have four spines, the first two supernumerary. Centrarchids have from two to eight spines, pentacerotids from two to six and gerreids from three to five, all with the first two supernumerary. The only other percoids characterized by more than three anal spines (eight to eleven) are the Acanthoclinidae, where one or two may be supernumerary. Several groups have fewer than three anal spines, and, as in the dorsal fin, it is important to understand the nature of this reduction. Apogonids, for example, have only two spines and only one of these is supernumerary, suggesting that the anteriormost spine was lost. The mesopelagic epigonines (*sensu* Fraser, 1972a) have usually been treated as a subfamily of the Apogonidae, for they also have only two anal spines. The epigonine anal spines, however, are both supernumerary (as are those of the Sciaenidae), suggesting that the usually spinous third (serial) element has not transformed into a spine. Hence, the two anal spine conditions of epigonines and apogonids are not homologous. In bathylupeids, the single anal spine is serially associated with the first pterygiophore, suggesting that the first two spines have been lost. Only a few groups, Bramidae, Caristiidae, Congrogadidae, Coryphaenidae and some cepolids and grammistine serranids, lack anal spines. The presence of 1-3 supernumerary elements on the first pterygiophore in all these groups indicates transformation rather than loss of the pre-existing spines. Anal soft rays range in number from 4 in the Acanthoclinidae to 101 in the Cepolidae and, with some exception, the range of variability within families is comparable (frequently within two or three rays) to that of the dorsal soft rays.

Predorsal bones.—In most percoids, one to three strut-like bones precede the anteriormost pterygiophores of the dorsal fin. It has been proposed (Smith and Bailey, 1961), but never conclusively demonstrated, that these predorsal bones were derived from true pterygiophores that once bore spines or rays, but Fraser

TABLE 120. CONTINUED.

	Vertebrae	Dorsal fin	TRISEG. PTERYG. D — A	Pelvic fin	Predorsal formulae	CAUDAL FIN Principal
		Anal fin (SS)	Stay			Procurent
Centropomidae	10 + 14 11 + 14	<u>VII-VIII, 8-13</u> <u>III, 6-9 (2)</u>	$\frac{0-5}{0-4} +$	1, 5	0/0/0+2/1+1/ 0/0/0+1/1+1/	$\frac{9+8}{8-12+7-11}$
Cepolidae						
Cepolinae	12 + 44-66 14 + 55 16 + 53	<u>0-III, 65-89</u> <u>0-I, 62-101</u>	$\frac{0}{0} +$	1, 5	//2/1/	$\frac{6-7+6}{1-2+1-2}$
Owstoniinae	11 + 17 13 + 16 14 + 16	<u>III-IV, 21-27</u> <u>I-II, 14-19</u>	$\frac{0}{0} +$	1, 5	//2/1/	$\frac{8+7}{3-4+3-4}$
Chaetodontidae	10 + 14 11 + 13	<u>VI-XVI, 15-30</u> <u>III-V, 14-23 (2)</u>	$\frac{0}{0} -$ $\frac{0}{0} - (+)$	1, 5	0/0+2/1/ 0/2/1/1/	$\frac{9+8}{2-4+2-3}$
Cheilodactylidae	14 + 21	<u>XIV-XXII, 15-39</u> <u>III, 6-19 (2)</u>	$\frac{0}{0} +$	1, 5	0+0/2+1+1/1/ 0+0/2+1/1+1/	$\frac{8+7}{9-11+8-10}$
Chironemidae	13 + 20 14 + 19	<u>XIV-XVI, 15-21</u> <u>III, 6-8 (2)</u>	$\frac{0}{0} +$	1, 5	0/0/2+1/1/	$\frac{8+7}{13-16+10-12}$
Cirrhitidae	10 + 16	<u>X, 11-17</u> <u>III, 5-7 (2)</u>	$\frac{0}{0} +$	1, 5	0/0+0/2/1+1/ 0/0/0+2/1+1/	$\frac{8+7}{9-14+10-13}$
Congrogadidae	12-19 + 34-64	<u>0-II, 33-76</u> <u>28-63</u>	$\frac{0}{0} -$	1, 2-4 or absent	0/0/0/P+1 0/0//P+1 0/0//P+P ///P+P/	$\frac{4-6 \text{ br}+4-8 \text{ br}}{0-4+0-3}$
Coracinidae	10 + 15	<u>X, 18-23</u> <u>III, 13-14 (2)</u>	$\frac{10}{6} +$	1, 5	0/0/0+2/1+1/	$\frac{9+8}{9+8}$
Coryphaenidae	13-15 + 17-19 T:30-34	<u>52-66</u> <u>23-31 (2)</u>	$\frac{0}{0} -$	1, 5	1-3+1+1+1, etc./1/1/	$\frac{9+8}{10-14+10-14}$
<i>Datnioides</i>	10 + 14	<u>XII, 15</u> <u>III, 9 (2)</u>	$\frac{5}{1} +$	1, 5	0/0/0+2/1/	$\frac{9+8}{6+7}$
Dinolestidae	10 + 17	<u>VIII-I, 18-19</u> <u>I, 26-27 (1)</u>	$\frac{0-1}{0-1} +$	1, 5	0/0/0+1/1+1/ 0/0/0/1+1/	$\frac{9+8}{11+11}$
<i>Dinoperca</i>	10 + 16	<u>XI, 17-19</u> <u>III, 11-13 (2)</u>	$\frac{4}{3} +$	1, 5	0/0/0+2+1/1/	$\frac{9+8}{13+12}$
Drepanidae	10 + 14	<u>XIII-IX, 19-22</u> <u>III, 17-19 (2)</u>	$\frac{0 (+)}{0} -$	1, 5	0/0+0/2/1+1/	$\frac{9+8}{5+4}$
Echeneididae	12-18 + 14-22 T:26-40	<u>IX-XXVIII-17-42</u> <u>II, 14-36 (1)</u>	$\frac{0}{0} -$	1, 5	absent; D ₁ on head	$\frac{9+8}{8-13+7-13}$
Emmelichthyidae	10 + 14	<u>XI-XIV, 9-12</u> <u>III, 9-11 (2)</u>	$\frac{6-8}{6-8} +$	1, 5	0/0/0+2/1/	$\frac{9+8}{7-8+7-8}$
Enoplosidae	10 + 16	<u>VIII-I, 14-15</u> <u>III, 14-15 (2)</u>	$\frac{1-7}{4-8} +$	1, 5	0/0/0+2/1+1/	$\frac{9+8}{5-6+5-6}$
Ehippididae	10 + 14	<u>V-IX, 18-40</u> <u>III, 15-28 (2)</u>	$\frac{0 (11*)}{0 (11*)} - (+)$ *Ehippus	1, 5	0/0+0/2/1+1/ 0+0+0//2/1+1/ 0+0/2/1+1/ 0/0/0+1/1/ 0+0/0/P/1	$\frac{9+8}{3-7+3-6}$
Epigonidae	10 + 15 11 + 14	<u>VII-VIII-1, 7-10</u> <u>I-III, 7-9 (1-2)</u>	$\frac{0-1}{0-1} +$	1, 5	0/0/0+2/1+1/ /0+0/0+2/1+1/ /0+0/0+1/1/	$\frac{9+8}{9-10+7-10}$
Gerreidae	10 + 14	<u>IX-X, 9-17</u> <u>III-V, 13-17 (2)</u>	$\frac{0-2}{0-2} +$	1, 5	0/0/0+2/1+1/	$\frac{9+8}{9-11+9-10}$

TABLE 120. CONTINUED. EXTENDED.

CAUDAL SKELETON H/E/U/Ah H Fusions	Proc spur FU3 cart.	BR	IAC	Scales
<u>5/2-3/1-2/2</u> —	++ +	7	+	Ct
<u>2-4/1-2/1/2?</u> (1-2; 3-4; 5 absent)	-- ?	6	+	Cy
<u>3-4/3/1/2</u> (1-2; 3-4)	-- —	6	+	Cy
<u>5/3/2/2</u> —	-- —	6	+	Ct
<u>5/2-3/1/2</u> —	-- —	3-6	—	Cy
<u>5/3/1/2</u> —	-- ?	6	—	Cy
<u>5/3/2/2</u> —	-- +	6	r or —	Cy
<u>2/0-2/0/0-1</u> pH--1-2; 3-4-UR	-- —	6	—	Cy
<u>5/3/2/2</u> —	++ ?	6	+	Ct
<u>3/1/1/2</u> 1-2; 3-4	-- —	7	+	Cy
<u>5/3/2/2</u> —	++ +	6	+	Ct
<u>5/3/2/2</u> —	++ ?	7	+	Cy
<u>5/3/2/2</u> —	++ —	7	+	Ct
<u>5/2-3/2/2</u> —	++ +	6	+	Cy
<u>5/2/1/1-2/</u> —	- + (-) —	8-11	—	Cy
<u>5/3/2/2</u> —	++ ?	7	r or —	Ct
<u>5/3/2/2</u> —	++ ?	7	+	Cy
<u>4-5/3/2/2</u> (2-3)	+ + (- -)* (+) * <i>Rhinoprenes</i>	6	—	Ct or Cy
<u>5/3/2/2</u> —	++ +	7	+	Ct or Ct'
<u>3 or 5/3/2/2</u> (1-2; 3-4)	++ +	6	+	Ct

(1972a) argued that the first three predorsal elements of percoids may represent supraneurals. Ahlstrom et al. (1976) recognized the importance and utility of considering patterns of predorsal bones in early life history studies, and further developmental studies could resolve the origin of these elements.

The most common and presumably primitive number of predorsal bones in percoids is three; Table 120 shows that over half of 91 percoid groups (families and *incertae sedis* genera) have three predorsal bones exclusively, with three predorsals occurring in at least some members of 66 groups. The first dorsal pterygiophore inserts in the third interneural space in at least some members of 69 groups, bears two supernumerary spines in some members of 69 groups and exhibits both conditions in 57 groups. Therefore, the most common and ostensibly primitive predorsal formulae (using that defined by Ahlstrom et al., 1976) for the Percoidei are 0/0/0+2/ and 0/0+0/2/. The 0/0/1 pattern, considered by Smith and Bailey (1961) to be primitive for percoids occurs in only six families, frequently in the more derived members. Furthermore, Fraser (1972a) noted that derivation of the 0/0/0+2/ or 0/0+0/2/ patterns from the 0/0/1 pattern by backward shift of the first dorsal spine, hypothesized by Smith and Bailey (1961), is untenable and inconsistent with pterygiophore interdigitation. On the other hand, the 0/0/0+2/ pattern could be easily derived by a posterior shift of the first dorsal spine in the 0/0/1+1/ pattern that characterizes many beryciforms, including holocentrids and diretids. This latter pattern is found among percoids only in some ambassids.

Departures from the primitive predorsal pattern have apparently arisen independently in many families. In anterior shifts of the dorsal fin origin a compound first pterygiophore with two supernumerary spines is frequently retained, but it is invariably absent in posterior shifts. A possible conclusion is that forward shifts result from anterior displacement of the pterygiophores, whereas posterior shifts result only from loss of spines. Reductions in numbers of predorsal bones to fewer than three are almost certainly the result of simple losses as opposed to transformations, even when these reductions are accompanied, as they are occasionally (e.g., Chaetodontidae, Scatophagidae, Pentacerotidae, Priacanthidae), by a forward shift of the dorsal fin origin. Transformations of pre-existing predorsal bones to spinous pterygiophores would require the unlikely addition of *de novo* spines and distal radials, and modification of musculature. More than three "predorsal bones" are found in at least some members of 13 percoid groups, with a corresponding posterior shift of the dorsal fin origin. The additional elements are usually distinguishable from the anterior three ("true") predorsals. In *Bathyclupea*, Braminae, some carangids, Congrogadidae, *Mene*, *Neoscorpis*, *Platax*, some pempheridids and Toxotidae, these additional spineless elements (designated P in Table 120) resemble pterygiophores, may have separate distal elements, and often articulate with succeeding similar elements or with the anterior-most spine-bearing pterygiophore. In *Bathyclupea* and Toxotidae, they are also separated from the true predorsals by one interneural space. In the remaining groups with more than three "predorsals" (some percichthyids and centrarchids, *Brinkmanella* and *Leptobrama*), the additional elements are not morphologically distinguishable from the anterior three, but, as in the other groups, the dorsal fin originates posterior to the third interneural space (except in *Brinkmanella*), and it seems likely that these elements were also derived from pre-existing pterygiophores. Studies of the sequence of development of predorsal

TABLE 120. CONTINUED.

	Vertebrae	Dorsal fin	TRISEG. PTERYG. D A Stay	Pelvic fin	Predorsal formulae	CAUDAL FIN Principal
		Anal fin (SS)				Procurent
Gigantiidae	10 + 15	<u>IX, 13</u> III, 8 (2)	$\frac{11}{6} +$	I, 5	0/0/2/1+1/	$\frac{9+8}{10+9}$
Girellidae	11 + 16 11 + 17 14 + 20	<u>XII-XVI, 11-17</u> III, 10-13 (2)	$\frac{0-1}{0-1} +$	I, 5	0/0+0/2/1+1/ 0/0/2/1+1/	$\frac{9+8}{9-14+8-12}$
Glaucosomatidae	10 + 15	<u>VIII, 11</u> III, 9 (2)	$\frac{10}{7} +$	I, 5	0/0/0+2/1+1/	$\frac{9+8}{7-8+7-8}$
Grammatidae	10 + 15 10 + 17 10 + 18	<u>XII-XIV, 8-10</u> III, 7-11 (2)	$\frac{0}{0} +$	I, 5	0/0/0+2/1+1/ 0/0/0+1/1+1/	$\frac{8-10+7-9}{2-8+2-7}$
Haemulidae	10 + 16 11 + 16	<u>IX-XIV, 11-26</u> III, 6-13 (2)	$\frac{0}{0} +$	I, 5	0/0/0+2/1/ 0/0+0/2+1/1/ 0/0+0/2/1/	$\frac{9+8}{9-14+8-13}$
Haplogeny	10 + 14	<u>XI-XIV, 14-19</u> III, 9-13 (2)	$\frac{0}{0} +$	I, 5	0/0+0/2/1+1/	$\frac{9+8}{6+5-6}$
Hemilutjanus	10 + 15	<u>X, 10-11</u> III, 9 (2)	$\frac{6}{6} +$	I, 5	0/0/0+2/1+1/	$\frac{9+8}{11+10}$
Howella	10 + 16	<u>VIII-1, 9</u> III, 7 (2)	$\frac{0}{0} +$	I, 5	0/0/0+2/1+1/	$\frac{9+8}{9-10+9-10}$
Inermiidae	12 + 14 13 + 13	<u>X-II or XVII, 9-10</u> III, 8-10 (2)	$\frac{0}{0} +$	I, 5	/0/0+2/1/ /0+0/0+2/1/	$\frac{9+8}{10-12+10-12}$
Kuhliidae	10 + 15	<u>X, 9-12</u> III, 9-13 (2)	$\frac{4-7}{5-8} +$	I, 5	0/0/0+2/1+1/ 0/0/0+2/1/	$\frac{9+8}{11-13+10-12}$
Kyphosidae	10 + 15 10 + 16	<u>X-XII, 11-15</u> III, 10-16 (2)	$\frac{1-7}{3-5} +$	I, 5	0/0/0+2/1/	$\frac{9+8}{8-10+8-10}$
Lactariidae	10 + 14	<u>VII-VIII-1, 20-22</u> III, 25-28 (2)	$\frac{3-5}{2-3} +$	I, 5	0/0/0+2/1+1/	$\frac{9+8}{9+8}$
Lateolabrax	17 + 18	<u>XII-XIV, 12-16</u> III, 7-10 (2)	$\frac{6}{3} +$	I, 5	0/0/0+1/1+1/	$\frac{9+8}{13+12-13}$
Latrididae	14 + 21	<u>XIV-XXIII, 23-40</u> III, 18-35 (2)	$\frac{0}{0} +$	I, 5	0/0+2/1+1/1/ 0+0/2/1+1/1/	$\frac{8+7}{14+12}$
Leiognathidae	10 + 14	<u>VIII, 15-16</u> III, 14 (2)	$\frac{15-16}{13} +$	I, 5	0/1/1/1/	$\frac{9+8}{9-10+7-9}$
Leptobramidae	10 + 14	<u>IV, 16-18</u> III, 26-30 (2)	$\frac{0}{0} +$	I, 5	0/0/0/0//P/P/P/P/P/1/1+1+1/	$\frac{9+8}{6-8+7}$
Lethrinidae	10 + 14	<u>X, 9-11</u> III, 8-10 (2)	$\frac{2-3}{2-3} +$	I, 5	0/0+0/2+1/1/	$\frac{9+8}{7-9+7-9}$
Lobotidae	11 + 13 12 + 12	<u>XII, 15-16</u> III, 11 (2)	$\frac{0}{0} +$	I, 5	0/0/0+2/1+1/	$\frac{9+8}{3-5+3-5}$
Lutjanidae	10 + 14	<u>X-XII, 10-17</u> III, 7-11 (2)	$\frac{1-7}{1-7} +$	I, 5	0/0/0+2/1+1/ 0/0+0/2/1+1/	$\frac{9+8}{8-13+8-13}$
Malacanthidae	10 + 14 11 + 14 11 + 16	<u>I-X, 14-60</u> I-II, 11-55 (1-2)	$\frac{?-17}{?-14} +$	I, 5	0/0/2/1+1/ /0+0/2/1+1/ //2+1+1+1+1/1+1+1/	$\frac{9+8}{10-13+9-13}$
Menidae	10 + 14	<u>IV, 38-42</u> III, 28-32 (2)	$\frac{0}{0} +$	I, 5	0/0+0/P/1/	$\frac{9+8}{4+3-4}$
Microcanthidae	10 + 15	<u>X-XI, 16-22</u> III, 13-19 (2)	$\frac{10-16}{10-15} +$	I, 5	0/0+0/2/1+1/	$\frac{9+8}{7-10+7-10}$
Monodactylidae	10 + 14 10 + 15	<u>VII-IX, 26-36</u> III, 27-37 (2)	$\frac{0-2}{0-1} +$	I, 5	0/0/0+1/1+1/	$\frac{9+8}{6+5-6}$
Moronidae	11 + 14 12 + 13	<u>VIII-X-1, 10-13</u> III, 9-12 (2)	$\frac{2-4}{2-4} +$	I, 5	0/0/0+2/1+1/ 0/0/0+2/1/ 0/0/0/2+1/	$\frac{9+8}{10-13+9-13}$

TABLE 120. CONTINUED. EXTENDED.

CAUDAL SKELETON H/E/U/Ah H Fusions	Proc spur PU3 cart.	BR	IAC	Scales
<u>5/3/1/2</u> —	— — ?	7	+	Ct
<u>5/3/1/2</u> —	—(r) — +	6	+	Ct
<u>5/3/2/2</u> —	+ + —	7	+	Ct
<u>2-3/3/0/2</u> 1-2; 3-4-UR 5 absent	— — +	6	+	Ct
<u>5/3/2/2</u> —	+ + ?	7	+	Ct
<u>5/3/2/2</u> —	— — ?	7	+	Ct
<u>5/3/2/2</u> —	+ + ?	7	+	Ct
<u>5/3/2/2</u> —	— — +	7	+	Ct'
<u>3/3/2/2</u> 1-2; 3-4	+ + ?	7	+	Ct
<u>5/3/2/2</u> —	+ + +	6	+	Ct
<u>5/3/2/2</u> —	+ + +	7	+	Ct
<u>3/3/2/2</u> 1-2; 3-4	+ + +	7	+	Cy
<u>5/3/2/2</u> —	+ + +	7	+	Ct
<u>4/3/1/2</u> 3-4	— — ?	6	?	Cy
<u>3/3/1/2</u> 1-2; 3-4	— — —	5	—	Cy
<u>4/3/2/2</u> 3-4	+ + ?	6	+	Ct
<u>5/3/2/2</u> —	— — ?	6	+	Ct
<u>5/3/2/2</u> —	+ — —	6	+	Ct
<u>3 or 5/3/2/2</u> (1-2; 3-4)	— — —	7	+	Ct
<u>5/3/2/1-2</u> —	— — +	6	+	Ct
<u>2/3/0/0/</u> 1-2-3-4-UR	— — —	7	+	Cy
<u>5/3/2/2</u> —	+ + (+)	7	+	Ct
<u>2-5/3/2/2</u> (1-2; 2-3; 3-4)	+ — +	7	+	Ct
<u>5/3/2/2</u> —	+ + +	7	+	Ct

bones in relation to the development of the dorsal fin may prove useful in determining the homologies of these additional elements as well as the first three predorsals.

Caudal skeleton.—The primitive percoid caudal skeleton consists of one parhypural with a well-developed hypurapophysis, five hypurals, two pairs of uroneurals, three epurals, one ural centrum, a low neural crest on PU2 and autogenous haemal spines on PU2 and PU3. This configuration is found in at least some members of 54 percoid groups.

The most common reductions involve fusion of hypurals one and two and hypurals three and four and loss of the posterior uroneural pair. Loss of one epural occurs in only 14 groups, and epurals are completely lacking only in some congrogadids. More extreme reductions, including various combinations of fusions of the hypurals with the parhypural and/or urostyle, loss or fusion of the anterior uroneural pair and fusion of the autogenous haemal spines, occur in only a few groups: Acanthoclinidae, some apogonids, Congrogadidae, Grammatidae, Menidae, Mullidae, Opstognathidae, Plesiopidae, and Pseudochromidae.

The second preural centrum bears a full neural spine in only two groups, Echeneididae and Nandidae, except for occasional anomalous specimens. This full neural spine must be secondarily derived in the echeneidids because these fishes are unquestionably closely related to other percoids that bear the usual reduced neural crest on PU2 (see discussion on utility of larval morphology). Unfortunately, evidence for the origin of this *de novo* spine in echeneidids is lacking. Although it may represent a captured first epural (there are only two in echeneidids), it is attached and of full length at its earliest appearance in ontogeny. Another possibility is that the second preural centrum of other percoids has been lost in echeneidids, so that the last centrum bearing a full neural spine actually corresponds to PU3. However, presence of the usual autogenous haemal spines on both PU2 and PU3 in echeneidids refutes this hypothesis. The significance of a full neural spine on PU2 in the Nandidae is unclear, since the affinities of this family with the Percoidei remain problematic.

The presence of a procurrent spur and of radial cartilages anterior to the neural and haemal spines of PU3 are probably primitive features (Johnson, 1975, 1983). The procurrent spur is developed to some extent in 50 percoid groups, all but ten of which have a primitive caudal complex. Reductions among these ten groups usually involve only simple hypural fusion. The procurrent spur is never present in groups with fewer than 9 + 8 principal rays. Third preural radial cartilages are found in 45 of 66 groups examined for them, about half of which have primitive caudal complexes.

Vertebral number.—Vertebral number ranges from 23 to about 78 in percoids. Gosline (1968, 1971) noted that the "basal number" of vertebrae in percoids is 24–25 (10 + 14–15), and this number characterizes 45 of the 91 groups treated in Table 120; 63 groups have 24–27 vertebrae. Twenty-two groups have vertebral counts greater than thirty, but only five have more than 40 vertebrae. Only priacanthids and scatophagids have fewer than 24 (10 + 13).

Gill arches.—Primitively, percoid gill arches contain the following elements: one basihyal, four basibranchials (the fourth cartilaginous), three pairs of hypobranchials, five pairs of ceratobranchials, four pairs of epibranchials, four pairs of

TABLE 120. CONTINUED.

	Vertebrae	Dorsal fin	TRISEG. PTERYG. D — Stay A	Pelvic fin	Predorsal formulae	CAUDAL FIN
		Anal fin (SS)				Principal
Mullidae	10 + 14	$\frac{\text{VII-VIII}-\text{I}, 8-9}{\text{I-II}, 5-8 (0-1)}$	$\frac{0}{0} +$	I, 5	0/0/0+2/1+1/ 0/0/0+1/1+1/ 0/0/2/1+1/	$\frac{8+7}{8-10+8-10}$
Nematistiidae	10 + 14	$\frac{\text{IX}, 26-29}{\text{III}, 16-17 (2)}$	$\frac{1}{1} +$	I, 5	0+0+0//2/1/	$\frac{9+8}{9-10+8-9}$
Nemipteridae	10 + 14	$\frac{\text{X}, 9-10}{\text{III}, 7-8 (2)}$	$\frac{1}{1} +$	I, 5	0/0/2+1/1/	$\frac{9+8}{8-11+8-11}$
<i>Neoscorpis</i>	10 + 15	$\frac{\text{VI-VIII}, 20-22}{\text{III}, 23-26 (2)}$	$\frac{14}{11} +$	I, 5	0/0/0+P/P/P+1/	$\frac{9+8}{9+8}$
Opistognathidae	10 + 15-21 11 + 16-23 12 + 18-19 13 + 18-20	$\frac{\text{X-XII}, 11-22}{\text{II-III}, 10-20 (1-2)}$	$\frac{0}{0} +$	I, 5	/0+0/1/1+1/ /0/1/1+1/ //1/1+1/	$\frac{6-7+6-7}{3-8+3-7}$
Oplegnathidae	10 + 15	$\frac{\text{XI-XII}, 11-22}{\text{III}, 11-18 (2)}$	$\frac{11}{8} +$	I, 5	0/0+0/2/1+1/ 0/0/2/1+1/	$\frac{9+8}{9+8}$
Ostracoberycidae	10 + 15 10 + 16	$\frac{\text{IX}, 8-10}{\text{III}, 7-8 (2)}$	$\frac{4-7}{4} +$	I, 5	0/0/0+2/1+1/	$\frac{9+8}{10-12+10-11}$
Parascorpididae	12 + 15	$\frac{\text{XI-XII}, 14-17}{\text{III}, 13-15 (2)}$	$\frac{13}{11} +$	I, 5	0/0+0/2+1/1/	$\frac{9+8}{11+9}$
Pempheridae	10 + 15	$\frac{\text{IV-VII}, 7-12}{\text{III}, 17-45 (2)}$	$\frac{0}{0} +$	I, 5	0/0/0+1/1+1/ 0/0/0+1/1/ 0/0/0+P/1+1	$\frac{9+8}{3-7+3-7}$
Pentacerotidae	12 + 12 12 + 13 13 + 11 13 + 12 13 + 13 13 + 14	$\frac{\text{IV-XV}, 8-29}{\text{II-VI}, 6-17 (?-2)}$	$\frac{0}{0} +$	I, 5	0/0+2/1/ 0/0/2/1+1/	$\frac{9+8}{3-7+3-6}$
Percichthyidae	10-15 + 15-23 T:25-36	$\frac{\text{VII-XI}, 8-18}{\text{III}, 7-13 (2)}$	$\frac{0-16}{0-15} +$	I, 5	variable: 0-5 predorsals 0-2 sup. spines	$\frac{9+8}{5-16+5-14}$
<i>Gadopsis</i>	21 + 26	$\frac{\text{X-XII}, 25-28}{\text{III}, 17-19 (2)}$	$\frac{0}{0} -$	I, 1	//0/0/1/1/	$\frac{9+8}{5+5}$
Percidae	T:31-50	$\frac{\text{V-IXX}-0-\text{III}, 7-24}{\text{I-II}, 4-15 (1-2)}$	$\frac{0}{0} + (-)$	I, 5	0/1/1/1/ /1/1/1/ ///1/1/ ////1/1/	$\frac{8-9+7-8}{10-15+8-13}$
Plesiopidae	10 + 15 10 + 16 12 + 25	$\frac{\text{IX-XV}, 7-21}{\text{III}, 8-23 (2)}$	$\frac{6-16}{6-19} +$	I, 4	0/0/0+2/1+1/ 0/0/2/1+1/ 0/0/0+1/1+1/ 0/0/1/1+1/	$\frac{9-10+8-9}{3-10+3-9}$
Pomacanthidae	10 + 14	$\frac{\text{IX-XV}, 15-33}{\text{III-IV}, 14-25 (2)}$	$\frac{0}{0} +$	I, 5	0/0/2/1+1/ 0//2/1+1/	$\frac{9+8}{4+3-4}$
Pomatomidae	11 + 15	$\frac{\text{VII-IX}, 23-28}{\text{III}, 22-28 (2)}$	$\frac{2-3}{3} +$	I, 5	0/0/0+1/1+1/	$\frac{9+8}{9-10+8-9}$
<i>Polyprion</i>	13 + 14	$\frac{\text{XI-XII}, 11-13}{\text{III}, 8-10 (2)}$	$\frac{8-10}{5-6} +$	I, 5	0/0/0+2/1+1/	$\frac{9+8}{8-9+7-8}$
Priacanthidae	10 + 13	$\frac{\text{X}, 11-15}{\text{III}, 9-16 (2)}$	$\frac{0-1}{0-1} +$	I, 5	0+2/1/1/1/ 2/1/1/1/	$\frac{8+8}{4-6+4-6}$
Pseudochromidae	10-13 + 16-25 T:26-35	$\frac{\text{I-III}, 21-37}{\text{I-III}, 13-30}$	$\frac{0-\text{many}}{0-\text{many}} +$	I, 3-5	0/0/0+2/1+1/ 0/0/0+1/1+1/ 0/0/2/1+1/ 0/0/1/1+1/	$\frac{7-9+7-8}{5-7+5-7}$

TABLE 120. CONTINUED. EXTENDED.

CAUDAL SKELETON H/E/U/Ab H Fusions	Proc spur PU3 cart.	BR	IAC	Scales
<u>3/2/1-2/2</u> 1-2; 3-4-UR	-- ?	4	-	Ct
<u>3/3/2/2</u> 1-2; 3-4	-- -	7	+	Cy
<u>5/3/2/2</u> -	-- +	6	r or -	Ct
<u>5/3/2/2</u> -	++ -	6	+	Ct
<u>2-3/3/0/1</u> pH-1-2; 3-4-UR; (5 absent)	-- +	6	+	Cy
<u>5/3/2/2</u> -	++ ?	7	+	Ct
<u>5/3/2/2</u> -	++ +	7	+	Ct'
<u>5/3/2/2</u> -	++ ?	7	+	Ct
<u>3 or 5/3/1-2/0-2</u> (1-2; 3-4)	-(+) + +	7	+	Ct or Cy
<u>5/3/1/2</u> -	+ -(+) +	7	+	Ct
<u>?/2-3/1-2/2</u> ?	++ (-) + (-)	5-7	+	Ct or Cy
<u>5/2/1/2</u> -	-- -	7	+	Cy
<u>5/3/1/2</u> -	-- + (-)	5-8	+	Ct
<u>3/3/0-2/1</u> 1-2-(pH); 3-4-UR	-- +	6	+	Ct
<u>5/3/2/2</u> -	-- +	6	+	Ct'
<u>5/3/2/2</u> -	++ -	7	+	Cy
<u>5/3/2/2</u> -	++ ?	7	+	Ct
<u>5/3/2/2</u> -	-- -	6	-	Ct'
<u>3/2-3/0/0-1/</u> (pH)-1-2; 3-4-UR	-- +	6	-	Ct

pharyngobranchials, and an interarcual cartilage between the uncinat process of epibranchial 1 and pharyngobranchial 2. The first pharyngobranchial is rod-like and serves to suspend the dorsal gill arches from the neurocranium. The fourth pharyngobranchial is reduced and cartilaginous, but consistently bears a well-developed dermal tooth plate, as do the second and third pharyngobranchials and the fifth ceratobranchials. Small tooth-plates on the second and third epibranchials are variously present or absent.

Reductive departures from the primitive branchial complex are few and involve only the basihyal, first pharyngobranchial or interarcual cartilage. The basihyal is reduced or absent in ephippidids. Pseudochromids lack a first pharyngobranchial (Springer et al., 1977). Of 88 percoid groups examined for it, only 13 lack a well-developed interarcual cartilage and at least three of these (Cirrhitidae, Emmelichthyidae and Nemipteridae) may have a vestigial element. The remaining eleven groups completely lack the interarcual cartilage, but most have an uncinat process with the cartilaginous tip separated by a decided gap from the second pharyngobranchial and frequently pointing away from it. This condition differs from the primitive state (as represented in most beryciforms) wherein the uncinat process of the first epibranchial directly contacts that of the second pharyngobranchial, and suggests that these percoids have secondarily lost the interarcual cartilage. A condition resembling that of the beryciforms was observed among percoids only in some anthiine serranids, where it must be secondary. In eche-neidids the uncinat process of the first epibranchial also articulates directly with that of the second, but there is a concomitant extreme reduction of the main arm of the first epibranchial not seen in beryciforms. Again this condition must be derived if the relationships of the eche-neidids are as postulated here (see discussion on utility of larval morphology).

Scales.—The unpublished work of McCully (1961) on comparative anatomy of serranid scales provides an excellent illustration of the wealth of information available in the scales of percoid fishes that has largely been ignored in systematic studies. More recent work on ctenoid scales of other groups (DeLamater and Courtenay, 1973a, b, 1974; Hughes, 1981) using scanning electron microscopy also demonstrates the systematic value of ctenoid scales. Details of the scale morphology of most percoids are unknown. On a gross level, three basic scale types (Ct, Ct' and Cy in Table 120) are found among percoids. Although beryciforms and some myctophids are said to have ctenoid scales, these scales (Ct') differ from the type possessed by most percoids and other perciforms (Ct). In beryciforms and myctophids the "ctenii" are continuous spinous projections from the lateral surface and posterior margin of the scale. A few percoids (Bramidae, Epigonidae, *Howella*, Pomacanthidae, Priacanthidae, Ostracoberycidae and Scatophagidae) possess similar scales that may represent retention of the plesiomorphic beryciform condition, or may have been secondarily derived. In the "true" ctenoid scale that characterizes most percoids (59 groups), the ctenii are separate bony plates, or scalelets (McCully, 1961, 1970), that are continually added in the posterior field as the scale grows. In most groups the posterior field becomes filled with remnants of old ctenii, the tips of which are amputated (or, more likely, resorbed), as each new row of ctenii is added. In a few groups, however (e.g., anthiine serranids and callanthiids), only a primary and secondary row of marginal ctenii are evident. This second variation of "true" ctenoid scale also characterizes

TABLE 120. CONTINUED.

	Vertebrae	Dorsal fin	TRISEG. PTERYG	Pelvic fin	Predorsal formulae	CAUDAL FIN
		Anal fin (SS)	D — A			Stay
						Procurent
Rachycentridae	11 + 14	VII-IX, 26-34 I-II, 22-28 (1)	0 0	-	1, 5	/1+1/1/1/ 15-16+12-14
Scatophagidae	10 + 13	XI-XII, 16-18 IV, 14-16 (2)	0 0	+	1, 5	0/0+2/1/1/ 4-6+4-5
Sciaenidae	10-15 + 12-18 T:24-29	VII-XV-1, 17-46 I-II, 5-23 (1-2)	0 0	+	1, 5	0/0/0+2/1+1/ //2+1+1+1, etc./ 9+8 7-10+6-9
Scombroptidae	10 + 16	VIII-IX-1, 12-13 II, 11-12 (1)	5 4	+	1, 5	0/0/0+2/1+1/ 9+8 11+10
Scorpididae	10 + 15 10 + 16	IX-X, 22-28 III, 17-28 (2)	7-18 9-22	+	1, 5	0/0/0+2/1+1/ 11-13+10-12
Serranidae	10 + 14 11 + 13 10 + 15 10 + 16 11 + 15 10 + 18	VI-XII, 9-24 or II-IV, 20-29 II-III, 6-22 (2) or 13-17 (1)	0-24 0-19	+	1, 5	0/0/0+2/1+1/ 0/0+0/2/1+1/ 0/0/2/1+1/ 0+0/2/1/1/ 0/0/1/1+1/ 0/0/P/1+1/ 0//P/1+1/ //1/1+1/ 8-9+7-8 3-12+3-10
Sillaginidae	14-20 + 19-27 T:33-44	X-XIII-1, 16-27 II, 14-26	0 0	+	1, 5	0/0/0/1+1/ 0/0/0/1/ 0//0/1/1+1/ 9+8 17-19+14-19
<i>Siniperca</i>	12 + 16 13 + 15 13 + 18	XI-XV, 10-17 III, 7-13 (2)	7-10 4-6	+	1, 5	0/0/0+2/1+1/ 0/0/0/2/1+1/ 9+8 6-12+6-12
Sparidae	10 + 14	X-XIII, 10-15 III, 7-14 (2)	1-4 1-4	+	1, 5	0/0+0/2+1/1/ 9+8 7-11+7-11
<i>Stereolepis</i>	12 + 14	XI-XII, 9-10 III, 7-9 (2)	6-8 3-6	+	1, 5	0/0+0/2/1+1/ 0/0/0+2/1+1/ 9+8 10-11+8-9
<i>Symphysanodon</i>	10 + 15	IX, 10 III, 7-8 (2)	2-3 2-3	+	1, 5	0/0/0+2+1/1/ 9+8 12-14+12-14
Teraponidae	10 + 15 10 + 16 10 + 17 11 + 14 11 + 16	XI-XIV, 8-14 III, 7-12 (2)	0 0	+	1, 5	0/0+0/2/1+1/ 0/0+0/1/1+1/ 0+0/0+2/1/1/ 9+8 9-10+5-8
Toxotidae	10 + 14	IV-VI, 11-14 III, 15-18 (2)	0 (+) 0	-	1, 5	0/0/0//P/P/1/ 0/0/0//P/1/ 0//0//P/P/1/ 9+8 4-5+4-5

Aphredoderus, gobies and some flatfishes, and the mechanism of growth of the posterior field is not understood. As shown by the authors mentioned above, there is extensive diversity in configuration and processes of formation of marginal and sub-marginal ctenii, and this diversity undoubtedly holds useful phylogenetic information.

The third major scale type found among percoids is the cycloid scale (Cy in Table 120), characteristic of most groups below the Percomorpha. Although the cycloid scales of some percoids may represent a plesiomorphic state, they are clearly secondary in a number of families where they occur only in some members (acanthoclinids, acropomatids, apogonids, ephippidids, pempheridids, percichthyids, sciaenids and serranids). Cycloid scales also characterize all members of two groups of percoid families,

each of which probably comprises a monophyletic lineage. The cirrhitoid fishes (Aplodactylidae, Cheilodactylidae, Chironemidae, Cirrhitidae, and Latrididae) have large cycloid scales of similar morphology, and the carangoid fishes (Carangidae, Coryphaenidae, Nematistiidae, Rachycentridae and Echeneidae) have very small adherent cycloid scales. Cycloid scales characterize five other families of moderate size, Ambassidae, Cepolidae, Congrogadidae, Leiognathidae and Opistognathidae. Otherwise, cycloid scales are restricted to a few monotypic families and *incertae sedis* genera (Bathyclupeidae, Caristiidae, Dinolestidae, Drepanidae, Enoplosidae, Lactariidae, Menidae, Pomatomidae, Scombroptidae and *Siniperca*). The widespread occurrence of true ctenoid scales in the Percoidae, including most of the less specialized forms, and the distribution of cycloid

TABLE 120. CONTINUED. EXTENDED.

CAUDAL SKELETON H/E/U/Ah H Fusions	Proc spur PU3 cart.	BR	IAC	Scales
<u>5/3/2/2</u> —	— + —	7	+	Cy
<u>5/3/1/2</u> —	— —	6	—	Ct'
<u>5/3/2/2</u> —	+ + (— —) ?	7	+	Ct or Cy
<u>5/3/2/2</u> —	+ + +	7	+	Cy
3 or 5/3/2/2 (1-2; 3-4)	+ + (+)	7	+	Ct
3 or 5/3/1/2 (1-2; 3-4)	— — —	6-7	+ (—)	Ct or Cy
<u>5/2-3/1-2/2</u> —	+ + +	6	+	Ct
<u>4-5/3/1/2</u> (3-4)	r(—) + —	7	+	Cy
3 or 5/3/2/2 (1-2; 3-4)	— — +	6	+	Ct
<u>5/3/2/2</u> —	+ + ?	7	+	Ct
<u>5/3/2/2</u> —	— + +	7	+	Ct
<u>5/3/2/2</u> —	+ + +	6	+	Ct
<u>5/3/0-1/2</u> —	+ — +	7	+	Ct

scales just described, suggests that cycloid scales in most percoids have been secondarily acquired.

DEVELOPMENT

Eggs

Most percoids have buoyant, spherical eggs about 1 mm in diameter, with a single oil globule. The total size range is about .5 to 4.6 mm, but eggs larger than 2 mm are found only in a few freshwater-associated groups, Centrarchidae, Moronidae, Percichthyidae, Percidae, *Siniperca* and Teraponidae, and in the marine Echeneididae (Table 121). Multiple oil globules occur in some centrarchids, percichthyids and sciaenids, and in *Hapalogenys*, moronids and *Polyprion*, but they are generally

fully coalesced by hatching. Most members of the three primary freshwater families, Centrarchidae, Percichthyidae and Percidae have demersal eggs as do some members of the Ambassidae and Teraponidae, however only six families of exclusively marine percoids are known to possess non-buoyant eggs. The Acanthoclinidae, Congrogadidae, Plesiopidae and Pseudochromidae have specialized demersal eggs with adhesive threads that bind them together in attached, sheet-like (Plesiopidae) or free, spherical (Acanthoclinidae and Pseudochromidae) masses that are guarded by the male. These eggs also have numerous small oil globules that gradually coalesce with a single, much larger globule. The possibility that these four families are closely related has remained unresolved (Böhlke, 1960a; Springer et al., 1977), but the similar egg morphology and parental care shared by them may represent synapomorphies not heretofore considered. The other two marine families with adhesive demersal eggs, Apogonidae and Opistognathidae are oral brooders, and oral brooding has also been reported for the plesiopid *Assessor* (Allen and Kuiter, 1976).

Larvae

Diversity of general body form and morphological specialization among the larvae of percoid fishes is extensive, and, as with the adults, no single feature shared by larval percoids characterizes the suborder. Representative postflexion larvae of 62 percoid groups are illustrated in Figs. 254-262. Larval serranids and carangids were excluded from these figures because they are illustrated elsewhere in this volume. I was unable to obtain specimens or illustrations of larvae of the remaining 30 groups and most are probably unknown, or at least undescribed. Of these, 19 are monotypic.

Larval body form ranges from elongate to deep-bodied, by the criteria of Leis and Rennis (1983), and frequently, but not always, reflects adult body form. Thus, some of the most deep-bodied percoid larvae are found among the Chaetodontidae, Pomacanthidae, Menidae, Bramidae, and Caristiidae, whereas the elongate Congrogadidae and Cepolidae have elongate larvae. On the other hand, the moderately elongate larvae of groups like the Girellidae or the Cirrhitidae are not particularly reflective of the adult body form, nor are the deeper-bodied larvae of the Emmelichthyidae.

In Table 121, selected aspects of known larvae of percoid families and *incertae sedis* genera are given. This table should prove a useful guide to identification of postflexion larval percoids at the family level, particularly when used in conjunction with the meristic data in Table 120 and the illustrations in Figs. 254-262. Features included in Table 121 are discussed below.

Fin development. — Formation of median fin rays occurs at very small sizes in most percoids. Flexion may begin as early as 2.5-3 mm and is complete in most groups by 4-5 mm, at which time the full complement of principal caudal rays is present. Dorsal and anal fin rays begin to form during or shortly after flexion and are usually complete, including spinous rays, by 5-8 mm. Size at flexion and completion of full median fin ray complements is relatively consistent within families, the range usually not varying more than 2 mm. Groups characterized by notably later flexion (6-18 mm) include the Caristiidae, Centranchidae, Centrarchidae, Cheilodactylidae, Girellidae, *Latolabrax*, *Morone*, Percichthyidae, Percidae, *Polyprion*, Scorpididae, Sillaginidae, and *Siniperca*. These groups also exhibit somewhat delayed dorsal and anal fin ray completion (7-18 mm). Among marine percoids, the most extreme delay in com-

TABLE 121. SELECTED EARLY LIFE HISTORY FEATURES OF PERCOIDEI. Parentheses enclose features known to characterize only some members of a group. Head spination abbreviations—Supraoccipital: S1—small peak-like crest; S2—S1 with serrations; S3—large vaulted spine-like crest with serrations; S4—low serrated median ridge; S5—entire surface rugose. Frontal: F1—entire surface rugose; F2—one or more parallel or converging serrated ridges; F3—serrated supraorbital ridges; F4—single spine on supraorbital ridge; F5—large posteriorly projecting serrated spine. Preopercle: P1—posterior margin with moderate to large simple spines; P2—P1 plus lateral ridge with one or more small simple spines; P3—P2 with spine at angle notably elongate; P4—P3 with marginal spines serrate; P5—posterior margin and sometimes lateral ridge with very small spines or serrations. Other bones with simple spines, serrations or serrated ridges: Op—opercle; Sb—subopercle; Io—interopercle; Ta—tabular; Pt—posttemporal; Scl—supracleithrum; Cl—cleithrum; La—lacrima; Co—circumorbitals; Na—nasal; Mx—maxillary shaft; D—dentary; Br—branchiostegals; Pe—pterotic; Pa—parietal; Sp—sphenotic. Sequence of completion of fin rays: A. D₂-A-D₁-P₂-P₁; B. D₁-P₂-D₂-A-P₁; C. P₁-P₂-D₂-A-D₁; D. P₁-D₂-A-D₁-P₂; E. A-D₂-P₂-P₁-D₁; F. P₂-D₂-A-D₁-P₁. Egg type: P—pelagic, buoyant; D—demersal; A—adhesive; M—egg mass; O—oral brooder.

Taxon	Text figures	Egg type	Size (mm)					Sequence of fin completion	Head spination	Other specializations
			Egg	Hatch	Flex	D & A rays complete	First scales			
Acanthoclinidae	255D	D, A, M	~1.4	~4.7	5-6	?	?	A	P5	None
Acropomatidae	254A-D	P	?	?	~4	~5	12-15	A	(S1), (S4), (F2), F3, (P4), (P5), Op, Sb, Io, Pt, Scl, (Pcl), (Co), (D), (Pe)	(D and P ₂ spines serrate)
Ambassidae	255A	(D, A) (P)	.7-8	1.8	~3.5	5.5-6	9-10	A	P5	None
Apogonidae	257D-G	D, A, M, O	<1	2.5-3	3-4	4-6	12 or >	A (B)	(S1), (S5), (F1), (P2), (P3), (P5), (Op), (Sb), (Pt) (...?)	(Elongate D spines and P ₂ rays)
Bramidae	261E	P	?	~3	4-7	6-10	7-10	C (D)	(F1), P1, Op, Sb, Io	Spinous scales (large P ₁ and P ₂)
Callanthiidae	255E-F	P	?	?	5	7	7-14	A	P2, Op, Sb, Io, Pt	None
Carangidae	—	P	.7-1.3	1-3.5	~3-5	~6-10	~7-14	A (D)	(S1), (F3), (F4), P3, (P4), Pt, Scl, (Pe)	(Elongate D spines and P ₂ rays)
Caristiidae	261D	P	1.1-1.3	2.3-2.9	~7	~8	?	A	P5	None
Centracanthidae	258J	P	1.1-1.3	2.3-2.9	6-7	8-9	?	A	P5	None
Centropomidae	260G	P	.7	1.4-1.5	3.6-3.8	~7	~14	A	P5	None
Centrarchidae	260A	D, A	.8-2.8	2.2-5.5	6-9	~7-13	~14-18	A	None	None
Cepolidae	262G	P	.7	<3	8-9	7-9	?	A	S3, F1, F3, P4, Scl, D	None
Chaetodontidae	262A-C	P	.7-9	1.5-2.0	4-5	5-8	7-11	A (B)	All exposed head bones thick and ru- gose. Pt and Scl ex- panded poste- riorly. P expanded to cover cheek and with broad flat spine poste- riorly.	(P ₂ spine long and serrate) (Ant. D spines long and ru- gose)
Cheilodactylidae	258E	P	.9-1	2.9-3.3	7-8	10-12	~10	A	None	Postlarvae deep, com- pressed, sil- very to 70- 90 mm
Cirrhitidae	258F	P	?	?	~4	~8	10 or <	A	P5	Chin barbel
Congrogadidae	255G	D, A, M	?	?	?	?	?	?	None	None
Coryphaenidae	261A	P	~1.6	~4	6.5-7.5	D 13-24 A 8-11	~25-30	E	F4, P2, Pt	Minute epithe- lial "prick- les" by ~6 mm; "swollen" pterotics
Echeneididae	261C	P	1.4-2.6	4.7-7.5	5-9	D 12-30 A 6-12	~15-30	E	None	Large hook- like teeth on dentary
Emmelichthyidae	259I	P	?	?	?	?	?	A	P1, Op, Io, Pt, Scl	None

TABLE 121. CONTINUED.

Taxon	Text figures	Egg type	Size (mm)					Sequence of fin completion	Head spination	Other specializations
			Egg	Hatch	Flex	D & A rays complete	First scales			
Ephippididae										
<i>Chaetodipterus</i>	256G	P	~1	~2.5	~4	~5	~8-9	A	S1, F3, P2, Op, Io, Ta, Pt	Spinous scales to ~15 mm
Epigonidae										
<i>Epigonus</i>	257B	P	?	?	?	?	?	?	None	None
<i>Sphyraenops</i>	257A	P	?	?	?	?	~12	?	S1, S5, F1, F3, P3, Op, Pt, Pe	None
Gerreidae	259A	P	.6-.75	~1.4	3.5-4.4	~6	>15	A	P5, (Scl)	None
Girellidae	258C	P	~1	~2.3	~6	11-13	~15-16	A	P5, Scl	None
Haemulidae	259B-D	P	.8-1.0	1.7-2.8	3.9-5.4	6-8 (earlier in in <i>P. nigra</i>)	~13 (much earlier in <i>Conodon</i>)	A	(F3), (P1), (P5), (Op), Sb, Io, (Pt), Scl, Pe (also F2, Pcl, La, Co, Na, D in <i>Conodon</i>)	None (spinous scales in <i>Conodon</i>)
<i>Hapalogenys</i>	254H	P	1.2	~3	~4.5	~5-6	>10	F	S3, S5, F1, F3, P2, Op, Sb, Io, Pt, Scl, La, Pe	P ₂ precocious, large
<i>Howella</i>	257C	P	?	?	~3.5	~4.5	?	A	P5, Op, Io, Pt, Cl	None
Kyphosidae	259J	P	~1	2.4-2.9	3.8-5.5	6-7	~7	A	P5, Op, Sb, Io, Scl, Pcl	Spinous scales
<i>Lateolabrax</i>	260E	P	1.3-1.4	4.4-4.6	~9	~15	>15	A	P5	None
Leiognathidae	256C	P	.6	1.4	~4	~5	?	?	S3, F3, P4, Pt, Scl	Ant. D spines serrate
Leptobramidae	258D	?	?	?	?	>8	>9	?	None	None
Lethrinidae	262F	P	.7-8	1.3-1.7	4.4-5.2	5.5-7.0	8	A	S3, F3, P4, Op, Sb, Io, Ta, Pt, Scl, Pcl, La, Co, Mx, D, Pe	Spinous scales
Lobotidae	254G	P	~1	?	<6	<6	~8	?	S3, S5, F1, F4, P2, Op, Sb, Io, Pt, Scl	P ₂ large (precocious?)
Lutjanidae (including Caesionidae)	256A-B	P	~.5-8	1.7-2.2	4.2-5.3	5-6	~12-14	B	F3, (P2), (P3), (P4), Op, Io, Pt, Scl, Pcl	(2nd dorsal spine and P ₂ spine and soft rays elongate) (anterior D, A, and P ₂ spines serrate)
Malacanthidae	256E-F	P	1.2	2.2-2.6	4-6	5-8	3-4	A	F2, F3, P4, Op, Sb, Io, Ta, Pt, Scl, La, Na, D, Pe, Pa	Spinous scales to ~30 mm or >; fused nasals
Menidae	256D	?	?	?	<4.5	<4.5	?	?	None	None
Microcanthidae	259G	P	?	?	~4	5-6	~15	A	P2, Op, Sb, Io, Pt, Scl	None
Monodactylidae	255H	P	.6-.7	1.8	3.5-4.0	5-6	9-10	F	F3, P2, Op, Io, Pt, Scl	P ₂ large, precocious
Moronidae	260F	(P) (D, A)	.7-4.6	1.7-3.7	7-9	10-13	16-25	A	P5	None
Mullidae	259E	P	.6-.9	1.6-3.4	3.5-4.5	~7	~12-13	A	None	Silvery, pelagic postlarvae to ~40-60 mm
Nemipteridae	258H	P	.7-8	1.5-1.6	~4	6-8	~11	A	None	None
Opistognathidae	255B	D, A, M, O	?	?	~5.5	~7	?	A	P5, Io	None
Oplegnathidae	255J	P	.9	2.3	~5	~7	~12	A	P5, Op, Io, Scl	None
Pempheridae	255I	P	?	?	3.6-4.3	~6	?	F	P5, Io, Scl	P ₂ precocious
Pentacerotidae	262J	P	?	?	?	?	~12	?	S3, S5, F1, F3, F4, P4, Op, Pt, Cl, La, Pe	P ₂ spines serrate; spinous scales
Percichthyidae	260D	(P) (D, A)	1.2-4.2	3.1-9.0	7-9	9-13	10-20	D	None	None

TABLE 121. CONTINUED.

Taxon	Text figures	Egg type	Size (mm)					Sequence of fin completion	Head spination	Other specializations
			Egg	Hatch	Flex	D & A rays complete	First scales			
Percidae	260C	(P) (D, A) (M)	.7-2.8	4.7-8.7	7-15	9-18	13-24	A (D)	(P5)	None
Plesiopidae	—	D, A, M, (O)	~.9 × .6	2.8-2.9	?	?	?	?	?	?
<i>Polyprion</i>	254E	P	1.6	3.7	~7	~9	?	A	S2, F3, P2, Op, Sb, Io, Pt, Scl	None
Pomacanthidae	256H	P	.7-.9	1.5-1.8	3.4-4.3	4-5	2.5-2.8	A	F3, P2, Sb, Io, Ta, Pt, Scl, La, Co, Na, D	Spinous scales to 17-19 mm
Pomatomidae	258G	P	.8-1.2	2-2.5	5-6	~7	~12	A	P5	None
Priacanthidae	262H-1	P	?	?	4-5	~7	~6	A	S3, F2, F3, P4, Op, Sb, Io, Ta, Pt, Scl, La, Co, Na, D, Br	D ₁ , A, P ₂ spines and soft rays serrate; spinous scales to ~20 mm
Pseudochromidae	255C	D, A, M	?	3-4	4.4-5.8	~8	12-13	A	P5	None
Rachycentridae	261B	P	1.2-1.4	?	~7	D 16-18 A 9-10	30-35	E	F4, P2, Pt	Minute epithelial prickles by ~6 mm "swollen" pteriotics
Scatophagidae	262D	P	?	~3	~4	~4-5	~4	D	Most exposed head bones thick and rugose; P and Pt expanded posteriorly; Pt with posterior spatulate "spine"; Pe swollen and with separate rugose "shield"	Spinous scales
Sciaenidae	257H	P	.7-1.3	1.5-2.5	3.0-4.6	~5-9	14-20	A (B)	(S4), (F3), (P2), P5, Pt, Scl, Io	None
Scombroptidae	262E	P	?	?	?	>6	?	A	S2, F3, P4, Op, Sb, Io, Pt	None
Scorpididae	258A-B	P	?	?	~6	9-10	9-11	A	P2, Op, Sb, Io, Scl	None
Serranidae										
Serraninae	—	P	.8-1.0	~2.2	4.3-5	~6	~11-12	A (B)	P2, Op, Sb, Io, Pt, Scl	None
Anthiinae	—	P	.6-.8	1.2-1.4	3.5-5	4.6-5.5	~6->10	B (A)	(S1), (S2), (F1), (F2), (F3), (F4), (P3), (P4), Op, Sb, Io, (Ta), Pt, Scl, (La), (Co), (D), (Pe), (Pa)	(D ₁ , A and P ₂ spines serrate) (ant D spines and P ₂ rays elongate)
Epinephelinae										
Epinephelini	—	P	.7-1.0	1.4-2.4	~4-5	~6	>15	B	(F1), F3, P4, Op, Sb, Io, Pt, Scl	D ₁ , A and P ₂ spines serrate; second D ₁ spine and P ₂ spines elongate
Grammistini	—	P	~1	<2.9	3.3-4.6	~6	?	P ₁ , D ₁ , D ₂ , A, P ₂	P2, Op, Sb, Io	Ant D spines flexible, elongate, pigmented; P ₁ large, precocious

TABLE 121. CONTINUED.

Taxon	Text figures	Egg type	Size (mm)					Sequence of fin completion	Head spination	Other specializations
			Egg	Hatch	Flex	D & A rays complete	First scales			
Liopropomini	—	P	~1	?	?	~6	?	D ₁ , D ₂ , A, P ₁ , P ₂	(F4), P2, Op, (1o)	Ant D spines flexible, elongate, ornamented
Sillaginidae	259F	P	.6-.7	1.3	~6	~9	?	A	P5, Pt	None
<i>Siniperca</i>	260B	D, A	~2	~5	~10	~11	?	A	P5	None
Sparidae	258I	P	.8-1.2	2.0-2.7	4-7	6-11	8-20	A	P5, 1o, Pt, Scl (also S2, F3, P2, in <i>Pagrus</i>)	None (spinous scales in <i>Pagrus</i>)
<i>Stereolepis</i>	254F	P	?	?	?	<7	>10	?	F3, P2, Sb, 1o, Pt, Scl, Pe	None
<i>Symphysanodon</i>	254A	P	?	?	3.5-4.0	~4.5	~13-14	A	F2, F5, P4, Pt, Scl, Ta, La, Co, D, Pe	None
Teraponidae	259H	(P) (D)	.7-2.8	1.7-3.7	~4-8	~7-11	14-18	A	P5, Op, Sb, 1o, Scl, Cl, Pcl	None

pletion of dorsal fin rays (12-30 mm) occurs in the elongate larvae of *Coryphaena*, *Rachycentron* and the Echeneidae.

The most commonly observed sequence of fin completion (pattern A in Table 121) is that described for *Morone* by Fritzsche and Johnson (1980) and for *Anisotremus* by Potthoff et al. (1984). Soft rays of the dorsal and anal fins begin to form during or just prior to flexion. Fin rays appear first near the future middle of these fins and are added in an anterior and posterior direction. Full complements of dorsal and anal soft rays are usually achieved at about the same time as the full principal caudal fin complement. The spinous dorsal fin is completed next (usually from posterior to anterior) followed by the pelvic and pectoral fins.

Precocious development of the anterior portion of the spinous dorsal and the pelvic fins, pattern B, is usually associated with ornamentation and/or elongation of the spines. It characterizes all larvae of lutjanids and epinepheline serranids, and a few apogonids, chaetodontids and sciaenids. In liopropomine serranids, the anterior portion of the spinous dorsal is precocious, but the pelvic fins develop last. Precocious development of pectoral and pelvic fins, pattern C, is unique to some members of the Bramidae. Pattern D, precocious pectorals only, is found in scatophagids, some bramids, and interestingly, is also shared by the freshwater Percichthyidae and some Percidae. The pectoral fin and anterior portion of the spinous dorsal are precocious in the serranid tribe Grammistini. In pattern E, the full anal fin ray complement tends to be complete prior to that of the dorsal, and the spinous dorsal is the last fin to be completed. This pattern is unique to the echeneoid fishes (*Coryphaenidae*, *Rachycentridae* and *Echeneidae*). Pattern F, in which only the pelvics are precocious, is found in *Hapalogenys*, *Monodactylidae* and *Pempheridae*.

Scales.—Most percoids begin to develop scales well after completion of fins near the end of the larval period, frequently after settling. In several families (e.g., *Chaetodontidae*, *Cheilodactylidae*, *Cirrhitidae*, and *Scorpididae*) unspecialized scales first appear at or slightly before completion of the median fins and are thus present during the late larval stages. Larvae of a few groups are characterized by early development of specialized

spinous scales that eventually transform into the typical adult ctenoid scale. In the ephippidid *Chaetodipterus*, the haemulid *Conodon*, malacanthids, pomacanthids and scatophagids these consist of small, roughly circular, non-imbricate bony plates from the center of which one to several spines project outward at right angles. Larvae of the Bramidae, *Kyphosidae*, *Pentacerotidae*, *Priacanthidae*, some anthiine serranids, the sparid *Pagrus* and the sparoid family *Lethrinidae* possess spinous scales in which one or more spines project outward at less than right angles from the posterior field or margin of imbricate plates that more closely resemble scales of the adults. Among non-percoid fishes, spinous larval scales occur in trachichthyids, chiasmodontids, acanthurids, *Xiphias*, *Antigonia* and some pleuronectiforms, tetraodontiforms, scorpaeniforms and gasterosteiforms. The function of specialized larval scales is unknown, but it seems likely that they provide some defense against small biting predators, parasites and/or nematocysts.

Head spination.—The simple to elaborate spinous ornamentation of various bones of the head in larvae of many percoid fishes is an area ripe for future detailed investigations. Nowhere is the potential utility of larval morphology in phylogenetic studies more evident, for it is in this feature that larval percoids frequently exhibit far more complexity and diversity than adults. Although more work is needed to determine if patterns of head spination will prove useful in studies of interfamilial relationships, there can be no doubt that the diversity of these patterns within some well-defined families or subfamilies (e.g., anthiine serranids, chaetodontids, priacanthids, malacanthids, pomacanthids, haemulids, etc.) offer critical information for intra-familial phylogenetic analyses.

Extensive head spination appears to have arisen independently numerous times within the Percoidei. Nevertheless, an ordered progression of increasing complexity is evident in the sequence in which ornamentation is added to various bones. Most families are characterized by a single level of complexity, but some are more diverse. In the larvae of several unrelated families (e.g., *Cheilodactylidae*, *Echeneidae*, *Menidae*, *Mullidae*, *Percichthyidae*) head spines are completely lacking. A

somewhat larger, equally heterogeneous assemblage of percoid groups (including the Ambassidae, Centranchidae, Centropomidae, Cirrhitidae, Moronidae, Percidae, Pomatomidae and Pseudochromidae) has minimal head spination, consisting of only a few small spines along the posterior, and usually lateral, margins of the preopercle. In most instances, these spines are so small and isolated that it is difficult to imagine that they serve any useful function.

The most common pattern of head spination among larval percoids is one in which, in addition to small to moderate preopercular spines, small spines may also occur on other bones of the opercular series (interopercle, subopercle and opercle) and on various bones of the pectoral series (cleithrum, postcleithrum, supracleithrum, posttemporal and tabulars). This pattern occurs in many of the more generalized families that have usually been considered "basal" percoids, including the Acropomatidae, Gerreidae, Girellidae, Haemulidae, Kyphosidae, Sciaenidae, Scorpionidae, Sparidae and Teraponidae, and it must be primitive for at least some large subgroup of percoid families.

Two additional levels of complexity in this artificial hierarchy involve modifications of cranial bones (frontal and supraoccipital) in addition to opercular and pectoral series spination. Modifications of the frontal bones occur only in those larvae with opercular and pectoral series spination and encompass several types of ornamentation. Frontal surface rugosity is found in a few apogonids, bramids and serranids as well as in *Acanthocephala*, *Lobotes*, *Hapalogenys*, *Pseudopenaceros* and *Sphyraenops*. Johnson and Keener (1984) noted this condition in larval *Alphistes*, but it was not previously considered in descriptions of percoid larvae. With closer examination, cranial rugosity will undoubtedly be detected in larvae of other percoid and non-percoid groups. It probably offers an efficient way to strengthen the neurocranium during early development. Frontal spines or serrations are most frequently borne along the supraorbital ridge. *Coryphaena*, *Rachycentron*, *Lobotes*, and some carangids have one large, broad-based supraorbital spine, but the more common condition is a series of supraorbital spines or serrations. These are found in lutjanids, malacanthids, monodactylids, pomacanthids, *Stereolepis*, some acropomatids, carangids, haemulids, sciaenids, and serranids as well as in most groups with supraoccipital modifications. More elaborate ornamentation, consisting of a series of parallel serrated ridges on the dorsal surface of the frontals, characterizes larval malacanthids, priacanthids, *Synagrops* and some anthiin serranids.

The most extreme example of frontal spination is seen in *Symphysanodon* (Fig. 254A). A longitudinal serrated crest above the supraorbital ridge on each frontal bone continues posteriorly as a long, spike-like serrated spine extending to about the middle of the spinous dorsal fin. The only other example of large paired cranial spines among larval perciforms is found in istiophorids, where the spines originate from the pterotics. This "horned" effect occurs elsewhere in larvae of many scorpaeniform groups (e.g., Scorpaenidae and Triglidae) and in the beryciforms, *Diretmus* and *Anoplogaster*, but in these groups the large paired spines are parietal in origin. With the exception of occasional minute spines or small ridges, larvae of perciform fishes never develop parietal ornamentation, and it is tempting to speculate that the presence of variously developed parietal spines among larvae of many scorpaeniform groups offers support for the often questioned monophyly of the Scorpaeniformes. In any case, this uncommon feature should be examined in future considerations of higher relationships among acanthopterygian fishes. The

monophyly of the Beryciformes has recently been questioned (Zehren, 1979), and it is interesting to note that although *Diretmus*, *Anoplogaster* and at least some trachichthyoids share larval parietal spines with scorpaeniforms, holocentrids lack them, instead possessing frontal, supraoccipital and preopercular spination similar to that seen in more elaborately ornamented larval percoids.

Modifications of the supraoccipital, representing the last category of complexity in head spination, occur in those larvae which also have opercular series, pectoral series and frontal ornamentation. Simple forms of supraoccipital ornamentation include a small peak-like median crest (*Chaetodipterus*, *Pagrus*, *Polyprion*, *Sphyraenops*, and some acropomatids, apogonids, carangids and anthiin serranids) or a serrated, ridge-like crest (*Synagrops*, some sciaenids and anthiin serranids). The more extreme form is a large, vaulted, variously serrate spine-like crest that projects beyond the posterior margin of the cranium and is well-developed in preflexion larvae soon after hatching. This type of crest characterizes larval cepolids, *Hapalogenys*, leiognathids, lethrinids, (lobotids?), pentacerotids, priacanthids and *Scombrops*. To my knowledge, it occurs elsewhere only in the larvae of holocentrid beryciforms and the caproid *Antigonia*.

The so called "tholichthys" larvae of the Chaetodontidae and Scatophagidae (Fig. 262A–D) perhaps represent the ultimate in head bone modification among larval percoids. The cranial bones and many of the other exposed bones of the head are thickened and rugose, effecting an armor-like protective covering. In chaetodontids the posttemporal and supracleithrum are rugose and expanded posteriorly as large laminar plates. The preopercle is similarly expanded anteriorly and posteriorly and at its angle bears a broad, flattened or serrated, terete spine. In scatophagids the preopercle is rugose and expanded, but, unlike chaetodontids, the supracleithrum is unmodified. The posttemporal is rugose, its dorsal portion is somewhat expanded, and its ventral half extends posteriorly as a very blunt, thick, spine-like projection. Also notable is a large, thick, rugose protuberance covering the pterotic. Although not identical, the larvae of chaetodontids and scatophagids share a unique physiognomy, the details of which should be investigated in relation to possible close affinity of these two families.

Spination on circumorbital, nasal, premaxillary and maxillary bones is generally found only in those larval percoids with cranial ornamentation, and it is almost exclusively in these larvae that other specializations, such as elongate serrate fin spines and spinous scales occur. In addition, opercular and pectoral series spination is usually more extensive and almost always includes an elongate and/or serrate spine at the angle of the preopercle.

In summary, there seem to have been some common evolutionary constraints on the order in which morphological complexity and specialization of larval percoids has progressed, but a simple direct relationship between this ordered progression and phylogenetic affinity among families is not apparent. In fact, the assemblages of taxa that characterize the various levels of complexity discussed above are quite diverse and not compatible with what little we do understand about percoid affinities based on adult morphology. Furthermore, it is clear that elaborately ornamented larvae have arisen independently several times within monophyletic groups otherwise characterized by larvae with only generalized opercular and preopercular spination. Examples include the haemulid *Conodon*, the sparoid family Lethrinidae and the serranid subfamily Anthiinae. Resolution of the phylogenetic significance of intricate patterns of

head spination among larval percoids will entail more precise study than has characterized much previous work. Determination of homology will require detailed information about location, conformation and processes of development of head spines prior to considering the question of compatibility with adult characters.

Utility of Larval Morphology in Phylogenetic Studies

The preceding two decades have seen notable advances in our understanding of the evolutionary relationships of teleost fishes; however, as noted above, progress in elucidating the phylogeny of the Percoidei has not kept pace. Many families are poorly delineated and hypotheses about inter- and intrafamilial relationships are few. Lack of progress is chiefly attributable to the size and diversity of the Percoidei, the adaptive malleability and convergence that have characterized percoid evolution and the paucity of conspicuous morphological specializations that can be readily identified as true synapomorphies. With few exceptions (Burgess, 1974; Dooley, 1978; Kendall, 1979; Johnson, 1983), previous studies of percoid phylogeny and classification have failed to consider early life history stages, even though it is obvious that the prodigious variety of larval form and specialization among percoids offers a rich suite of additional characters.

Within many families there is a complexity of larval morphology or diversity of larval form that suggests excellent potential for the application of larval characters in elucidating generic interrelationships. Particularly promising families in this regard include the Acropomatidae, Apogonidae, Bramidae, Carangidae, Cepolidae, Chaetodontidae, Haemulidae, Lutjanidae, Malacanthidae, Pentacerotidae, Pomacanthidae, Priacanthidae, Sciaenidae, and Serranidae. The intricate bony ornamentation of the larvae of anthiine serranids, for instance, is considerably more complex than that of the adults, and preliminary studies of details of larval head spination and scale development among New World genera indicate that the current generic classification, based exclusively on adult morphology, should be reexamined (Carole Baldwin, Abstracts of 1983 ASIH Annual Meeting). Larvae of groups like the apogonids and carangids exhibit a less complex morphology, but the wide range of form and specialization should prove useful in phylogenetic analyses.

Larval morphology will undoubtedly also prove useful in considerations of higher relationships among percoids. At the family level, a rather simplistic approach is to consider that larvae offer independent tests of hypotheses of monophyly. In other words, do the larvae of each percoid family share one or more derived features that corroborate the monophyly of that family as currently defined on the basis of adult morphology? The answer to this question appears to be yes for many groups, but problems stem from an inadequate understanding of character polarity and the fact that, for most families, larvae of many genera and most species remain undescribed. Nonetheless, this is a useful concept, and the validity and power of such a test will increase as we gain more knowledge of the larvae of various percoid groups.

Consider, for example, the bearing of larval morphology on several hypotheses of relationship resulting from the recent redefinition of Schultz's (1945) Emmelichthyidae, a polyphyletic assemblage of planktivorous fishes. Heemstra and Randall (1977) transferred *Dipterygonotus* to the Caesionidae and Johnson (1980) hypothesized that caesionids are lutjanoid fishes most

closely related to the lutjanid subfamily Lutjaninae. Caesionids are quite distinctive in body form and upper jaw configuration, but share with the lutjanines a number of osteological features and a specialized adductor mandibulae (similar to that of most carangids) in which a separate division of A_1 originates on the subocular shelf. Subsequent descriptions of larval lutjanines and caesionids (see Table 122) show that they share a distinctive body form, pattern of head spination, precocious first dorsal and pelvic fins with elongate spines and soft rays, and sparse pigmentation (Fig. 256A, B). The hypothesized sister group relationship is thus corroborated by larval morphology.

The Centranchidae were also removed from the Emmelichthyidae and hypothesized to be most closely related to the Sparidae (Heemstra and Randall, 1977; Johnson, 1980) based on adult morphology. Although the larvae of these two groups share no obvious specializations, they are quite similar (Fig. 258I, J), and are distinguishable from those of the Emmelichthyidae (Fig. 259I) and the other reassigned groups. *Labracoglossa*, placed in a separate family by Heemstra and Randall (1977) is here placed in the family Scorpididae (see section on classification), and the larval form corroborates this placement (Fig. 258A, B). The larvae of inermiids, *Inermia* and *Emmelichthyops*, also removed from the Emmelichthyidae, remain undescribed, but their identification can provide a test of the hypothesis that they are most closely related to the Haemulidae (Johnson, 1980).

These examples and those that follow demonstrate that early life history stages offer important information that can be used to test previous phylogenetic hypotheses or incorporated with adult characters into new phylogenetic analyses. Additional examples are mentioned in the discussion of familial classification. Where the larvae are known, failure to consider their morphology in studies of percoid phylogeny seems hardly justifiable, and may inhibit progress or lead to false conclusions. This point is well-illustrated in the two examples discussed below, in which details of larval morphology provide critical evidence in support of new or previously rejected phylogenetic hypotheses.

The families Branchiostegidae (=Latilidae) and Malacanthidae have been variously united and separated in past classifications. In the most recent revision, Dooley (1978) concluded that "the branchiostegids and malacanthids have few characters in common that might be used to justify their consolidation into a single family" and noted that they "could as easily be aligned with several other percoid families as with each other." He suggested that the malacanthids are possibly "a branch of the labrid-scarid lineage, while the branchiostegids show closer affinities to the serranid-percid line of perciform evolution." In contrast, Robins et al. (1980) recognized a close affinity between the two groups by treating them as subfamilies of the Malacanthidae. Marino and Dooley (1982) took issue with this classification and stated that there are "several more myological (differences) why the families are distinct." Actually, Marino and Dooley listed only one myological difference, the absence of adductor mandibulae section A_{3b} . This difference and the other 13 listed by Dooley (1978, Table 1), including body depth, body shape, and skull contour, have little relevance to the phylogenetic affinity of these two groups. As for features common to the malacanthids and branchiostegids, Dooley found only three: dorsal and anal fins relatively long and continuous, a single opercular spine, and "grossly similar larval stages." Dooley correctly noted that the first two of these are not particularly meaningful because they are fairly common percoid features, but he

TABLE 122. REFERENCES TO LARVAL PERCOIDEI.

Taxon	Eggs	Yolk-sac	Preflexion	Postflexion
Acanthoclinidae	Jillett, 1968	Jillett, 1968	Jillett, 1968	Crossland, 1981 Crossland, 1982 Jillett, 1968
Acropomatidae	—	—	—	Fourmanoir, 1976 Okiyama, 1982b
Ambassidae	Breder and Rosen, 1966 Eng, 1969 Nair, 1958	Eng, 1969	—	Nair, 1952b Gopinath, 1946 Nair, 1958
Apogonidae	Breder and Rosen, 1966 Leis and Rennis, 1983 Allen, 1975b Bertolini, 1933a	Leis and Rennis, 1983 Miller et al., 1979 Allen, 1975b Bertolini, 1933a	Leis and Rennis, 1983 Miller et al., 1979 Allen, 1975b De Gaetani, 1937	Leis and Rennis, 1983 Miller et al., 1979 Allen, 1975b Fourmanoir, 1976 Okiyama, 1982b Bertolini, 1933a Fahay, 1975 Whitley, 1926 Vatanachi, 1972 De Gaetani, 1937
Bramidae	—	Johnson, 1978 Mead, 1972	Johnson, 1978 Mead, 1972	Johnson, 1978 Mead, 1972 Fahay, 1983
Caesionidae	—	—	—	Leis and Rennis, 1983
Callanthiidae	—	—	Leis and Rennis, 1983 Bertolini, 1933b Fage, 1918	Leis and Rennis, 1983 Fourmanoir, 1976 Bertolini, 1933b Fage, 1918
Carangidae	Laroche et al., this volume			
Caristiidae	—	—	—	Belyanina, 1982b
Centracanthidae	Brownell, 1979 Thomopoulos, 1954 Aboussouan, 1964 Montalenti, 1933 Sanzo, 1939c	Brownell, 1979 Sanzo, 1939c	Brownell, 1979 Sanzo, 1939c	Brownell, 1979 Fage, 1918 Montalenti, 1933
Centrarchidae	Numerous references, see Breder and Rosen, 1966; Hardy, 1978b; and Auer, 1982			
Centropomidae	Lau and Shafland, 1982	Lau and Shafland, 1982	Lau and Shafland, 1982	Lau and Shafland, 1982
Cepolidae	Breder and Rosen, 1966 Russell, 1976 Holt, 1891 Montalenti, 1937b	—	Russell, 1976 Fage, 1918 Montalenti, 1937b Okiyama, 1982b	Russell, 1976 Fourmanoir, 1976 Clark, 1920 Fage, 1918 Montalenti, 1937 Fourmanoir, 1973
Chaetodontidae	Leis and Rennis, 1983 Burgess, 1978 Suzuki et al., 1980	Leis and Rennis, 1983 Suzuki et al., 1980	Leis and Rennis, 1983 Suzuki et al., 1980	Leis and Rennis, 1983 Burgess, 1978 Fourmanoir, 1976 Kendall and Goldsborough, 1911 Burgess, 1974
Cheilodactylidae	Brownell, 1979 Mito, 1963 Robertson, 1978 Gilchrist and Hunter, 1919 Barnard, 1927	Brownell, 1979 Robertson, 1978	Brownell, 1979 Gilchrist and Hunter, 1919 Hattori, 1964	Brownell, 1979 Dudnik, 1977 Vooren, 1972 Tong and Saito, 1977 Nielsen, 1963a Hattori, 1964
Cirrhitidae	—	—	Leis and Rennis, 1983	Leis and Rennis, 1983 Fourmanoir, 1973 Fourmanoir, 1971a
Congrogadidae	—	—	—	Whitley, 1926
Coracinidae	—	—	—	Smith, 1938
Coryphaenidae	Johnson, 1978 Miller et al., 1979 Mito, 1960	Johnson, 1978 Miller et al., 1979 Mito, 1960	Johnson, 1978 Miller et al., 1979 Mito, 1960 Potthoff, 1980	Johnson, 1978 Miller et al., 1979 Gibbs and Collette, 1959 Aboussouan, 1969 Potthoff, 1980

TABLE 122. CONTINUED.

Taxon	Eggs	Yolk-sac	Preflexion	Postflexion
Echeneididae	John, 1950 Sanzo, 1930a Martin and Drewry, 1978 Sanzo, 1928 Akazaki et al., 1976	John, 1950 Sanzo, 1930a Martin and Drewry, 1978 Sanzo, 1928 Akazaki et al., 1976	John, 1950 Martin and Drewry, 1978 Sanzo, 1928 Akazaki et al., 1976	Gudger, 1926 Gudger, 1928 Akazaki et al., 1976
Emmelichthyidae	—	—	—	Nakahara, 1962
Ehippididae	Breder and Rosen, 1966 Johnson, 1978 Ryder, 1887	Johnson, 1978 Ryder, 1887	Johnson, 1978 Hildebrand and Cable, 1938 Fahay, 1983	Johnson, 1978 Hildebrand and Cable, 1938 Fahay, 1983
Epigonidae	—	—	—	Mayer, 1972
Gerreidae	Leis and Rennis, 1983 Rass, 1972	Leis and Rennis, 1983	Leis and Rennis, 1983	Leis and Rennis, 1983 Nair, 1952b Uchida et al., 1958
Girellidae	Breder and Rosen, 1966 Uchida et al., 1958 Mito, 1957a	Uchida et al., 1958 Mito, 1957a	Uchida et al., 1958 Mito, 1957a	Kobayashi and Igarashi, 1961 Munro, 1945 Uchida et al., 1958
Haemulidae	Breder and Rosen, 1966 Leis and Rennis, 1983 Johnson, 1978 Mito, 1966 Podosinnikov, 1977 Saksena and Richards, 1975 Hildebrand and Cable, 1930 Fahay, 1983	Leis and Rennis, 1983 Johnson, 1978 Mito, 1966 Podosinnikov, 1977 Saksena and Richards, 1975 Hildebrand and Cable, 1930 Fahay, 1983	Leis and Rennis, 1983 Johnson, 1978 Saksena and Richards, 1975 Hildebrand and Cable, 1930 Fahay, 1983	Leis and Rennis, 1983 Johnson, 1978 Saksena and Richards, 1975 Hildebrand and Cable, 1930 Nellen, 1973b Fahay, 1983 Heemstra, 1974
<i>Haplogenyis</i>	Suzuki et al., 1983	Suzuki et al., 1983	Suzuki et al., 1983	Okiyama, 1982b Suzuki et al., 1983
<i>Howella</i>	—	—	Gonzales, 1946	Gonzales, 1946
Kyphosidae	Leis and Rennis, 1983 Miller et al., 1979 Watson and Leis, 1974	Leis and Rennis, 1983 Miller et al., 1979	Leis and Rennis, 1983 Miller et al., 1979	Leis and Rennis, 1983 Moore, 1962 Johnson, 1978 Uchida et al., 1958 Nair, 1952b
Lactariidae	Breder and Rosen, 1966 Chacko, 1944	—	—	Nair, 1952b
<i>Lateolabrax</i>	Breder and Rosen, 1966 Mito, 1957b Uchida et al., 1958	Mito, 1957b Uchida et al., 1958	Mito, 1957b Uchida et al., 1958	Okiyama, 1982b Mito, 1957b Uchida et al., 1958
Leiognathidae	Breder and Rosen, 1966 Fujita, 1960	Fujita, 1960	Fujita, 1960	Nair, 1952b Vatanachi, 1972 Gopinath, 1946
Lethrinidae	Leis and Rennis, 1983 Suzuki and Hioki, 1978 Renzhai and Suifen, 1980a Mito, 1956a	Leis and Rennis, 1983 Suzuki and Hioki, 1978 Renzhai and Suifen, 1980a Mito, 1956a	Leis and Rennis, 1983	Leis and Rennis, 1983
Lobotidae	Hardy, 1978b Gudger, 1931	—	Hardy, 1978b Uchida et al., 1958	Hardy, 1978b Okiyama, 1982b Uchida et al., 1958
Lutjanidae	Leis and Rennis, 1983 Suzuki and Hioki, 1979b Rabalais et al., 1980 Stark, 1971 Mori, 1984	Leis and Rennis, 1983 Suzuki and Hioki, 1979b Rabalais et al., 1980 Mori, 1984	Leis and Rennis, 1983 Richards and Saksena, 1980 Collins et al., 1980 Laroche, 1977 Mori, 1984	Leis and Rennis, 1983 Fourmanoir, 1976 Okiyama, 1982b Richards and Saksena, 1980 Collins et al., 1980 Fahay, 1975 Heemstra, 1974 Vatanachi, 1972 Stark, 1971 Musiy and Sergiyenko, 1977 Laroche, 1977; Mori, 1984
Malacanthidae	Breder and Rosen, 1966 Fischer, 1958	Fischer, 1958a Fahay, 1983	Fischer, 1958a Okiyama, 1964	Fourmanoir, 1970, 1976 Dooley, 1978

TABLE 122. CONTINUED.

Taxon	Eggs	Yolk-sac	Preflexion	Postflexion
	Fahay, 1983		Fahay, 1983	Moser, 1981 Okiyama, 1964 Okiyama, 1982b Fahay, 1983 Berry, 1958 Hubbs, 1958
Microcanthidae	—	—	Leis and Rennis, 1983 Uchida et al., 1958	Leis and Rennis, 1983 Uchida et al., 1958
Monodactylidae	Akatsu et al., 1977	Akatsu et al., 1977	Akatsu et al., 1977	Akatsu et al., 1977 Ogasawara et al., 1978
Moronidae	Breder and Rosen, 1966 Hardy, 1978b Mansueti, 1964 Ryder, 1887 Ryder, 1887 Mansueti, 1958 Pearson, 1938	Hardy, 1978b Mansueti, 1964 Ryder, 1887 Mansueti, 1958 Pearson, 1938 Doroshev, 1970	Hardy, 1978b Mansueti, 1964 Ryder, 1887 Mansueti, 1958 Pearson, 1938 Doroshev, 1970 Fritzsche and Johnson, 1980	Hardy, 1978b Mansueti, 1964 Mansueti, 1958 Pearson, 1938 Doroshev, 1970 Okiyama, 1982b Fritzsche and Johnson, 1980
Mullidae	Breder and Rosen, 1966 Leis and Rennis, 1983 Russell, 1976 Miller et al., 1979 Marinaro, 1971 Raffaële, 1888 Heincke and Ehrenbaum, 1900	Leis and Rennis, 1983 Russell, 1976 Marinaro, 1971 Raffaële, 1888 Heincke and Ehrenbaum, 1900	Leis and Rennis, 1983 Russell, 1976 Miller et al., 1979 Heincke and Ehrenbaum, 1900 Montalenti, 1937 Uchida et al., 1958 Lo Bianco, 1908b	Leis and Rennis, 1983 Johnson, 1978 Russell, 1976 Miller et al., 1979 Uchida et al., 1958 Vatanachi, 1972 M. C. Caldwell, 1962 Lo Bianco, 1908b
Nemipteridae	Leis and Rennis, 1983 Aoyama and Sotogaki, 1955 Renzhai and Suifen, 1980b	Leis and Rennis, 1983 Aoyama and Sotogaki, 1955 Renzhai and Suifen, 1980b	Leis and Rennis, 1983	Leis and Rennis, 1983
Opistognathidae	—	—	—	Vatanachi, 1972
Oplegnathidae	Breder and Rosen, 1966 Mito, 1956b Uchida et al., 1958	Fukuhara and Ito, 1978 Mito, 1956b Uchida et al., 1958	Fukuhara and Ito, 1978 Uchida et al., 1958	Fukuhara and Ito, 1978 Fuskusho, 1975
Pempheridae	Leis and Rennis, 1983	Leis and Rennis, 1983	Leis and Rennis, 1983	Leis and Rennis, 1983
Pentacerotidae	—	—	—	Zama et al., 1977 Hardy, 1982
Percichthyidae	Breder and Rosen, 1966 Dakin and Kesteven, 1938 Llewellyn, 1974 Lake, 1967 Jackson, 1978 Fuster de Plaza and Plaza, 1955	Dakin and Kesteven, 1938 Llewellyn, 1974 Lake, 1967 Jackson, 1978	Dakin and Kesteven, 1938 Llewellyn, 1974 Lake, 1967 Jackson, 1978	Dakin and Kesteven, 1938 Lake, 1967 Jackson, 1978
Percidae	Numerous references, see Breder and Rosen, 1966; Hardy, 1978b; and Auer, 1982			
Plesiopodae	Breder and Rosen, 1966 Mito, 1955	Mito, 1955	—	—
<i>Polyprion</i>	Hardy, 1978b Sparta, 1939a Thomson and Anderton, 1921	Hardy, 1978b Sparta, 1939a	Hardy, 1978b Sparta, 1939a	Hardy, 1978b Sparta, 1939a Bertolini, 1933b
Pomacanthidae	Leis and Rennis, 1983 Suzuki et al., 1979 Fujita and Mito, 1960	Leis and Rennis, 1983 Suzuki et al., 1979 Fujita and Mito, 1960	Leis and Rennis, 1983 Burgess, 1974	Leis and Rennis, 1983 Burgess, 1978 Fourmanoir, 1976 Burgess, 1974
Pomatomidae	Hardy, 1978b Deuel et al., 1966 Dekhnik, 1973 Salekhova, 1959 Sparta, 1962 Fahay, 1983	Hardy, 1978b Deuel et al., 1966 Dikhnik, 1973 Salekhova, 1959 Sparta, 1962 Fahay, 1983	Hardy, 1978b Deuel et al., 1966 Dekhnik, 1973 Salekhova, 1959 Sparta, 1962 Norcross et al., 1974 Pearson, 1941 Fahay, 1983	Hardy, 1978b Dekhnik, 1973 Salekhova, 1959 Norcross et al., 1974 Pearson, 1941 Silverman, 1975

TABLE 122. CONTINUED.

Taxon	Eggs	Yolk-sac	Preflexion	Postflexion
Priacanthidae	Leis and Rennis, 1983 Suzuki et al., 1980	—	Leis and Rennis, 1983 Hardy, 1978b D. K. Caldwell, 1962 Aboussouan, 1969	Leis and Rennis, 1983 Hardy, 1978b D. K. Caldwell, 1962 Fourmanoir, 1976 Okiyama, 1982b
Pseudochromidae	Leis and Rennis, 1983 Lubbock, 1975	Leis and Rennis, 1983 Lubbock, 1975	Leis and Rennis, 1983	Leis and Rennis, 1983
Rachycentridae	Hardy, 1978b	—	—	Hardy, 1978b Dawson, 1971a
Scatophagidae	—	Weber and de Beaufort, 1936	—	Nair, 1952b Weber and de Beaufort, 1936
Sciaenidae	Numerous references, see Breder and Rosen, 1966; Hardy,	1978b; and Auer, 1982		
Scorpididae	—	—	Hattori, 1964	Hattori, 1964
Serranidae	Kendall, this volume			
Sillaginidae	Breder and Rosen, 1966 Ueno and Fujita, 1954 Uchida et al., 1958	Ueno and Fujita, 1954 Uchida et al., 1958	Munro, 1945 Uchida et al., 1958	Okiyama, 1982b Munro, 1945 Uchida et al., 1958 Gopinath, 1946
<i>Siniperca</i>	Imai and Nakahara, 1957 Chyung, 1977	Imai and Nakahara, 1957 Chyung, 1977	Imai and Nakahara, 1957 Chyung, 1977	Okiyama, 1982b Imai and Nakahara, 1957 Chyung, 1977
Sparidae	Breder and Rosen, 1966 Johnson, 1978 Russell, 1976 Ranzi, 1933 Rathbun, 1893 Cardeilhac, 1976 Kuntz and Radcliffe, 1917 Houde and Potthoff, 1976 Uchida et al., 1958 Fahay, 1983 Hussain et al., 1981	Johnson, 1978 Russell, 1976 Ranzi, 1933 Kuntz and Radcliffe, 1917 Houde and Potthoff, 1976 Uchida et al., 1958 Fahay, 1983 Kohno et al., 1983 Hussain et al., 1981	Johnson, 1978 Russell, 1976 Ranzi, 1933 Hildebrand and Cable, 1930 Kuntz and Radcliffe, 1917 Houde and Potthoff, 1976 Fahay, 1983 Kohno et al., 1983 Hussain et al., 1981	Johnson, 1978 Russell, 1976 Ranzi, 1933 Hildebrand and Cable, 1930 Kuntz and Radcliffe, 1917 Okiyama, 1982b Munro, 1945 Houde and Potthoff, 1976 Uchida et al., 1958 Fahay, 1983 Kohno et al., 1983 Hussain et al., 1981
<i>Stereolepis</i>	—	—	—	Okiyama, 1982b
<i>Symphysanodon</i>	—	—	—	Fourmanoir, 1973
Terapontidae	Breder and Rosen, 1966 Llewellyn, 1973 Zvjagina, 1965b Lake, 1967	Llewellyn, 1973 Lake, 1967	Llewellyn, 1973 Zvjagina, 1965b Lake, 1967	Llewellyn, 1973 Nair, 1952b Munro, 1945 Zvjagina, 1965b Lake, 1967 Vatanachi, 1972

incorrectly dismissed the significance of the larvae, which, as Okiyama (1982b) pointed out, are remarkably similar and distinctive among the percoids. I believe the larval morphology of these two groups offers conclusive evidence for a sister-group relationship between them, including a synapomorphy unique among percoids, and perhaps all teleosts.

Larval malacanthids and branchiostegids (Fig. 256E, F), are among the most elaborately ornamented in the Percoidei. They share early developing spinous scales, a series of serrate ridges on the frontals, and have very similar configurations of spines and serrate ridges on many of the exposed bones of the head. The most distinctive feature is a median rostral bony structure, forming a blunt, serrate-ridged projection in *Caulolatilus*, *Lopholatilus* and *Branchiostegus*, a smooth anchor-shaped projection in *Malacanthus* and a long spike-like spine with serrate ridges in *Hoplolatilus*. Dooley (1978) stated that larvae with similar rostra and head spination occur among holocentrids, lutjanids, serranids and istiophorids and that the similarity "could

be considered as convergence or perhaps a relict characteristic carried over from a common beryciform ancestor." In fact, the larvae of these groups are quite different morphologically, and misconceptions about their similarity apparently result from superficial considerations that have often characterized earlier larval descriptions. Neither larval lutjanids nor serranids have rostral projections or (with the exception of some anthiini serranids) particularly elaborate head spination. The rostral projection of istiophorids is a premaxillary beak or bill, supported internally by a fixed, horizontally-oriented rostral cartilage and is structurally homologous to that of larval *Xiphias* and scombrids (except Scombrini). Although the spinous rostrum of holocentrids bears a strong resemblance to that of *Hoplolatilus*, it is an entirely different structure, formed by enlargement of the supraethmoid and supported by a greatly enlarged ethmoid cartilage. The median rostral projection of malacanthids and branchiostegids has been described as an ethmoid spine (Okiyama, 1964, 1982b), but it actually originates from a modification of

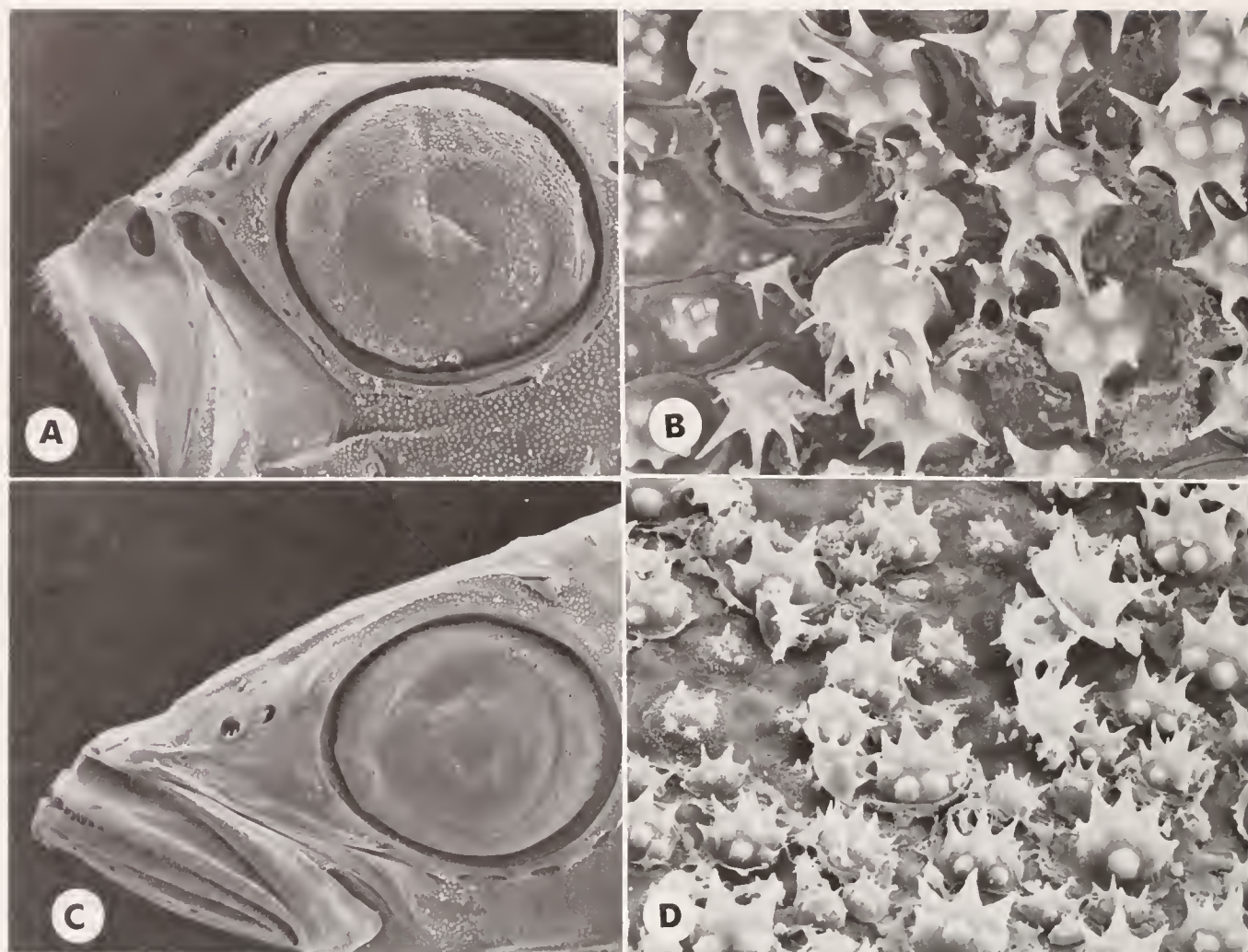


Fig. 263. Scanning electromicrographs of epithelium of juvenile dolphins and cobia at various magnifications. (A) *Coryphaena hippurus*, 28 mm SL, 15 \times ; (B) *C. hippurus*, 28 mm SL, 360 \times ; (C) *Rachycentron canadum*, 30 mm SL, 15 \times ; and (D) *R. canadum*, 80 mm SL, 360 \times .

the nasal bones. The nasal bones first appear as separate structures, but prior to or during flexion, they become fused anteriorly by a median bony bridge. This modified nasal structure then develops the various ornamentations that characterize malacanthid and branchiostegid larvae. At transformation, the bony bridge begins to fragment and is eventually entirely resorbed, so that the nasal bones once again become completely separate. I know of no other example in fishes of transient ontogenetic fusion of nasal bones. This unique synapomorphy, in conjunction with the other shared larval specializations, cogently supports the hypothesis that malacanthids and branchiostegids are sister groups. Classification of the two lineages of tilefishes as subfamilies of the Malacanthidae seems an appropriate way to express this relationship.

The evolutionary relationships of the dolphins, Coryphaenidae, have remained uncertain, but the family has usually been placed close to the Carangidae as have the Echeneididae and the monotypic Rachycentridae. Examination of the larvae of these groups during this investigation and subsequent considerations of adult morphology have led to further resolution of the interrelationships of these families (Johnson, Abstracts of 1983 ASIH Annual Meeting). This final example provides the

most convincing illustration of the importance of larval characters to studies of phylogeny among percoids. Consequently I discuss it in considerable detail.

Freihofer (1978) noted that the Nematistiidae, Carangidae, Coryphaenidae, Rachycentridae and Echeneididae share a unique specialization in the lateralis system on the snout—an anterior extension of the nasal canal consisting of one (Nematistiidae) or two prenasal canal units, with one (Nematistiidae and Carangidae) or both (remaining three families) surrounded by tubular ossifications. In addition, they share small, adherent cycloid scales. Based on two presumed synapomorphies, then, these five families constitute a monophyletic group, hereafter referred to as the carangoids.

Three synapomorphies unite the Carangidae, Coryphaenidae, Rachycentridae and Echeneididae as a monophyletic group. These four families lack the bony stay (Potthoff, 1975) posterior to the ultimate dorsal and anal pterygiophores found in almost all other percoids (see Table 120), have two prenasal canal units and have a lamellar expansion along the anterior margin of the coracoid. *Nematistius*, placed in separate family by Rosenblatt and Bell (1976), is apparently the sister group of these four families (see cladogram, Fig. 276, in Smith-Vaniz, this volume).

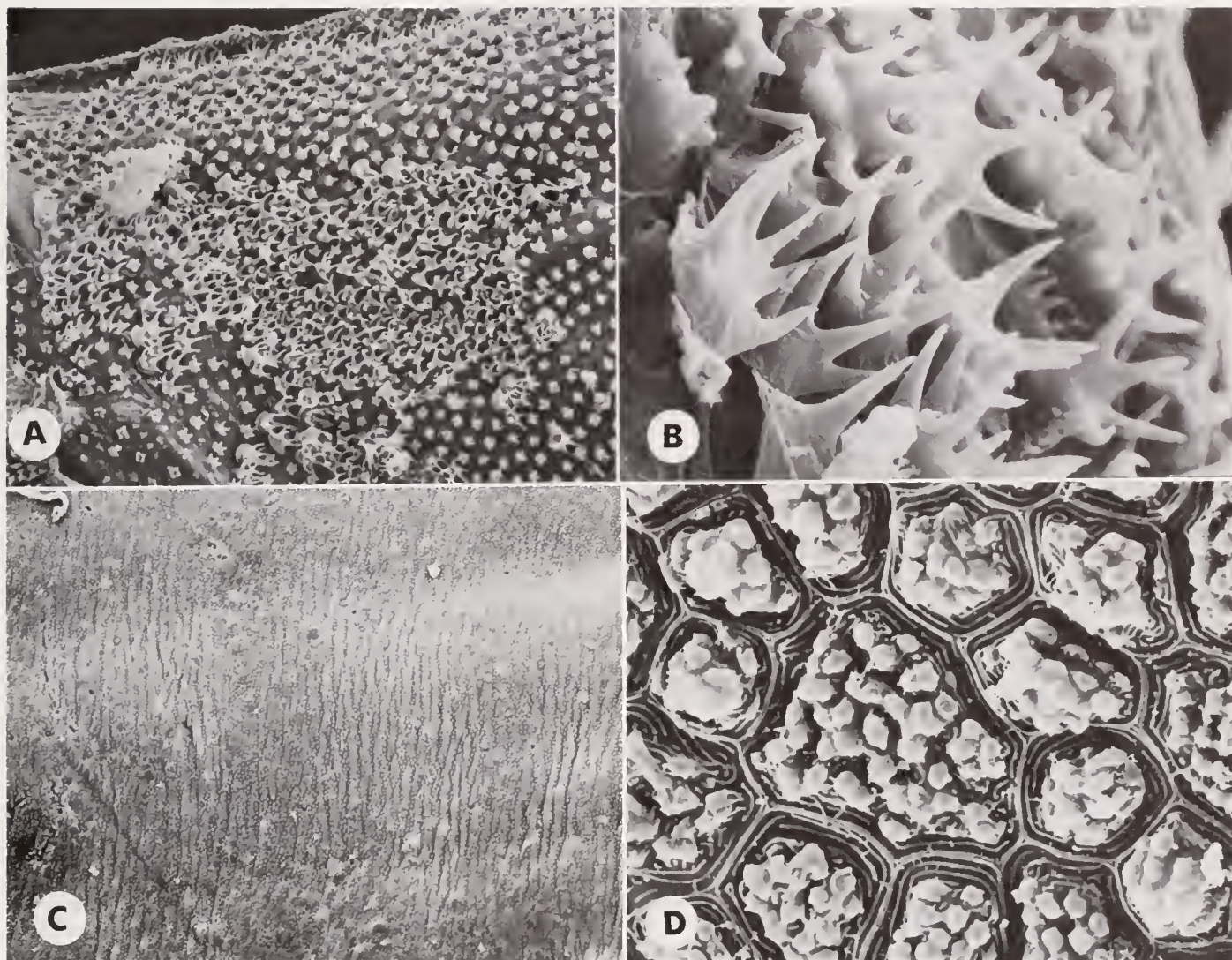


Fig. 264. Scanning electromicrographs of epithelium of larval dolphin and amberjack at various magnifications. (A) *Coryphaena hippurus*, 17.0 mm SL, 55 \times ; (B) *C. hippurus*, 17.0 mm SL, 400 \times ; (C) *Seriola* sp., 11.2 mm SL, 55 \times ; and (D) *S. sp.*, 11.2 mm SL, 2,000 \times .

it has a well developed bony stay, a single, partly ossified prenasal canal unit and an unmodified coracoid.

Within the carangoids, the Coryphaenidae, Rachycentridae and Echeneididae form a monophyletic group, here referred to as the echeneoids. Adult echeneoids are specialized with respect to the Carangidae in the following features: absence of predorsal bones; anterior shift of the first dorsal pterygiophore forward of the third interneural space; presence of several anal pterygiophores anterior to the first haemal spine (vs. one in carangids and most other percoids); loss of the so-called beryciform foramen in the anterior ceratohyal; and tubular ossifications surrounding both prenasal canal units. Larval echeneoids are also specialized with respect to carangids (larvae of *Nematistius* are unknown). Whereas larval carangids are moderate to deep-bodied, hatch at small sizes (1–3.5 mm) and complete dorsal fin and anal fin rays in conjunction with or soon after flexion, echeneoid larvae (Fig. 261A–C) are very elongate, hatch at large sizes and complete dorsal fin rays at two to three times the size at flexion (see Table 121). Larval morphology thereby corroborates the hypothesized monophyly of the echeneoids.

Although a sister-group relationship between the Coryphaenidae and either the Rachycentridae or the Echeneididae has not been previously proposed, it has often been suggested that *Rachycentron* and the echeneidids are sister groups. This hypothesis was based on general external similarity including the remarkable resemblance in body form, color pattern and caudal fin shape between juveniles of *Rachycentron* and *Echeneis naucrates* (Böhlke and Chaplin, 1968). Because the juvenile features of *Rachycentron* are shared by only one species of echeneidid, they do not provide evidence for a sister-group relationship between the Rachycentridae and the Echeneididae, nor does a detailed osteological comparison of the two groups. The echeneidids are highly modified in almost every aspect of their osteology compared to both *Rachycentron* and *Coryphaena*, and with two exceptions (absence of a median cranial crest and fusion of the prenasal ossifications), the only specializations shared by both *Rachycentron* and the echeneidids are also shared by *Coryphaena*. The following are autapomorphies of the Echeneididae: spinous dorsal fin modified as an attachment disc covering the dorsal surface of the cranium; first neural arch fused

to its centrum, spine absent; endopterygoid absent; quadrate with a lateral shelf; palatine and upper jaw bones distinctively modified; postcleithra absent; supracleithrum extremely reduced; medial tabular bones absent; posttemporal modified in shape and angle of articulation with supracleithrum; pelvic girdle broad and short, with two distinct anterior processes; caudal skeleton with a full neural spine on the second preural centrum; branchial skeleton with main arm of first epibranchial reduced to a nubbin, uncinat process enlarged and articulating directly with second pharyngobranchial, and interarcual cartilage absent. None of these extreme modifications (those of the caudal and branchial skeletons being unique among percoids) are even foreshadowed in the skeleton of *Rachycentron*, which is instead remarkably similar to that of *Coryphaena*, except in the anterior portion of the dorsal fin and the neurocranium.

In *Coryphaena*, the dorsal fin is elaborated anteriorly and extended into the first interneural space (second in *Rachycentron*) and there is an extreme supraoccipito-frontal crest on the neurocranium. The dorsal fin modification is autapomorphic for *Coryphaena*, but the median cranial crest is probably primitive for echeeneids since it is variously developed in all carangids and well-developed in *Nematistius*. The absence of this crest in *Rachycentron*, associated with a slight flattening of the neurocranium, is the only specialization shared with the Echeeneidae. Here again, however, there is little similarity between the slightly flattened neurocranium of *Rachycentron* and the extremely flattened and restructured neurocranium of the echeeneids, in which, for instance, the supraethmoid and vomer have become flat plates and the orbit is completely occluded by enlargement and anterior extension of the pterospheneids. This extreme restructuring of most cranial bones is evident even in larval echeeneids at the earliest development of the neurocranium, whereas the neurocrania of *Rachycentron* and *Coryphaena* exhibit a generalized development similar to that of carangids. Prior to development of the median crest in *Coryphaena* (>100 mm), the neurocrania of cobia and dolphin differ mainly in relative depth. Echeeneids also have an exceptionally modified adductor mandibulae in which A_1 is absent and A_2 and A_3 are distinctively subdivided. *Coryphaena* and *Rachycentron* share a relatively generalized adductor mandibulae, specialized with respect to the primitive carangids (see section on Carangidae) in having A_1 somewhat reduced and inserting narrowly on the maxillo-mandibular ligament.

The pronounced similarities between *Coryphaena* and *Rachycentron* in the adductor mandibulae and most osteological features merely serve to reiterate the lack of evidence for the frequently proposed sister-group relationship between *Rachycentron* and the echeeneids. Further comparison with character states throughout the Carangidae will be required to define these adult similarities as primitive or derived features. The most compelling evidence for a sister-group relationship between *Coryphaena* and *Rachycentron* is found in the morphology of their larvae. As noted above all echeeneid larvae have a similar body form and pattern of development, but the elongate, flattened head of larval echeeneids lacks ornamentation. In contrast, larval dolphin and cobia share identical patterns of head spination: a small posttemporal spine; several spines on the posterior and lateral margin of the preopercle, including one enlarged spine on either side of its angle; and a very large, posterolaterally directed spine on the supraorbital ridge of each frontal bone. Another obvious feature is the presence of laterally swollen pterotics, previously described in *Coryphaena* as blunt

sphenotic spines (Gibbs and Collette, 1959). This specific pattern of head spines is distinctive, but similar features occur in various combinations among carangid larvae, and it is premature to interpret this configuration as synapomorphic for *Coryphaena* and *Rachycentron* until detailed comparisons with carangids have been made.

A specialization clearly unique to the larvae of dolphin and cobia, however, is a modified epithelial cuticle in which are borne minute crown-shaped spicules (Figs. 263A–D, 264A, B). The cuticle itself is composed of large, multinucleate "cells," 40–100 μ in diameter, that appear to continually produce and slough-off the thorny spicules. Each epithelial "cell" produces one spicule, so that these extraordinary structures cover all exposed body surfaces, excluding the pupil of the eye, giving the integument a bristly appearance under magnification (Fig. 264A). They first appear at about 8mm and are present in some individuals as large as 100 mm. Further histological work and electron microscopy will be necessary to determine the composition of the spicules, which may be keratinous. It is clear, however, that they are neither bony nor cartilaginous. Their function is unknown, but as with spinous scales, it seems likely that they are defensive.

The surface and cellular composition of the epithelium of larval echeeneids appear normal, but some modification of the larval epithelium may actually be a primitive feature of carangoids. In larvae of trachinotine and naucratine carangids examined thus far (*Trachinotus*, *Naucrates*, *Seriola*) the epithelial cells are of normal size (~8–12 μ), but their surfaces bear clusters of bumplike structures, seemingly the result of keratinization (Fig. 264C, D). Absence of these modified epithelial cells in larvae of carangine carangids is parsimoniously interpreted as secondary (see Laroche et al., this volume). Their presence in the larvae of *Nematistius* (currently unknown) would corroborate the hypothesis that modified larval epithelium is primitive for carangoids and thus also for echeeneids, suggesting that it has been lost in carangines and echeeneids.

The multinucleate epithelial cells and enlarged, thorny spicules of larval *Coryphaena* and *Rachycentron* represent a complex, shared specialization, unique among percoids. The phylogenetic significance of this synapomorphy is lessened only by the unlikely possibility that loss of a modified epithelium in echeeneids occurred after development of multinucleate cells and spicules. Available evidence strongly points to a *Coryphaena-Rachycentron* sister-group relationship, and it should be clear that further investigations testing this hypothesis must integrate larval, adult and developmental characters.

In conclusion, the study of early life history stages of fishes has traditionally been treated as a discipline somewhat removed from the mainstream of systematic ichthyology. As a result, larval morphology has rarely been incorporated into studies of evolutionary relationships of fishes. It is evident that the larvae of percid fishes exhibit a prodigious array of complexity and diversity that offers exceptional potential applicability to phylogenetic studies. Recognition and application of this potential will be an important step in understanding the complex evolutionary history of the Percoidei.

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