Scorpaeniformes: Development

B. B. Washington, H. G. Moser, W. A. Laroche and W. J. Richards

THE Scorpaeniformes are the fourth largest order of fishes encompassing about 20 families (depending on classification used), 250 genera and over 1,000 species. Representatives of the order are widely distributed from tropical to arctic and antarctic waters. Most scorpaeniforms are benthic or epibenthic with representatives ranging from freshwater to the deep ocean.

The morphologically diverse "mail-cheeked fishes" are named for the bony suborbital stay which extends posteriorly from the third infraorbital to the preopercle. The suborbital stay is the only known character that defines the order; however, some workers have suggested that the stay evolved independently in several lineages and may not indicate monophyly (Matsubara, 1943; Quast, 1965; Poss, 1975). The classification of the scorpaeniforms is controversial, not only in terms of monophyly but also at the subordinal and familial levels. Discussion of the taxonomic status and current hypotheses of relationships is presented in Scorpaeniformes: Relationships (this volume).

Modes of reproduction vary widely within the scorpaeniforms. Many families spawn individual pelagic eggs (Anoplopomatidae, Congiopodidae, Hoplichthyidae and Triglidae), while others spawn demersal clusters of adhesive eggs (Agonidae, Cottidae, Cyclopteridae and Hexagrammidae). Where known, most scorpaenids produce pelagic egg masses enclosed in a gelatinous matrix. Notable exceptions include the scorpaenid genus *Sebastes* and the comephorids of Lake Baikal which give birth to live young.

Larvae of only about 20% of scorpaeniform genera and approximately 10% of the species are known. Because of the wide diversity of form, we are not able to characterize a typical scorpaeniform larva. Early life stages of many scorpaeniforms are characterized by strong head spination as depicted in the generalized scorpaenid larva *Sebastes* (Fig. 220). However, the expression of head spination is variable within the order with elaborations and losses in many groups.

For the purposes of this paper, we consider the Scorpaeniformes to be monophyletic and utilize the broad suborders Scorpaenoidei and Cottoidei as a framework for presentation and discussion. Because of the order's morphological diversity and the lack of an agreed upon classification, discussion of larval taxonomy is focused upon each family. The scorpaeniform family Cyclopteridae is presented in the subsequent article in this volume.

Scorpaenoidei

Eggs

Eggs are known for seven of the scorpaenoid families recognized in Washington et al. (this volume), however, they are known only for a few species (Table 107). Most scorpaenoid families are oviparous and spawn pelagic eggs; however, reproductive modes are varied in the Scorpaenidae. In the scorpaenid subfamilies Scorpaeninae, Pteroinae, and Sebastolobinae the eggs are extruded in bilobed gelatinous egg masses which float at the surface. The eggs are slightly elliptical and have homogeneous yolk, a narrow perivitelline space, and a smooth chorion. A single oil globule is present in *Pterois* (0.16–0.17 mm) and *Sebastolobus* (0.18–0.20 mm); *Scorpaena* lacks an oil globule. In the choridactyline genus *Inimicus,* eggs are extruded singly, are spherical, and lack an oil globule (Table 107). Members of the scorpaenid subfamily Sebastinae are viviparous and give birth to large broods of young which are comparable in stage of development to first-feeding larvae of oviparous scorpaenids. The eggs are retained in the lumen of the ovary after ovulation, range between 0.75 and 1.9 mm, have homogeneous yolk, a narrow perivitelline space, smooth chorion, and one to many oil globules. For the other families for which eggs are known, the eggs are pelagic with none to multiple oil globules (Table 107).

Larvae

At least one larval stage is known for 64 of the more than 600 species of scorpaenoids and for 20 of the 100+ genera. Major reviews of larval scorpaenoids include Sparta (1956b)

TABLE 107. SUMMARY OF EGGS AND LARVAL SIZE CHARACTERISTICS OF THE SCORPAENIFORMES BASED ON AVAILABLE LITERATURE (EXCLUDING CYCLOPTERIDAE).

Family/subfamily species	Type of egg pelagic (P), demersal (D) or viviparous (V)	Egg size (mm)	Number of oil globules	Largest oil globule size (mm)	Body length (mm) at			References
					Hatching	Flexion	Transformation	
SCORPAENOIDEI								
Scorpaenidae								
Sebastinae[1]								
Sebastes capensis	V	—	—	—	3.8	6.2–7.0	ca. 20	Moser et al., 1977
S. fasciatus	V	—	—	—	ca. 5.8	8.5–10.0	—	Moser et al., 1977; Fahay, 1983
S. marinus	V	1.5	—	—	6.7–7.2	8.5–11.8	ca. 24	Moser et al., 1977; Tåning, 1961
S. viviparous	V	—	—	—	5.4–5.8	7.8–10.6	—	Tåning, 1961
S. hubbsi	V	—	—	—	ca. 4.4	ca. 6	—	Uchida et al., 1958
S. inermis	V	—	—	—	4.5	ca. 7	ca. 18	Harada, 1962
S. longispinis	V	1.36	1	—	5.8–6.1	6.4–7.1	—	Takai and Fukunaga, 1971
S. marmoratus	V	0.75–0.95	1	0.2	ca. 4.5	ca. 8	ca. 17	Tsukahara, 1962
S. nigricans	V	1.6	many to 1	—	6.9–7.0	—	ca. 10	Fujita, 1957b, 1959
S. oblongus	V	1.56–1.60	many	—	7.2–7.5	ca. 8.5	12–14	Fujita, 1958
S. pachycephalus	V	1.5–1.9	many	—	6.0–7.0	ca. 8	>13	Shiokawa and Tsukahara, 1961
S. schlegeli	V	—	—	—	ca. 6.1	—	—	Sasaki, 1974
S. steindachneri	V	—	—	—	ca. 4.8	—	—	Sasaki, 1974
S. taczanowskii	V	—	—	—	ca. 5.4	—	—	Sasaki, 1974
S. constellatus	V	—	—	—	4.0–5.0	<7.1	—	Moser and Butler, in press
S. cortezi	V	—	—	—	4.1	7.0–8.3	ca. 17	Moser et al., 1977
S. crameri	V	—	—	—	ca. 5.7	8.0–9.3	16–21	Westrheim, 1975; Richardson and Laroche, 1979
S. dallii	V	—	—	—	5.0	6.2–8.0	<20	Moser and Butler, 1981
S. entomelas	V	—	—	—	4.5–4.6	9.9–12.9	21.7–30.6	Laroche and Richardson, 1981; Moser and Butler, in press
S. flavidus	V	—	—	—	4.5	—	23.6–26.7	DeLacy et al., 1964; Laroche and Richardson, 1980
S. helvomaculatus	V	—	—	—	4.1	7.7–8.0	12.0–18.6	Richardson and Laroche, 1979; Westrheim, 1975
S. jordani	V	—	—	—	5.4	8.0–10.0	27–30	Moser et al., 1977
S. levis	V	—	—	—	5.0	7.6–10.4	ca. 19	Moser et al., 1977
S. macdonaldi	V	—	—	—	4.0–5.0	7.7–9.0	ca. 15	Moser et al., 1977
S. melanops	V	—	—	—	—	—	23.2–30.6	Laroche and Richardson, 1980
S. melanostomus	V	—	—	—	4.5	6.2–7.2	ca. 16	Moser and Ahlstrom, 1978
S. ovalis	V	—	—	—	4.9–5.1	ca. 6.8	—	Moser and Butler, in press
S. paucispinis	V	1.0	1	ca. 0.20	4.6	7.2–9.7	15	Moser et al., 1977
S. pinniger	V	—	—	—	4.0	ca. 7.8	12.8–18.4	Waldron, 1968; Richardson and Laroche, 1979
S. rufus	V	—	—	—	4.6–4.8	6.1–7.6	—	Moser and Butler, in press
S. zacentrus	V	—	—	—	ca. 4.3	7.4–8.5	13.7–19.6	Laroche and Richardson, 1981; Westrheim, 1975
Sebastes Type A	V	—	—	—	4.2	7.0–7.6	—	Moser et al., 1977
Helicolenis dactylopterus	V	—	—	—	2.2	6.0–7.9	>19	Graham, 1939; Sparta, 1956b; Tåning, 1961; Moser et al., 1977; Fahay, 1983
Scorpaeninae								
Pontinus Type A	—	—	—	—	<2.3	4.1–4.6	ca. 15	Moser et al., 1977
Pontinus Type B	—	—	—	—	—	<5.0–5.5	ca. 10	Moser et al., 1977

TABLE 107. CONTINUED.

Family/subfamily species	Type of egg pelagic (P), demersal (D) or viviparous (V)	Egg size (mm)	Number of oil globules	Largest oil globule size (mm)	Body length (mm) at Hatching	Flexion	Transformation	References
Scorpaena guttata	P	1.22–1.29 × 1.16–1.19	0	—	1.9–2.0	4.5–5.7	>13	David, 1939; Orton, 1955d; Moser et al., 1977
S. notata	P	0.76 × 0.88	0	—	<2.7	ca. 6.0	—	Sparta, 1956b
S. porcus	P	0.84 × 0.92	0	—	1.72	ca. 6.7	ca. 12	Sparta, 1956b
S. scrofa	P	0.68 × 0.88	0	—	<2.8	ca. 6.0	ca. 17	Sparta, 1956b
Scorpaena Type A	—	—	—	—	ca. 2.0	4.0–5.5	>12	Moser et al., 1977
Scorpaenodes xyris	—	—	—	—	1.8	4.0–5.4	11–14	Moser et al., 1977
Pteroinae								
Pterois lunulata	P	0.81–0.83	1	0.16–0.17	1.52–1.58	—	—	Mito and Uchida, 1958; Mito, 1963
Dendrochirus brachypterus	P	—	0	—	ca. 1.1	—	—	Fishelson, 1975
Sebastolobinae								
Sebastolobus alascanus	P	1.2–1.4	1	0.18–0.20	ca. 2.6	6.0–7.3	14–20	Pearcy, 1962; Moser, 1974; Moser et al., 1977
S. altivelis	P	1.2–1.4	1	0.18–0.20	ca. 2.6	6.0–7.3	14–20	Moser et al., 1977
Setarchinae								
Ectreposebastes imus	—	—	—	—	<2.8	ca. 5.5	ca. 28	Moser et al., 1977
Choridactylinae								
Inimicus japonicus	P	1.31–1.43	0	—	3.18–3.27	6.4–8.2	ca. 10.4	Fujita and Nakahara, 1955; Mito, 1963; Sha et al., 1981
Minoinae								
Minous sp. (?)	—	—	—	—	ca. 1.8	3.7–5.9	>9.0	Leis and Rennis, 1983
Triglidae								
Chelidonichthys cuculus	P	1.45–1.65	1	—	—	—	—	Padoa, 1956e
C. gurnardus	P	1.45–1.5	1	0.19–0.33	3.2	9.0	17.0	Padoa, 1956e
C. kumu	P	1.20–1.27	1	0.25–0.27	3.12–3.26	—	—	Uchida et al., 1958
C. lastoviza	P	1.29–1.33	1	0.24	—	—	—	Padoa, 1956e
C. lucerna	P	1.25–1.36	1	0.26–0.28	3.2	9.0	17.0	Padoa, 1956e
C. obscurus	P	—	—	—	—	—	—	Padoa, 1956e
Lepidotrigla alata	P	1.22–1.25	1	0.25	2.78–2.92	—	—	Mito, 1963
L. aspera	P	1.16	1	0.21–0.22	3.2	7.0	19.0	Padoa, 1956e
L. japonica	P	1.20–1.40	1	0.25–0.26	—	—	—	Mito, 1963
L. microptera	P	1.26–1.31	1	0.25–0.28	—	—	—	Mito, 1963
Prionotus carolinus	P	0.94–1.15	10–25	—	2.6–2.8	—	8.6	Fritzsche, 1978; Fahay, 1983
P. evolans	P	—	—	—	—	6.3	8.7	Fahay, 1983
Peristediidae								
Peristedion	P	1.7	—	—	—	<11.5	15.0	Padoa, 1956e; Breder and Rosen, 1966
Congiopodidae								
Congiopodus leucopaecilus[2]	P	1.9–2.2	0	NA	—	—	—	Robertson, 1974, 1975a
C. spinifer[2]	P	1.82	0	NA	5–6	—	>12.4	Brownell, 1979; Gilchrist, 1904; Gilchrist and Hunter, 1919; Robertson, 1975a
C. torvus[2]	P?	1.7–1.8	0	NA	—	—	—	Gilchrist, 1904
Platycephalidae								
Platycephalus indicus[2]	P	0.88–1.2	1	0.19–0.25	1.78–2.3	7.3	13	Ueno and Fujita, 1958; Chang et al., 1980
Platycephalidae spp.	—	—	—	—	~2.1	3.9–5.2	—	Leis and Rennis, 1983

TABLE 107. CONTINUED.

Family/subfamily species	Type of egg pelagic (P), demersal (D) or viviparous (V)	Egg size (mm)	Number of oil globules	Largest oil globule size (mm)	Body length (mm) at Hatching	Flexion	Transformation	References
Hoplichthyidae								
Hoplichthys haswelli[2]	P	0.85–0.90	1	0.15	—	—	—	Robertson, 1975a
Hoplichthys sp.[2]	—	—	—	—	—	≥8	—	Okiyama (unpubl. MS)
Dactylopteridae								
Dactylopterus volitans	P	~0.8	1	0.14	1.8	<7	ca. 16	Fritzsche, 1978; Sanzo, 1933c; Padoa, 1956e
Daicocus petersoni	—	—	—	—	—	4.3	ca. 10	Senta, 1958
Dactyloptena sp.	—	—	—	—	—	3.9–6.5	ca. 10	Leis and Rennis, 1983
COTTOIDEI								
Agonidae								
Agonomalus mozinoi	D	~1.0	—	—	5.5	—	—	Marliave, 1978
Agonopsis chiloensis[2]	—	—	—	—	—	—	—	de Ciechomski, 1981
Agonus cataphractus	D	1.7–2.2	Several coalesce	0.7–0.75	6.3–8.0	—	~14 mm	Russell, 1976; Ehrenbaum, 1904; McIntosh and Prince, 1890
A. decagonus[2]	—	—	—	—	—	—	—	Ehrenbaum, 1905–1909
Aspidophoroides monopterigius[2]	—	—	—	—	—	—	—	Dannevig, 1919; Bigelow and Schroeder, 1953
A. olriki[2]	—	—	—	—	—	—	—	Dunbar, 1947
Bothragonus swani	D	2	—	—	7.5	~10–12	>16	Marliave, 1975
Pallasina barbata[2]	—	—	—	—	—	—	—	Marliave, 1975
Xeneretmus latifrons[2]	—	—	—	—	~7	~10	—	Marliave, 1975
Anoplopomatidae								
Anoplopoma fimbria	P	2.0–2.1	—	—	<8.8	11–14	>33	Ahlstrom and Stevens, 1976; Hart, 1973; Kobayashi, 1957
Comephoridae								
Comephorus baicalensis	V	N/A	—	—	9.4	—	>48	Chernyayev, 1975
C. dybowskii	V	N/A	—	—	8.2	~13	~21	Chernyayev, 1971
Cottidae								
Artedius creaseri	—	—	—	—	~3.5	5.7–7.9	13–14	Washington, 1981
A. fenestralis	—	—	—	—	3.5–3.8	5.9–6.8	12–13	Washington, 1981; Marliave, 1975
A. harringtoni	—	—	—	—	~3.0	5.2–6.4	12–14	Washington, 1981
A. lateralis	D	1.07	1	0.22	3.9–4.5	5.0–6.3	9.5–10.5	Washington, 1981; Marliave, 1975; Budd, 1940
A. meanyi	—	—	—	—	~3	6.3–9.4	15–20	Washington, 1981
Ascelichthys rhodorus	D	1.7–2.0	—	—	6.0	8.8–9.0	12–15	Matarese and Marliave, 1982
Blepsias cirrhosus[2]	—	—	—	—	—	≤11	—	Marliave, 1975; Richardson, 1981a
Chitonotus pugetensis[2]	D	1.02–1.05	1 large 5–8 small	0.3	2.9–3.0	—	>16	Misitano, 1980; Richardson and Washington, 1980
Clinocottus acuticeps	D	1.0–1.2	—	—	3.1–3.3	5.5–7.3	12.6–15.0	Washington, 1981; Washington, pers. obs.
C. analis[2]	D	1.2–1.3	several large	0.18	4.2–4.5	—	—	Budd, 1940; Washington, 1981
C. embryum	—	—	—	—	~4.0	6.4–9.6	13–14	Washington, 1981
C. globiceps	D	1.5–2.0	—	—	5.1–5.4	6.2–8.1	12.9–13.5	Washington, 1981
C. recalvus	D	1.25–1.35	—	—	4.6–4.7	—	9–11	Morris, 1951
Cottus asper	D	—	—	—	5.5–6.3	~7.0	—	Stein, 1972; Richardson and Washington, 1980
C. bairdi	D	1–3	1	—	6.3–6.9	—	9–10	Heufelder, 1982
C. carolinae	D	2.6–3.3	—	—	6 [illegible]	—	9.5–10	Wallus and Granneman, 1979
C. cognatus	D	2–3	—	—	5.7–6.3	—	8–11	Wallus and Granneman, 1979
C. nozawae	D	3.1–3.5	—	—	10.5	—	—	Watanabe, 1976
C. reinii[2]	D	2.0–2.6	1	—	—	—	—	Watanabe, 1976

TABLE 107. CONTINUED.

Family/subfamily species	Type of egg pelagic (P), demersal (D) or viviparous (V)	Egg size (mm)	Number of oil globules	Largest oil globule size (mm)	Body length (mm) at Hatching	Body length (mm) at Flexion	Body length (mm) at Transformation	References
C. ricei[2]	D	—	—	—	7–8	—	—	Heufelder, 1982
Enophrys bison	D	1.7–1.8	1	0.36	4.9–5.2	5.2–7.0	7.6–7.8	Misitano, 1978; Richardson and Washington, 1980
E. bubalis (Taurulus)	D	1.5–1.8	several	—	5.5–5.8	—	12	Russell, 1976
E. lilljeborgi (Taurulus)[2]	D	2.0	1	0.38	~4.0	—	—	Russell, 1976
Gymnocanthus herzensteini	D	1.6–1.7	few	—	5.6–6.1	—	—	Kyushin, 1970
G. ventralis[2]	—	—	—	—	—	—	—	Ehrenbaum, 1905–1909
Hemilepidotus gilberti[2]	—	—	—	—	—	—	—	Hattori, 1964
H. hemilepidous	D	1.5–1.6	1	0.31–0.56	~5–6	~9.1	>19–23	Richardson and Washington, 1980
H. jordani	—	—	—	—	—	—	—	Gorbunova, 1964a[6]
H. spinosus	—	—	—	—	~5	7.6–10.1	19	Richardson and Washington, 1980
H. zapus	—	—	—	—	—	7–12	—	Matarese and Vinter (in prep.)
Hemitripterus americanus	D	4	1 large	0.8	10–14	~14.5	>18.8	Fahay, 1983; Fuiman, 1976
H. villosus	D	—	—	—	10.9–11.6	≤14.4	~20	Okiyama and Sando, 1976
Icelus bicornis[2]	—	—	—	—	—	—	—	Russell, 1976; Ehrenbaum, 1905–1909
Leptocottus armatus[2]	D	1.4–1.5	present	—	3.9–4.8	~8	15–20	Richardson and Washington, 1980; Jones, 1962
Myoxocephalus aenaeus	D	1.5–1.7	2+	0.2	4.7–6.3	6.8	—	Fahay, 1983; Lund and Marcy, 1975
M. octodecimspinosus	D	1.9–2.3	1 or more	diameter varies	6.3–7.3	9–11	~15	Fahay, 1983; Colton and Marak, 1969
M. quadricornus	D	1.5–2.2[3]	—	—	~8	ca. 10.5+	—	Khan and Faber, 1974
M. scorpius	D	1.8–2.5	several	0.4–0.5	7.4–8.6	9–15	17–20	Russell, 1976; Ehrenbaum, 1905–1909; McIntosh and Masterman, 1897
M. thompsoni[2]	—	—	—	—	8–10	—	—	Heufelder, 1982
Nautichthys oculofasciatus	D	2–2.5	—	—	9	~9–11	~26	Richardson and Washington, 1980; Marliave, 1975
Oligocottus maculosus	D	1.3–1.5	1 large many small	—	4.2–4.5	7.2–7.6	7.5–10	Washington, 1981; Stein, 1973
O. snyderi	D	1.2–1.3	—	—	4.47	6.2–8.4	11–13	Washington, 1981; Stein, 1972
Orthonopias triacis[2]	D	0.9–1.0	1 large 2 small	—	2.9–3.8	—	—	Bolin, 1941
Paricelinus hopliticus[2]	—	—	—	—	<5.6	—	~25	Richardson and Washington, 1980
Pseudoblennius cottoides[2]	D	2.0–2.2	—	—	12.5	—	—	Watanabe, 1976
Radulinus asprellus	—	—	—	—	≤4.7	7.2–10.9	≳15	Richardson and Washington, 1980
R. boleoides[2]	—	—	—	—	—	~8.7	—	Richardson and Washington, 1980
Rhamphocottus richardsoni	D	2.5–2.8	—	—	6–7	8.4	~14–15	Richardson and Washington, 1980; Marliave, 1975; Blackburn, 1973
Scorpaenichthys marmoratus	D	1.4–1.9	1 large several small	0.27	5.8–6.0	7.5–8.7	14–15[4]	Richardson and Washington, 1980; O'Connell, 1953
Triglops murrayi[2]	—	—	—	—	7–8	12	—	Fahay, 1983
T. pingeli[2]	D	2.0	many	—	—	—	—	Bigelow and Schroeder, 1953; Rass, 1949
Cottocomephoridae								
Abyssocottus bergianus[2]	D	3.2–3.3[3]	—	—	—	—	—	Taliev, 1955
A. godlewskii[2]	D	2.8–3.0[3]	—	—	~5	—	—	Taliev, 1955
A. korotneffi[2]	D	~4.5[3]	—	—	—	—	—	Taliev, 1955

TABLE 107. CONTINUED.

Family/subfamily species	Type of egg pelagic (P), demersal (D) or viviparous (V)	Egg size (mm)	Number of oil globules	Largest oil globule size (mm)	Body length (mm) at Hatching	Flexion	Transformation	References
A. pallidus[2]	D	2.6–2.8[3]	—	—	~6	—	~16	Taliev, 1955
Asprocottus gibbosus[2]	D	3.3–3.4[3]	—	—	—	—	—	Taliev, 1955
A. herzensteinii[2]	D	3.0–3.2[3]	—	—	—	—	≳9	Taliev, 1955
A. megalops[2]	D	3.5–3.7[3]	—	—	—	—	—	Taliev, 1955
Batrachocottus baicalensis	D	~3.0	3–10 small	—	10.0 post-flexion[5]	N/A	~16	Chernyayev, 1981
B. multiradiatus[2]		~4.0	—	—	~6.0	—	—	Taliev, 1955
B. nikolskii[2]	D	2.9–3.1	—	—	—	—	—	Taliev, 1955
B. uschkani[2]	—	—	—	—	—	—	—	Taliev, 1955
Cottinella boulengeri[2]	D	2.8[3]	—	—	—	—	—	Taliev, 1955
Cottocomephorus grewingki	D	1.2–1.8	—	—	~6.8–7.0	—	~19	Taliev, 1955
C. inermis[2]	D	1.5–1.7	—	—	—	—	—	Taliev, 1955
Paracottus kessleri	D	1.0–1.45	1 large	0.3	5.2–5.4	~6.2	~20	Chernyayev, 1978
P. kneri	D	2.0–2.3	—	—	6.8–7.1	—	>10.8	Taliev, 1955
Procottus jeittelesi[2]	D	2.5–3.3	—	—	—	—	—	Taliev, 1955
Hexagrammidae								
Hexagrammos agrammys	D	2.02–2.07	many coalesce to 1	—	8.15–8.61	~11	≲40–48	Fukuhara, 1971
H. decagrammus	D	—	—	—	ca. 8	15–18	~30[4]	Kendall and Vinter, 1984
H. lagocephalus	D	2.0–2.6	many	—	~8–9	12–15	ca. 29	Kendall and Vinter, 1984; Gorbunova, 1964b (as *H. decagrammas*)
H. octogrammus	D	1.75–2.10	many	0.8	6–7	~12–15	~30[4]	Gorbunova, 1964b
H. otakii	D	2.3–2.7	many	—	6.5–7.0	~11	—	Gorbunova, 1964b; Yusa, 1960c
H. stelleri	D	—	—	—	~7–9	~12–15	~30[4]	Kendall and Vinter, 1984
Ophiodon elongatus	D	2.9–3.2	1	—	~9.0	11–15	~30[4]	Kendall and Vinter, 1984
Pleurogrammus monopterygius	D	2.1–2.8	many	1.38–1.4	10–11	~14–19	~30[4]	Yusa, 1967; Gorbunova, 1964b
Oxylebius pictus	D	—	—	—	4–5	7–9	~45	Kendall and Vinter, 1984; DeMartini, 1976
Zaniolepis sp.	—	—	—	—	~2.5	~6	?15	Kendall and Vinter, 1984
Normanichthyidae								
Normanichthys crockeri	—	—	—	—	<4.4	7–9	>16	Balbontin and Perez, 1980
Psychrolutidae								
Dasycottus setiger[2]	—	—	—	—	—	~10	—	Richardson, 1981a
Gilbertidia sigalutes[2]	D	2.3	—	—	—	~13–15	~23	Marliave, 1975
Malacocottus sp.	—	—	—	—	—	~7–9.8	≲24	Richardson, 1981a
Psychrolutes paradoxus[2]	—	—	—	—	—	~10.5	~13–14	Marliave, 1975

[1] Ovarian or newborn larvae of 30 species of *Sebastes* not listed here are described in Efremenko and Lisovenko (1970), Westrheim (1975), and Moser et al. (1977).
[2] Incomplete description with illustration.
[3] Ripe ovarian egg diameter.
[4] Pelagic juvenile stage.
[5] Hatch at advanced postflexion stage.
[6] Confusion exists regarding correct identification [Matarese and Vinter (in prep.)].

and Moser et al. (1977) on scorpaenids and Sparta (1956b) and Richards (in prep.) on triglids and peristediids.

Scorpaenidae (Figs. 220–223).—This is the largest and most diverse scorpaenoid family with about 44 genera and more than 350 species. The classification and relationships of the family are in controversy (Washington et al., this volume) and we follow their subfamily groupings.

Sebastinae.—Barsukov (1981) includes 3 genera and 114 species in this temperate and boreal group. *Sebastes* with about 106 species accounts for almost ⅓ of the species in the order. At least a single larval stage is known for 62 species of *Sebastes* and flexion or postflexion stages have been described for about 32 of these (Table 107). Larval stages have been described for one of the 6 species of *Helicolenus* and are unknown for the two species of *Hozukius*.

In *Sebastes* most of the yolk is utilized before hatching while the eggs lie freely within the ovary. Hatching precedes extrusion and newborn larvae range from 3.8 to 7.5 mm in length among the various species and have functional eyes, jaws, and pectoral fins. The finfold is slightly inflated and has minute cell-like

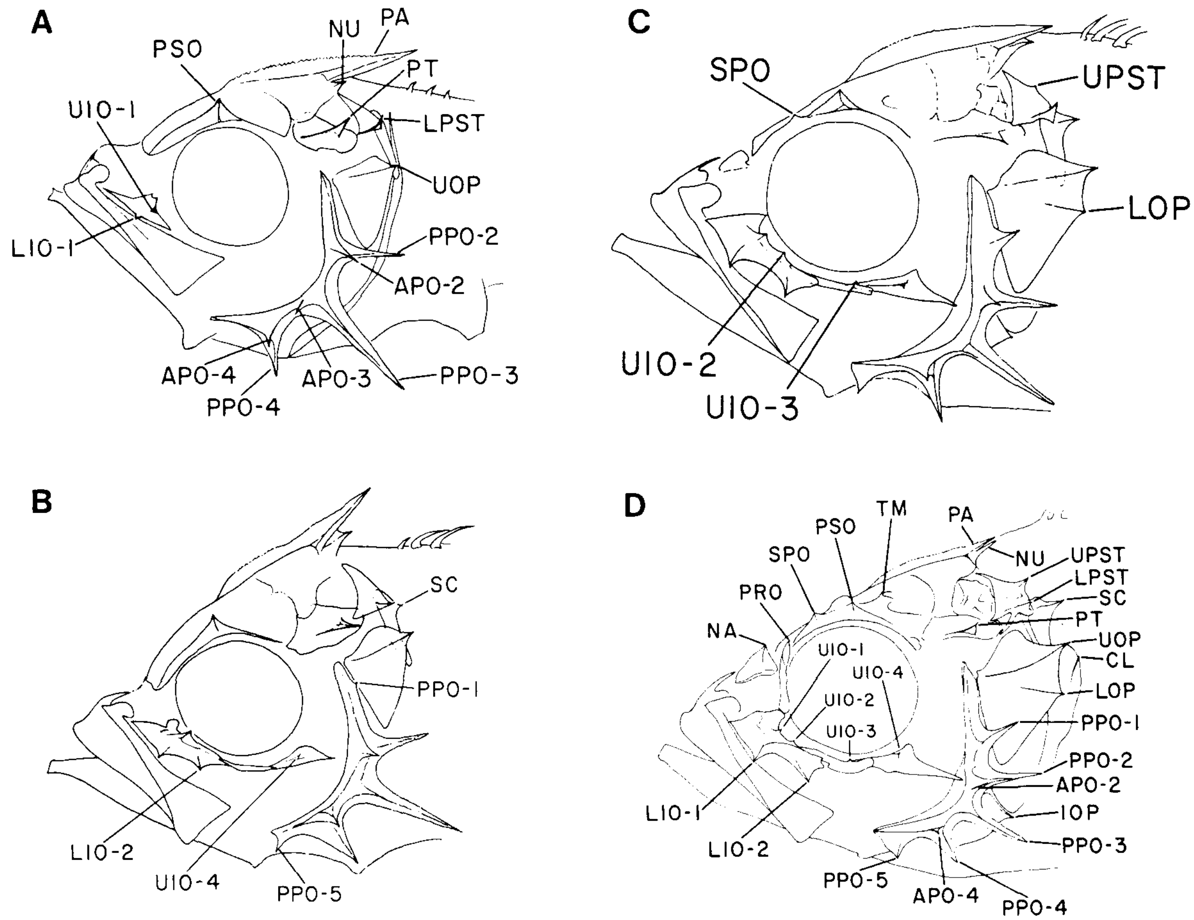


Fig. 220. Head spines in 6.2 mm (A), 8.2 mm (B), 10.0 mm (C) and 16.0 mm (D) stained larvae of *Sebastes melanostomus*. Abbreviations of head spines: APO-2, 2nd anterior preopercular; APO-3, 3rd anterior preopercular; APO-4, 4th anterior preopercular; CL, cleithral; IOP, interopercular; LIO-1, 1st lower infraorbital; LIO-2, 2nd lower infraorbital; LOP, lower opercular; LPST, lower posttemporal; NA, nasal; NU, nuchal; PA, parietal; PPO-1, 1st posterior preopercular; PPO-2, 2nd posterior preopercular; PPO-3, 3rd posterior preopercular; PPO-4, 4th posterior preopercular; PPO-5, 5th posterior preopercular; PRO, preocular; PSO, postocular; PT, pterotic; SC, supracleithral; SPO, supraocular; TM, tympanic; UIO-1, 1st upper infraorbital; UIO-2, 2nd upper infraorbital; UIO-3, 3rd upper infraorbital; UIO-4, 4th upper infraorbital; UOP, upper opercular; UPST, upper posttemporal. From Moser and Ahlstrom, 1978.

structures concentrated along the dorsal and ventral margins. Notochord flexion occurs at about 6–12 mm and transformation at 15–25 mm (Table 107). Many species have a distinct pelagic juvenile stage which can reach almost 60 mm body length.

Preflexion larvae have a slender body (body depth 13–23% of body length) and compact gut; snout–anus distance increases from about 40–50% of body length to over 60% in some species during the larval period. The caudal and pectoral fins begin forming first, followed by the pelvics and then the dorsal and anal fins. The pectoral fins range from short and rounded to elongate and fan-shaped, reaching almost 50% of body length in *S. levis* (Fig. 221). The pectoral fin base is shallow (typically 7–13% of body length) in comparison with other subfamilies. Ossification of skeletal elements begins early in the larval period and proceeds rapidly as in other scorpaenoids; vertebral ossification follows the pattern of other scorpaeniforms, with the neural arches ossifying before the centra (Moser, 1972).

Pigmentation in newborn larvae consists of a melanistic sheath over the gut and a postanal series along the ventral midline. Some species also have a dorsal midline series which may develop gradually. Pigment increases with development, appearing on the head (above brain, on jaws and opercular region), fins, and caudal peduncle. Often the pectoral fins (both base and blade) have diagnostic pigment patterns. Several of the western Pacific species are heavily pigmented with the head and body covered by a sheath of melanophores (Fig. 221).

Head spines are a prominent feature of all *Sebastes* larvae. Pterotics, parietals (usually serrated), and preopercular spines

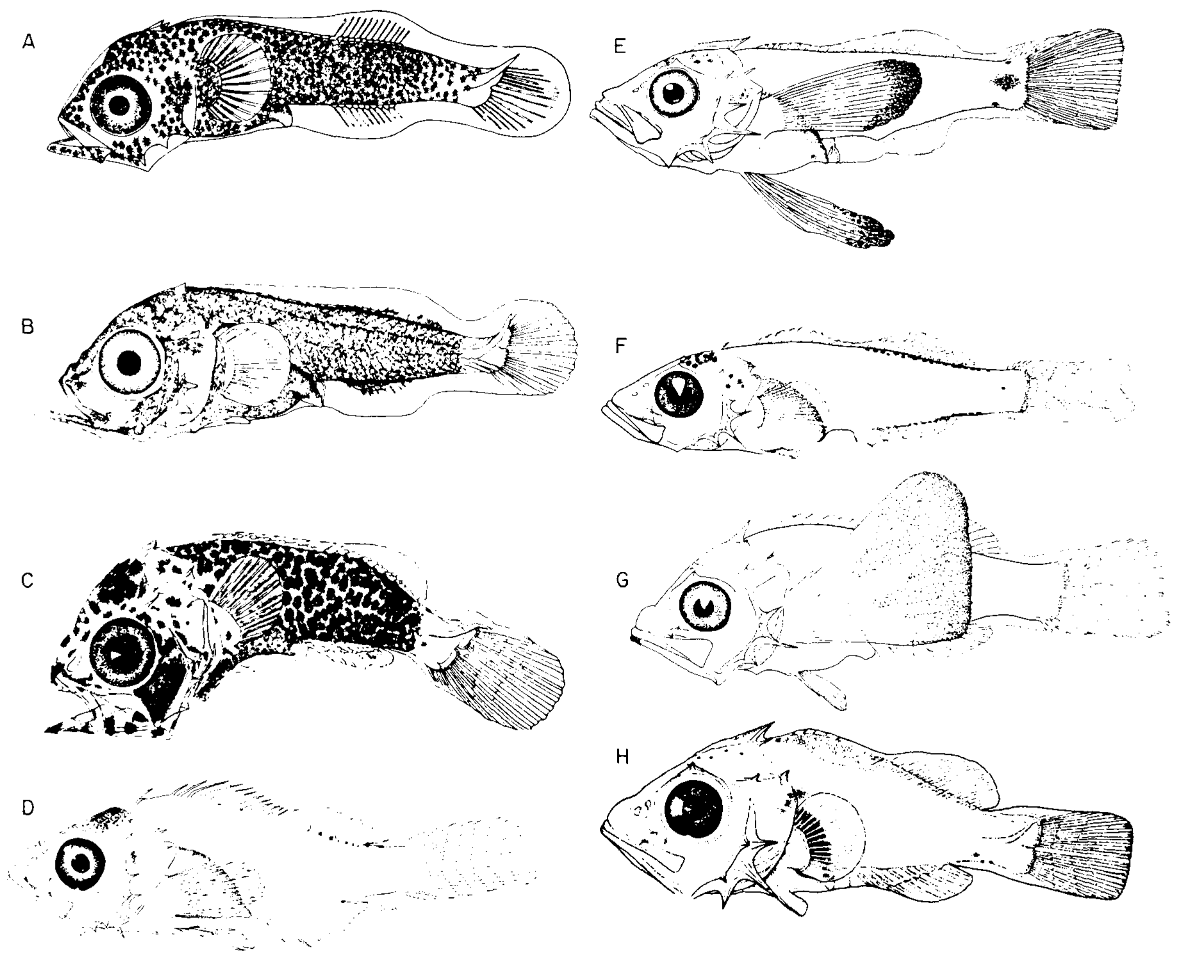


Fig. 221. Larvae of Scorpaenidae. (A) *Sebastes oblongus*, 8.5 mm TL (from Fujita, 1958); (B) *S. longispinis*, 7.1 mm TL (from Takai and Fukunaga, 1971); (C) *S. hubbsi*, 6.0 mm TL (from Uchida et al., 1958); (D) *S. zacentrus*, 12.7 mm SL (from Laroche and Richardson, 1981); (E) *S. paucispinis*, 10.5 mm SL (from Moser et al., 1977); (F) *S. jordani*, 15.5 mm SL (ibid.); (G) *S. levis*, 10.4 mm SL (ibid.); (H) *Helicolenus dactylopterus*, 10.0 mm (from Tåning, 1961).

form during the preflexion period in most species, and other spines appear gradually thereafter (Fig. 220). Although there is variation in larval spine complements (Moser and Ahlstrom, 1978; Moser and Butler, 1981; Richardson and Laroche, 1979; Laroche and Richardson, 1980, 1981), it is apparent that 1) the adult head spine complement develops during the larval period and 2) certain spines develop during the larval period but are not present in adults. Of the latter, the most prominent are the pterotic, anterior preoperculars, lower posttemporal, and upper infraorbitals.[1] The fact that these spines do occur in adults of other subfamilies is of possible phylogenetic significance (Moser and Ahlstrom, 1978).

[1] Upper infraorbitals are present in adults of a few species of *Sebastes*.

Helicolenus is viviparous, the fertilized eggs developing in a gelatinous matrix within the ovary (Graham, 1939; Krefft, 1961). Larvae of *H. dactylopterus* have been described; hatching and birth occur at a smaller size (2.2 mm) than in *Sebastes*, although sizes at notochord flexion and transformation are similar (Table 107). Larvae are moderately deep-bodied (Fig. 221); body depth averages 29%, 33%, and 49% of body length for preflexion, flexion and postflexion stages. Head and gut shape are similar to that of *Sebastes*. The pectoral fin is moderate in size and rounded; the base is slightly deeper than in most species of *Sebastes*. Sequence of fin formation is similar to that of *Sebastes*. A mass of spongy tissue develops anteriorly in the dorsal finfold in preflexion larvae and persists through most of the larval period; the structure is apparently unique. The early pigment pattern consists of a dorsolateral gut sheath, melanophores above the brain, on the lower jaw, in a short median ventral series just

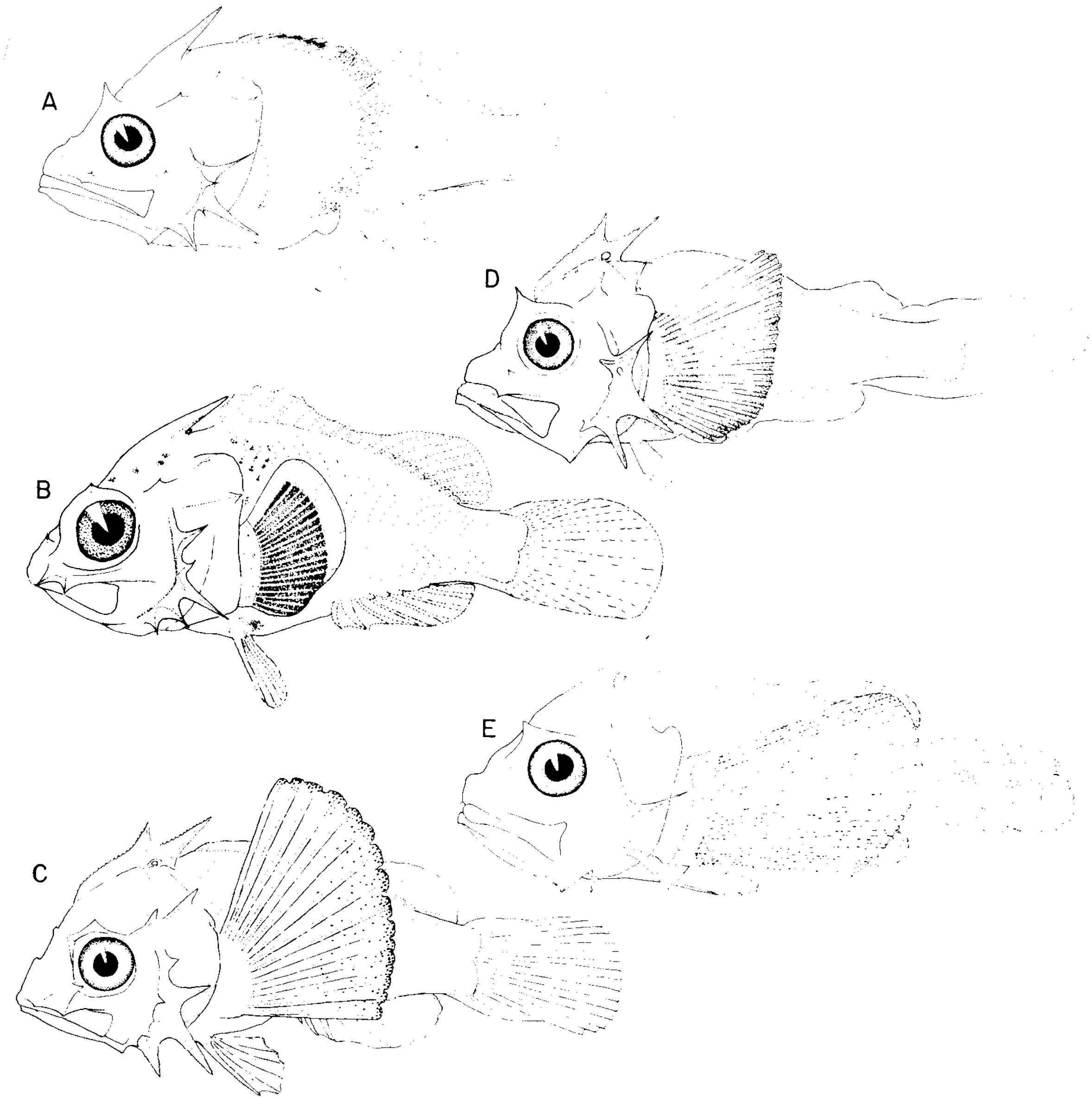


Fig. 222. Larvae of Scorpaenidae. (A) *Pontinus* Type A, 8.0 mm SL (from Moser et al., 1977); (B) *Scorpaena* Type A, 8.0 mm SL (ibid.); (C) *Scorpaenodes xyris*, 6.2 mm SL (ibid.); (D) *Sebastolobus* sp. 7.7 mm SL (ibid.); (E) *Ectreprosebastes imus*, 6.7 mm SL (ibid.).

anterior to the caudal fin, and on the distal and proximal regions of the pectoral fin blade (Fig. 221). Head spine formation is similar to that of *Sebastes* species which have full larval complements, except that spines are lacking on the 2nd infraorbital bone and the cleithrum.

Scorpaeninae.—Larval stages are known for only 3 of the 15 genera in this subfamily; a total of 8 species (or generic types) out of about 150 have been described (Table 107; see Sparta, 1956b and Moser et al., 1977, for major reviews). Hatching occurs at about 2.0 mm or less; newly-hatched larvae have a large elliptical yolk sac, unpigmented eyes, pectoral fin buds, and lack a mouth. The finfold is inflated and, along with the body skin, forms a balloon-like envelope that is attached principally at the snout and pectoral regions (Orton, 1955d). Cell-like granulations cover the entire envelope but are concentrated

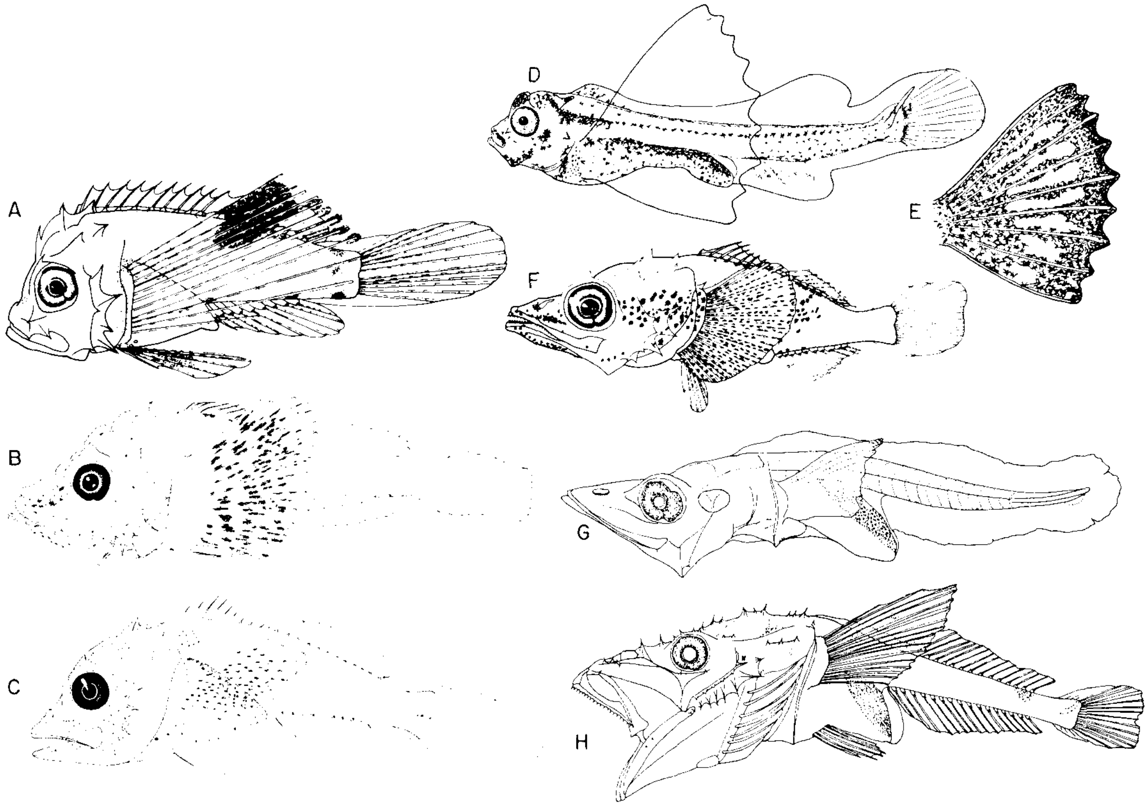


Fig. 223. Larvae of Minoinae (A), Triglidae (B, C), Congiopodidae (D, E), Platycephalidae (F), Hoplichthyidae (G, H). (A) *Minous* sp.?, 6.4 mm SL (from Leis and Rennis, 1983); (B) *Prionotus* sp., 6.4 mm SL (original); (C) *Prionotus stephanophrys*, 8.8 mm SL (CalCOFI 7510 sta. 117.70); (D) *Congiopodus spinifer*, 10.8 mm SL (from Brownell, 1979); (E) Detail of pectoral fin of *Congiopodus spinifer* (ibid.); (F) Platycephalidae, unidentified, 6.2 mm SL (from Leis and Rennis, 1983); (G) *Hoplichthys* sp., 7.1 mm SL (original, courtesy M. Okiyama); (H) *Hoplichthys* sp. 17.2 mm SL (ibid.).

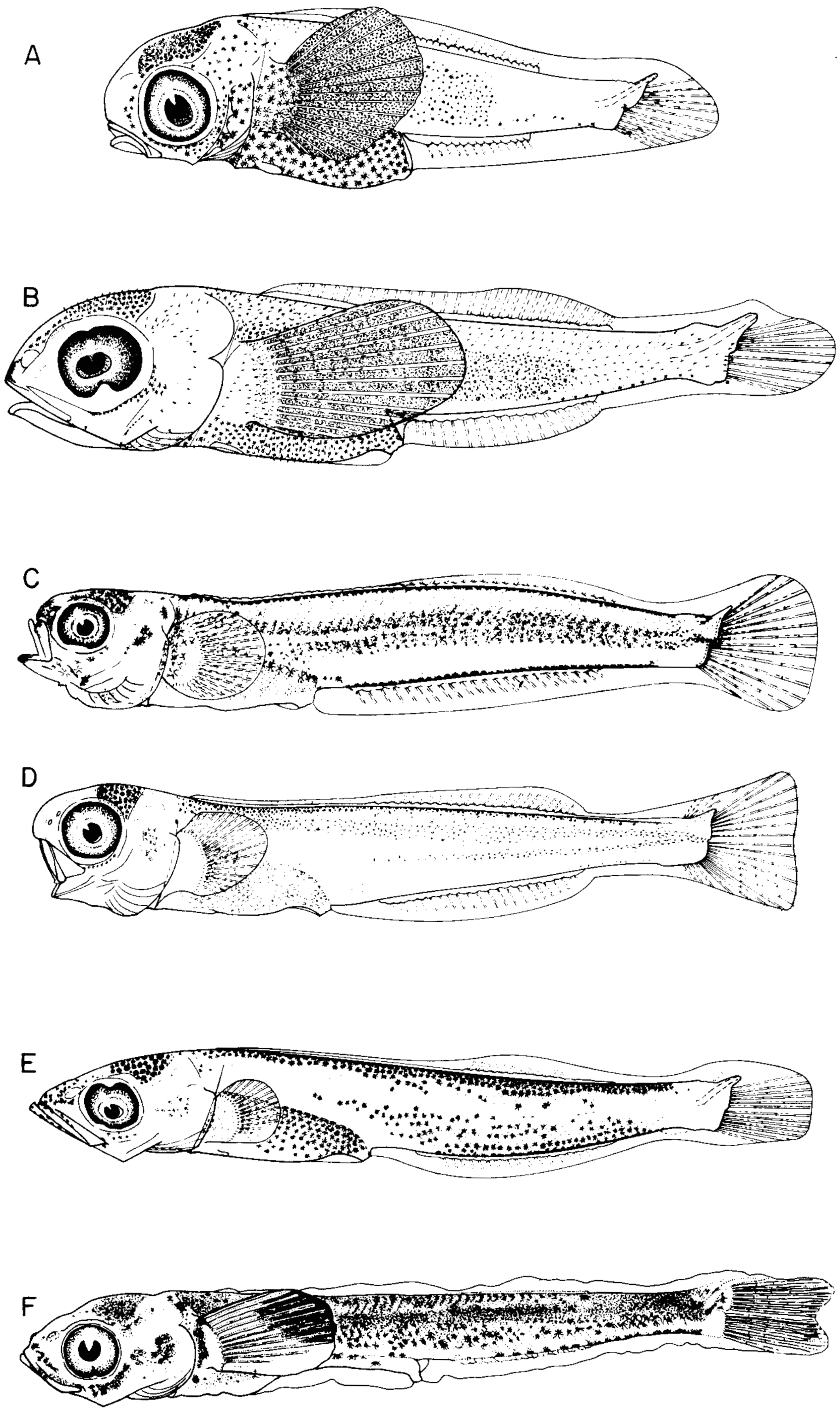
at the median edges of the finfold. Flexion occurs at a small size (4–6 mm) as does transformation (10–17 mm). Larvae are relatively deep-bodied during preflexion and flexion and more so during postflexion, when body depth averages 38–40% of body length for the genera listed in Table 107. The gut is compact and the head becomes massive. Snout-anus length increases from 46–50% of body length in preflexion larvae to 61–67% in postflexion larvae. The snout has a steep profile (Fig. 222).

The pectoral fins are well developed and deep-based; fin base depth is 13–15% of body length in preflexion larvae and 14–18% in flexion and postflexion larvae. They are fan-shaped and enlarged in *Scorpaenodes*; fin length attains 41% of body length during the postflexion stage. They are smaller but distinctively shaped in *Scorpaena* (fan-shaped with scalloped margin) and *Pontinus* (slightly wing-shaped). Ossification of fin rays, as well as skeletal elements, occurs in early larvae (4–5 mm). The caudal, pectoral, and pelvic rays begin ossifying almost simultaneously, followed immediately by the dorsal and anal fins.

Preflexion larvae have a postanal ventral midline series of melanophores ranging in number from 2–7 in *Scorpaena guttata* to 12–18 in *Scorpaenodes xyris*. The most prominent pigment is on the pectoral fins; typical patterns are a concentration at the distal margin (*Scorpaenodes*, some *Pontinus*, some *Scorpaena* spp.), a solid covering over most of the fin (some *Scorpaena* spp.), or a diagonal bar (some *Pontinus* spp.). A melanistic sheath develops over the dorsal surface of the gut and gas bladder in most species of *Scorpaena*, whereas in *Scorpaenodes* and *Pontinus* only the gas bladder is pigmented. Other pigment in *Scorpaena* forms at the cleithral juncture and above the brain (Fig. 222).

→

Fig. 224. Larvae of the *Oxylebius* scorpaeniform group (A, B) and the hexagrammid group (C–F) of Washington and Richardson (MS) (see Washington et al., this volume). (A) *Oxylebius pictus*, 8.5 mm SL (from Kendall and Vinter, 1984); (B) *Zaniolepis* sp., 7.7 mm SL (ibid.); (C) *Hexagrammos octogrammus*, 15.2 mm SL (ibid.); (D) *Pleurogrammus monopterygius*, 20.5 mm SL (ibid.); (E) *Ophiodon elongatus*, 15.4 mm SL (ibid.); (F) *Anoplopoma fimbria*, 13.8 mm SL (Ahlstrom and Stevens, 1976).


A
B
C
D
E
F

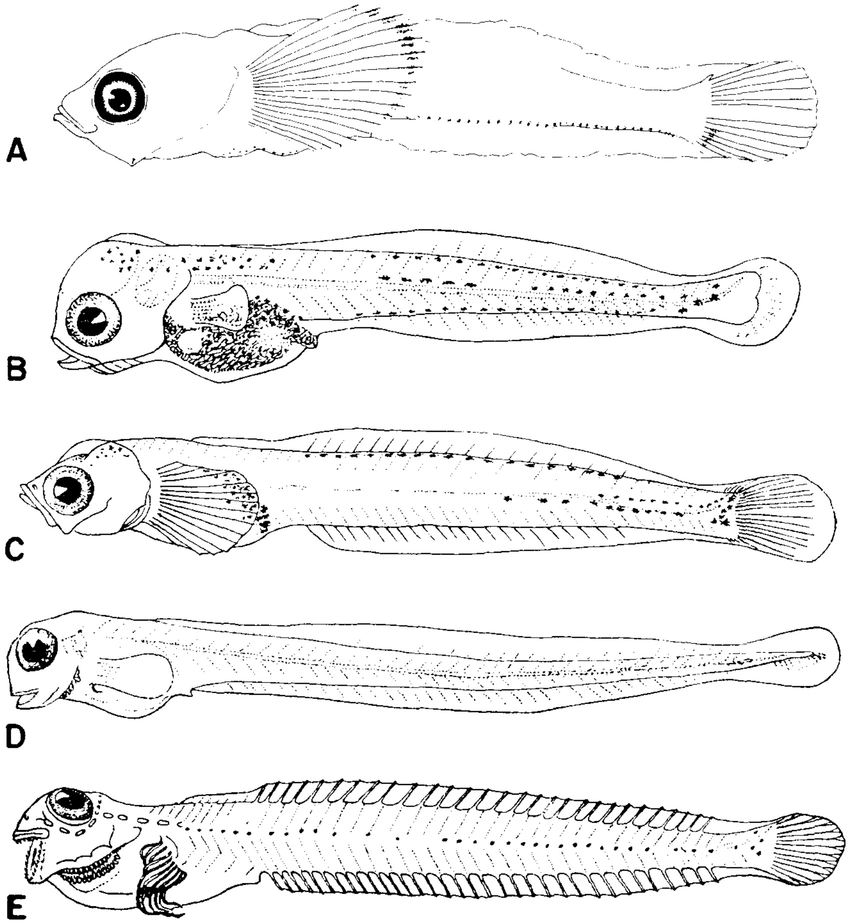


Fig. 225. Larvae of Normanichthyidae (A), Cottocomephoridae (B, C), Comephoridae (D, E). (A) *Normanichthys crockeri*, 8.5 mm SL (original); (B) *Cottocomephorus grewingki*, 7.4 mm (from Taliev, 1955); (C) *Cottocomephorus inermis*, 11.2 mm (ibid.); (D) *Comephorus baicalensis*, 6.9 mm (ibid.); (E) *Comephorus baicalensis*, 21.3 mm (ibid.).

Cranial spine development is similar to that in sebastines. The pterotic, parietal, postocular (supraocular crest), posterior preoperculars (2nd, 3rd, and 4th) anterior preoperculars (2nd and 4th) and lower posttemporal develop during the preflexion period. The lower infraorbital (1st), upper infraorbitals (1st and 4th), posterior preoperculars (1st and 5th), nuchal, supracleithral, cleithral, upper opercular, and lower opercular spines appear during postflexion. Late in the postflexion stage the lower infraorbital (2nd), nasal, preocular, and supraocular spines appear. Spines which do not develop in scorpaenine larvae but are present in adults of most genera are the upper infraorbitals (2nd and 3rd), upper posttemporal, tympanic, and sphenotic. In *Scorpaenodes* the nuchal spine develops during the preflexion period and exceeds the parietal spine in length, giving the parietal ridge a bifurcate appearance. In other scorpaenines and all other scorpaenids except *Sebastolobus*, the nuchal develops late and is excluded from the parietal ridge.

Pteroinae.—Early preflexion larvae have been described for *Pterois lunulata* and *Dendrochirus brachypterus* (Table 107). Newly-hatched larvae are small (1.1–1.6 mm) and similar in morphology to those of Scorpaeninae. The pectoral fins are large and fan-shaped with pigment at the distal margin. Postanal pigment in *Pterois* consists of ventral and dorsal midline series. In *Dendrochirus* this pigment coalesces to form a band.

Sebastolobinae.—Life history series have been described for *Sebastolobus alascanus* and *S. altivelis* (Moser, 1974). Larvae are 2.6 mm at hatching, 6.0–7.3 mm at notochord flexion, and 14–20 mm at transformation. The distinctive pelagic juveniles (up to 56 mm in *S. altivelis*) have a prolonged midwater existence before settling to the deep shelf and slope habitat of the adults. Larval morphology is similar to that of scorpaenines. The pectoral fins are large, deep-based, and fan-shaped (Fig. 222); their rays are the first to ossify, followed by the caudal rays and then

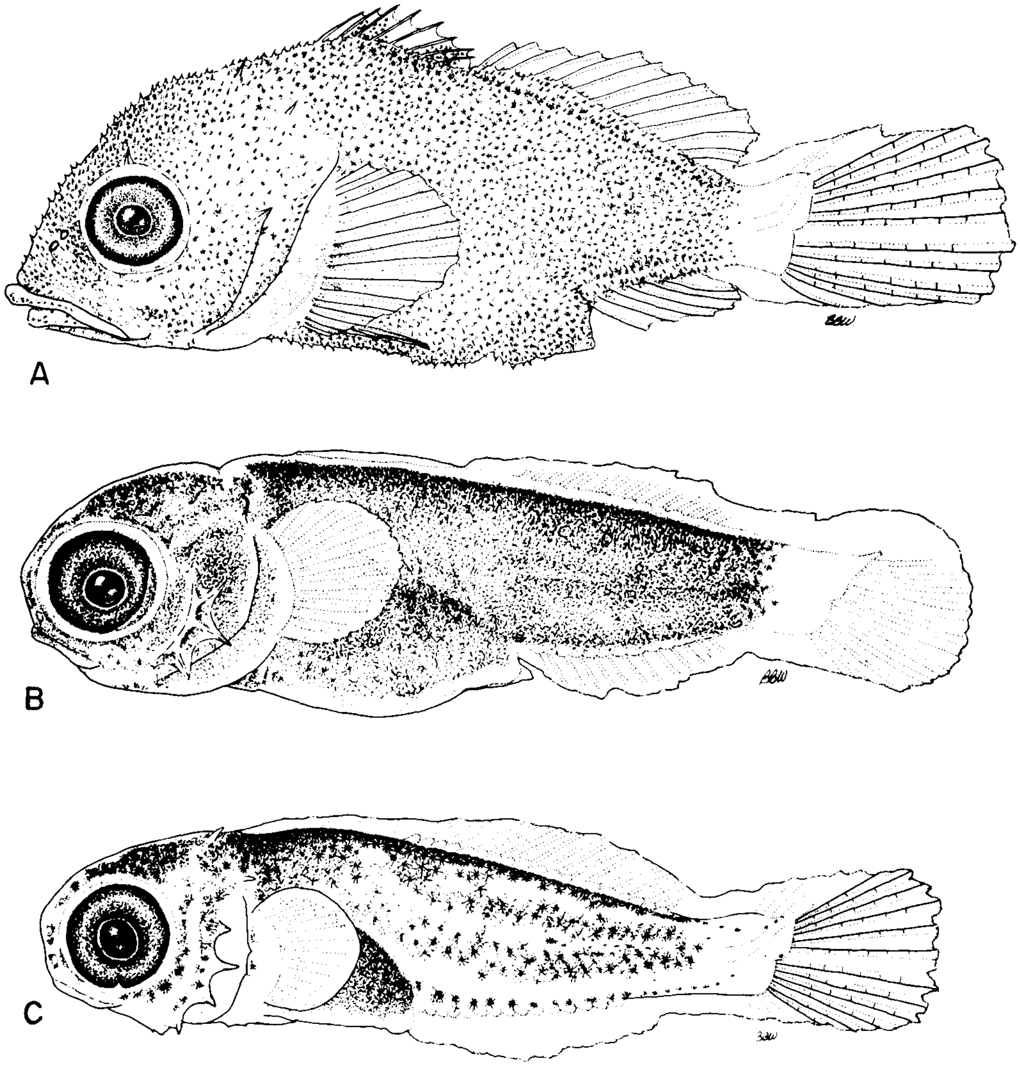
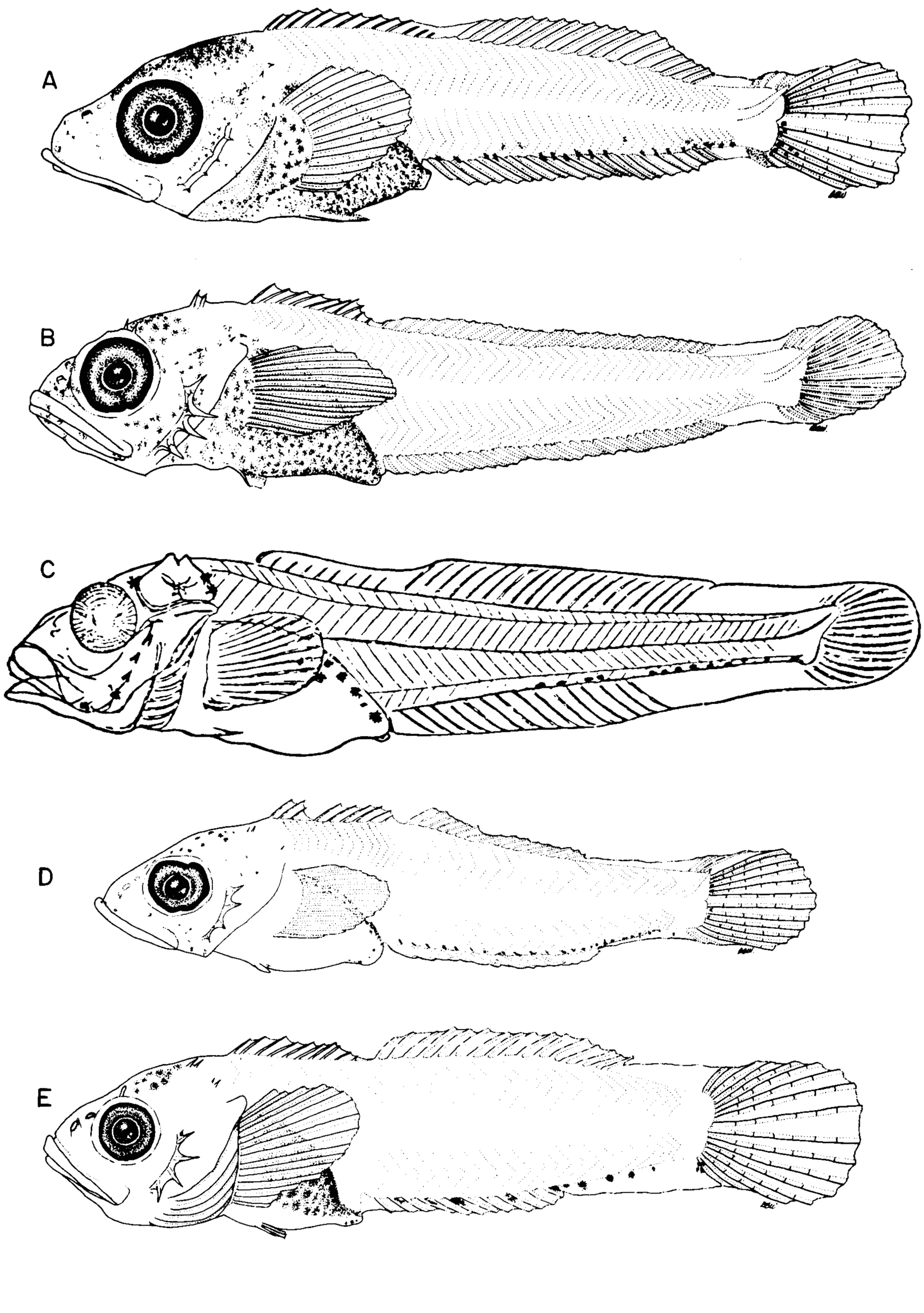


Fig. 226. Larvae of the *Rhamphocottus* group (A) and the *Scorpaenichthys* group (B, C) of cottids of Washington and Richardson (MS) (see Washington et al., this volume). (A) *Rhamphocottus richardsoni*, 10.6 mm SL (from Richardson and Washington, 1980); (B) *Scorpaenichthys marmoratus*, 8.7 mm SL (ibid.); (C) *Hemilepidotus spinosus*, 11.0 mm SL (ibid.).

those of the other fins. The pectoral fins are pigmented at the distal margin; other pigment includes a sheath over the gut and melanophores above the brain. Head spination is highly developed (Fig. 222); the sequence of development is similar to that of scorpaenines. In addition to the spine complement of scorpaenines, *Sebastolobus* larvae develop the 2nd and 3rd upper infraorbital spines and the 1st anterior preopercular spine.

Setarchinae.—Larvae are known for *Ectreposebastes imus* (Moser et al., 1977). Hatching and notochord flexion occur at a small size as in the scorpaenines; however, postflexion larvae attain a large size (Table 107). Larvae have the deepest body of known scorpaenids; body depth reaches 55% of body length in late postflexion stage. The gut is compact with an elongate terminal section; snout–anus distance averages 53% of body length in preflexion larvae and 76% in postflexion. The pectoral fins are deep-based, fan-shaped, and large, extending to the caudal peduncle (Fig. 222). Fin base depth and fin length reach 22% and 57% of the body length respectively. The pigment pattern consists of a postanal ventral series of 11–14 melanophores (not present after 4.0 mm), a blotch above the gas bladder, and an almost solid sheath over the pectoral fin, which recedes distally with development. Head spine development is similar to that of scorpaenines.


A
B
C
D
E

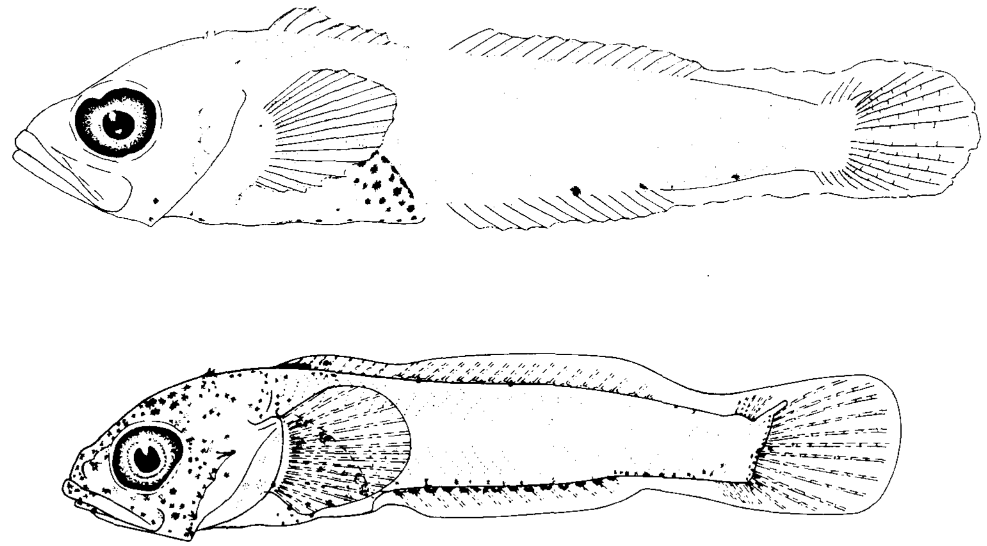


Fig. 227. Larvae of the *Myoxocephalus* group of cottids of Washington and Richardson (MS) (see Washington et al., this volume). (A) *Paricelinus hopliticus*, 13.8 mm SL (from Richardson and Washington, 1980); (B) *Triglops* sp., 15.4 mm SL (ibid.); (C) *Icelus bicornis*, 25 mm (from Ehrenbaum, 1905–1909); (D) *Chitonotus pugetensis*, 11.5 mm SL (from Richardson and Washington, 1980); (E) *Artedius meanyi*, 13.8 mm SL (ibid., as *Icelinus* sp.); (F) *Icelinus* sp., 11.9 mm SL (original); (G) *Ascelichthys rhodorus*, 11.0 mm SL (from Matarese and Marliave, 1982).

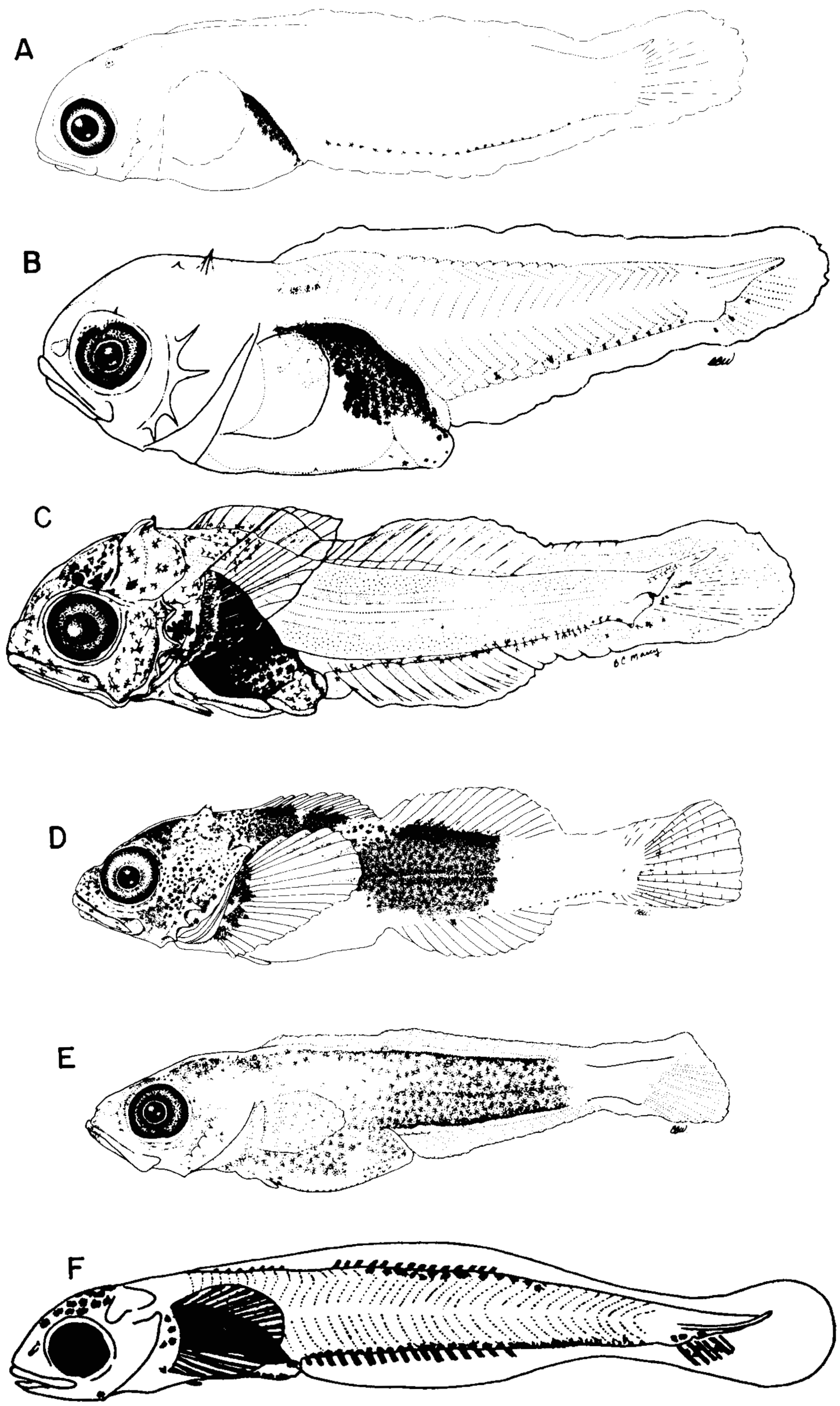
Choridactylinae.—The developmental stages of *Inimicus japonicus* have been described by Fujita and Nakahara (1955) and Sha et al. (1981). Larvae are 3.2 mm at hatching, 6.4–8.2 mm at flexion and about 10 mm at transformation. Yolk-sac larvae are similar to those of Scorpaeninae. Larvae are relatively slender and blunt-headed, with a compact short gut (Fig. 223). The pectoral fins are large and fan-shaped, with a scalloped margin; they develop a series of large blotches distally. One to several large postanal melanistic blotches form on the postanal ventral midline and the gas bladder region is pigmented. Sha et al. (1981) show the larvae to be heavily xanthic.

Minoinae.—Leis and Rennis (1983) described a larval series tentatively identified as *Minous* sp. It is generally similar in morphology and pigmentation to *Inimicus*; however, the pectoral fin is relatively larger and has a different pigment pattern.

Triglidae (Fig. 223).—Eggs are only known for 3 of the 8 genera of triglids. The new world genus *Prionotus* has multiple oil globules whereas single oil globules are known for *Chelidonichthys* and *Lepidotrigla*. Larvae are poorly known with complete series having been described for 4 species in 3 genera (Table 107). There are approximately 90 species in this family and many are very difficult to identify as adults. The genus *Lepidotrigla* has 40+ species and is poorly known in many areas. Diagnostic features include the depressed profile of the head and large pectoral fins of which the lowest three rays become detached during transformation. Meristics are very similar to platycephalids and caution is advised. However, most triglids have fewer pectoral rays than most scorpaenoids. *Prionotus*, including *Bellator*, has 13 to 15 plus 3 free rays; *Trigla*, *Chelidonichthys*, *Lepidotrigla*, and *Uradia* have 11 plus 3 free rays; and *Pterygotrigla* and *Parapterygotrigla* have 11 to 13 plus 3.

Peristediidae.—ELH information has been published only for *Peristedion cataphractum* of the eastern Atlantic (Table 107). Larvae and transforming juveniles have elongated upper pectoral rays and strong head spination (see plate 40 in Padoa, 1956e). This family is often combined with the Triglidae, but differs in many characters such as the presence of barbels, 2 rather than 3 free pectoral rays, and the body is encased in bony scutes rather than scales. Three genera (*Heminodus*, *Paraheminodus* and *Gargariscus*) have jaw teeth and two genera (*Peristedion* and *Satyrichthys*) lack jaw teeth. There are about 25 species found in the tropics of all oceans in deep water (>200 m).

Congiopodidae (Fig. 223).—Eggs are known for only 1 (*Congiopodus*) of the 4 genera of Congiopodidae (Brownell, 1978; Gilchrist, 1904; Robertson, 1974). The pelagic eggs are relatively large (1.7–2.18 mm) and spherical, with a narrow perivitelline space and no oil globules. The egg surface is covered with striations. Early life history stages have been illustrated for one species, *Congiopodus spinifer* (Brownell, 1979; Gilchrist and Hunter, 1919). Robertson (1975a), illustrated a well-developed embryo of *C. leucopaecilus*. Larvae hatch at about 5 to 6 mm NL and are elongate with long guts reaching 50% SL. The pectoral fins are extremely large and fan-shaped. Melanistic pigment is present on the head, nape and on the dorsal and ventral surface of the gut. Two large blotches of pigment on the dorsal and ventral midlines form a band midway between the vent and tail tip. The large pectoral fins have a distal band of pigment which gradually expands over the entire fin with development. Larvae develop large postocular and parietal spines. The presence of preopercular spines can not be determined from the description by Brownell (1975).


A
B
C
D
E
F

Platycephalidae (Fig. 223).—Platycephalids spawn small spherical eggs (< 1 mm) with a single oil globule (Chang et al., 1980; Uchida et al., 1958). Larvae have been described and illustrated for *Platycephalus indicus* (Ueno and Fujita, 1958) and for a series of larvae incorporating seven unidentified species (Leis and Rennis, 1983). Newly-hatched platycephalids are relatively small (1.7–2.3 mm) and slender-bodied, with unformed mouths, unpigmented eyes, and large yolk sacs. By the time of yolk absorption larvae have large heads and deep bodies which taper toward the tail. The gut is quite long reaching ⅔ SL during development. The pointed snout becomes distinctively long and flattened. Pigmentation is usually present on the head, jaws, ventral surface of the gut and along the postanal ventral midline. Pigment may also be present on the dorsolateral surface of the tail and pectoral fin. Larvae develop 4 to 9 preopercular spines. Other head spines include: supraocular, supracleithral, parietal and pterotic. Unlike most other scorpaeniforms, head spines persist and become more pronounced in juveniles. Fin development proceeds as follows: pectoral, caudal, dorsal, anal and pelvic.

Hoplichthyidae (Fig. 223).—The pelagic eggs of *Hoplichthys haswelli* are described by Robertson (1975a) as small and spherical with a smooth surface. A single oil globule is present. Descriptions of hoplichthyid larvae have not been published; however, based on Okiyama (in prep.) larvae are quite similar to platycephalids. Preflexion larvae (3.2 mm) are elongate with large heads and pointed snouts. The gut is moderately long (> 50% SL) and the early-developing pectoral fins are large and fan-shaped. The snout becomes increasingly long and depressed during development. Pigmentation is limited to the gut, distal tip of the pectoral fin and a band on the ventral finfold midway between the vent and notochord tip. Numerous clusters of small spines develop in the supraocular, parietal and pterotic regions. Seven spines form on the posterior margin of the preopercle with smaller spines at their base. As in platycephalids, head spines persist in juveniles.

Dactylopteridae (Fig. 233).—The pelagic eggs are small (0.8 mm) and slightly ovoid with a single oil globule. The egg surface is smooth and unsculptured. Larvae hatch at about 1.8 mm and undergo flexion of the notochord between 3.9–6.5 mm. Transformation to the juvenile form occurs at about 9 mm. Larvae are moderately deep-bodied with a distinctively blunt snout and small mouth. The gut is long, reaching about 75% SL in postflexion larvae. Pigmentation occurs over the head, gut, along the postanal ventral midline and around notochord tip. Pigmentation increases dramatically over most of the body in postflexion larvae. The distinctive head armature is quite different from all known scorpaeniform larvae and is present in larvae as small as 2.3 mm NL. A small supraoccipital spine is present only during the larval period. The extremely long posttemporal and preopercular spine extend posteriorly to the middle of the anal fin in larvae by about 6.5 mm and persist in juveniles and adults.

Cottoidei

Eggs

Eggs are known from representatives of six of the nine cottoid families recognized here (Table 107). Where known, most cottoids spawn demersal, adhesive eggs which often form clusters found under rocks. Eggs are frequently brightly colored, e.g., red, blue, green, yellow. The eggs of *Anoplopoma fimbria* are pelagic. The Comephoridae of Lake Baikal are reported to be viviparous.

Most eggs are spherical and average 1–2 mm in diameter, although eggs as large as 4 mm have been reported in the cottid *Hemitripterus* and some of the cottocomephorids. A single large oil globule, frequently accompanied by several small ones, occurs in many species. The surface of the eggs is often covered by a tough adhesive membrane, and may be smooth as in *Anoplopoma* and *Myoxocephalus aenaeus* (Fahay, 1983) or covered by tiny, radiating canals as in *Artedius lateralis* and *Clinocottus analis* (Budd, 1940).

Larvae

At least one larval stage is known for 88 of the 329+ species and for 46 of the 104 genera of cottoids. Major overviews of larval cottoid taxonomy include: Richardson and Washington (1980) on cottids; Kendall and Vinter (1984) on hexagrammids; Taliev (1955) and Chernyayev (1971, 1975, 1978, 1981) on comephorids and cottocomephorids; and, forthcoming Laroche (in prep.) on agonids.

Larval cottoids exhibit a broad diversity of form. Size at hatching varies from 2 to 12 mm. Planktonic life may be quite brief, several weeks in many cottids, or may be extended up to a year with a special pelagic juvenile stage as in the hexagrammids.

Cottoid larvae exhibit such a diversity of form and development that it is impossible to characterize a generalized "cottoid" larva.

Hexagrammidae (Fig. 224).—Larvae are known for 10 of the 11 species of the hexagrammid genera *Hexagrammos, Pleurogrammus,* and *Ophiodon.* Major works presenting descriptions and illustrations include Kendall and Vinter (1984) and Gorbunova (1964b). Hexagrammids hatch at a relatively large size (6–11 mm NL). Development is gradual from hatching to the juvenile stage with a prolonged epipelagic prejuvenile period (~30–50 mm SL). Larvae have elongate, slender bodies with large eyes. Larval *Hexagrammos* and *Pleurogrammus* have blunt heads, while *Ophiodon* larvae have pointed snouts and large terminal mouths.

Larvae are heavily pigmented especially dorsally. Melanophores are scattered over the head, gut and usually on the dorsal and ventral midlines. The extent of postanal, ventral midline and lateral pigmentation is useful in specific identification.

Fin formation proceeds in the following sequence: caudal, pectoral, second dorsal and anal, first dorsal and pelvic. Larvae exhibit delayed ossification. Vertebral ossification in hexagram-

←

Fig. 228. Larvae of the *Myoxocephalus* cottid group of Washington and Richardson (MS) (see Washington et al., this volume). (A) *Orthonopias triacis,* 7.0 mm SL (original); (B) *Enophrys bison,* 7.0 mm SL (from Richardson and Washington, 1980); (C) *Myoxocephalus aenaeus,* 7.0 mm SL (from Lund and Marcy, 1975); (D) *Myoxocephalus polyacanthocephalus,* 12.0 mm SL (from Richardson, 1981a); (E) *Radulinus asprellus,* 10.9 mm SL (from Richardson and Washington, 1980); (F) *Gymnocanthus tricuspis,* 13.0 mm (from Khan, 1972).

mids (and *Anoplopoma*) is similar to that in Scorpaenoidei with the neural and hemal arches ossifying before the associated vertebral centra. Vertebral counts are notably high (47–63). Head spines are absent in larval *Hexagrammos* and *Pleurogrammus* and extremely reduced in *Ophiodon,* with late-stage larvae developing 4 tiny preopercular spines.

Anoplopomatidae (Fig. 224, Table 107).—Larvae of only *Anoplopoma* have been described and illustrated by Kobayashi (1957) and Ahlstrom and Stevens (1976). Early development of *Anoplopoma* is similar to that of the hexagrammids. Larvae hatch at a large size (~9 mm NL) and development is gradual without great changes in form.

Larvae are slender and elongate with pointed snouts and long guts. The distinctive pectoral fins with heavy distal pigmentation are exceptionally large reaching nearly 33% SL late in the larval period. Larvae are heavily pigmented with melanophores over most of the head, gut and lateral surface of the body.

As in hexagrammid larvae, ossification is delayed with the neural and hemal arches ossifying before the associated vertebral centra. Vertebral counts (61–66) are distinctively high. Pectoral fin development is precocious. Head and preopercular spines are absent.

Oxylebius-Zaniolepis (Fig. 224).—*Oxylebius* and *Zaniolepis* are sometimes included in the Hexagrammidae, but are herein treated separately because of the distinctiveness of their larvae from hexagrammids (Washington and Richardson, MS; Kendall and Vinter, 1984). Larvae of *Oxylebius pictus* and *Zaniolepis* sp. are illustrated and described by Kendall and Vinter (1984). Larvae hatch at a small size (2.5–5 mm NL), undergo notochord flexion between 6 and 9 mm NL, and transform to a benthic juvenile at about 15 mm SL.

Oxylebius and *Zaniolepis* are relatively short and deep-bodied with large, bulging guts and rounded snouts. Pectoral fins develop early and are distinctively large and fan-shaped. Pigmentation is heavy over the anterior half of the body in preflexion larvae and increases over the postanal lateral body with development. *Zaniolepis* possesses characteristic snout pigment which is absent in *Oxylebius.* The pectoral fins of both species are densely pigmented.

Head spination is well-developed with preopercular (5 spines in *Oxylebius*; 6–7 in *Zaniolepis*), posttemporal and supracleithral spines present. *Zaniolepis* larvae develop distinctive prickle-scales over most of the body by about 7 mm.

Normanichthyidae (Fig. 225).—Larvae of the monotypic *Normanichthys crockeri* are illustrated and described by Balbontin and Perez (1980). Hatching occurs at a small size (4.4 mm NL) and flexion of the notochord occurs at 7 to 9 mm. Development from hatching to the juvenile stage is gradual without great change.

Larvae are elongate and slender with short, coiled guts and distinctive large pectoral fins. Pigmentation is restricted to the pectoral fins and the ventral midline extending from the isthmus to the tail. In small larvae several large melanophores are present on the dorsal midline.

Distinctive features of larval development include: the absence of head and preopercular spines, delayed ossification, early development of the pectoral fin, and presence of only 5 branchiostegal rays.

Comephoridae (Fig. 225).—The endemic comephorids of Lake Baikal in Russia are reported to be viviparous (Chernyayev, 1971, 1975) and are born at a relatively large size (8.2–9.4 mm) but are not well developed. Flexion of the notochord occurs at about 8.2 to 13 mm. Larvae develop very slowly with transformation occurring 3 or 4 months after birth.

Larvae are extremely slender and elongate with small heads and very short coiled guts. Comephorids are quite different from other cottoids morphologically and are blennioid in appearance. Pigmentation is usually limited to the gut and sometimes in a series along the postanal lateral midline. Four small preopercular spines develop in late-stage larvae; other head spines are absent.

Cottocomephoridae (Fig. 225).—Larvae of seven genera of Lake Baikal cottocomephorids have been described and illustrated (Chernyayev, 1971, 1975, 1978, 1981; Taliev, 1955). Larvae hatch at about 5 to 10 mm, and range from forms with large yolk sacs and no fin development (e.g., *Paracottus*) to well developed, postflexion forms with fins well developed (e.g., *Batrachocottus*). Size at transformation varies from 9 to 20 mm. Larvae are slender with moderately short guts and rounded snouts, somewhat similar to freshwater cottids (*Cottus*) in form. Pigmentation is variable with melanistic pigmentation usually present on the head, nape, gut and variously on the dorsal and ventral midline. Melanophores are frequently present in a row along the lateral midline near the tail tip.

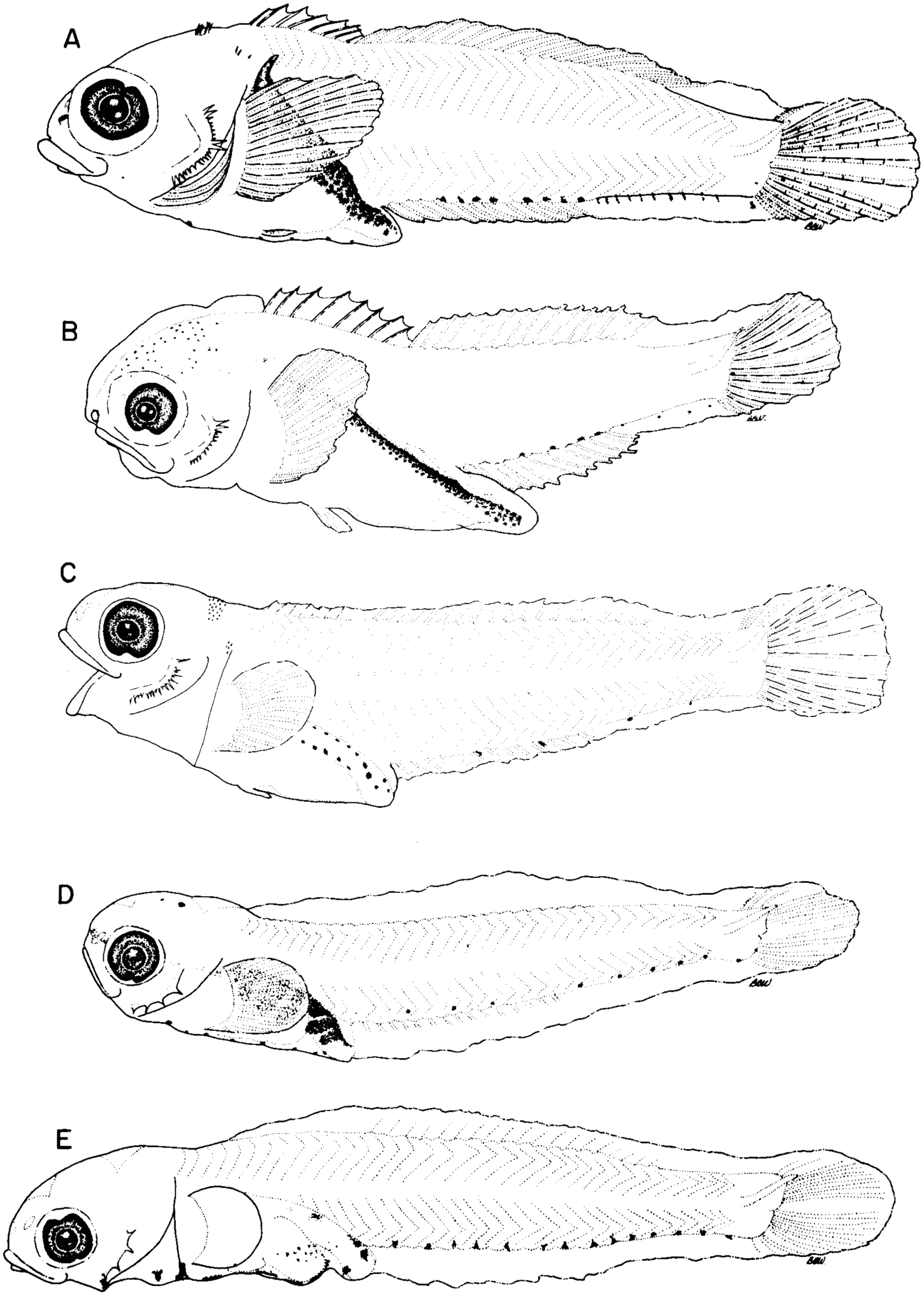
Larvae develop 4 small preopercular spines accompanied by two spiny projections from an inner preopercular shelf. Other head spines are lacking.

Cottidae (Figs. 226–231).—The taxonomic status of the family Cottidae is controversial with the number of recognized families ranging from 1 to 17 (see Washington and Richardson, MS). To minimize confusion, and because there is no generally agreed upon classification of this "family," we use the generic groupings identified by Washington and Richardson (MS) for our discussion of early life history information. Larvae are known for 28 of the 70+ cottid genera. A general overview of larval cottid taxonomy is presented in Richardson and Washington (1980), Richardson (1981a), Washington (1981) and Fahay (1983).

Rhamphocottus (Fig. 226).—Larvae of this distinctive, monotypic species hatch at a relatively large size (6–7 mm NL). Notochord flexion occurs at 7 to 8 mm and transformation to a

→

Fig. 229. Larvae of the *Artedius* Part A group (A–C) and the *Cottus* group of cottids of Washington and Richardson (MS) (see Washington et al., this volume). (A) *Artedius fenestralis,* 9.9 mm SL (from Richardson and Washington, 1980, as *Artedius* Type 2); (B) *Clinocottus acuticeps,* 10.4 mm SL (from Washington, in prep.); (C) *Oligocottus snyderi,* 10.2 mm SL (from Washington, 1981); (D) *Leptocottus armatus,* 8.1 mm SL (from Richardson and Washington, 1980); (E) *Cottus asper,* 8.2 mm SL (ibid.).


A
B
C
D
E

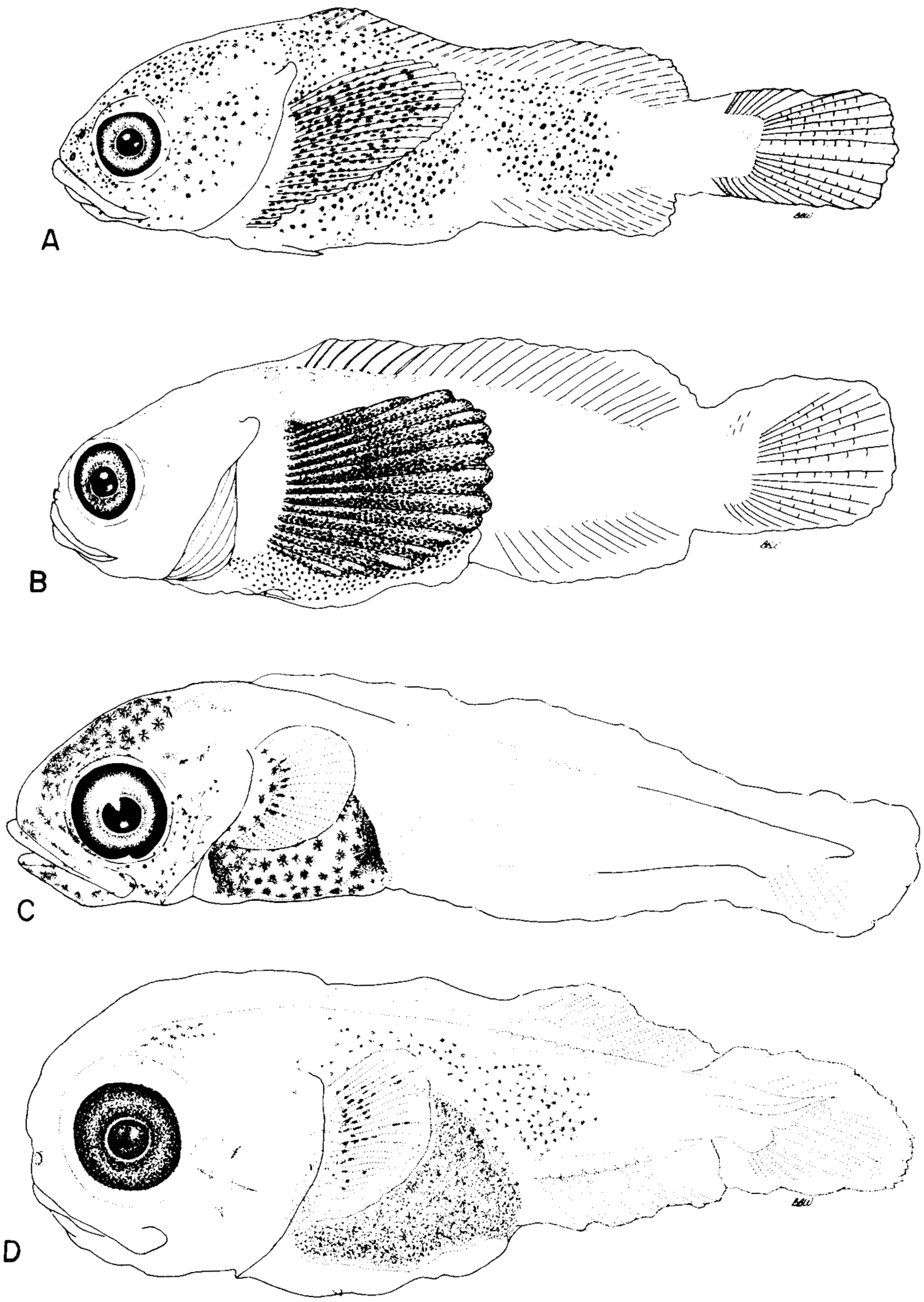


Fig. 230. Larvae of the *Psychrolutes* group (A, B) and the *Malacocottus* group (C, D) of cottids of Washington and Richardson (MS) (see Washington et al., this volume). (A) *Psychrolutes paradoxus,* 13.0 mm SL (from Richardson, 1981a); (B) *Gilbertidia sigalutes,* 13.0 mm SL (ibid.)· (C) *Dasycottus setiger,* 10.3 mm SL (original); (D) *Malacocottus zonurus,* 9.8 mm SL (original).

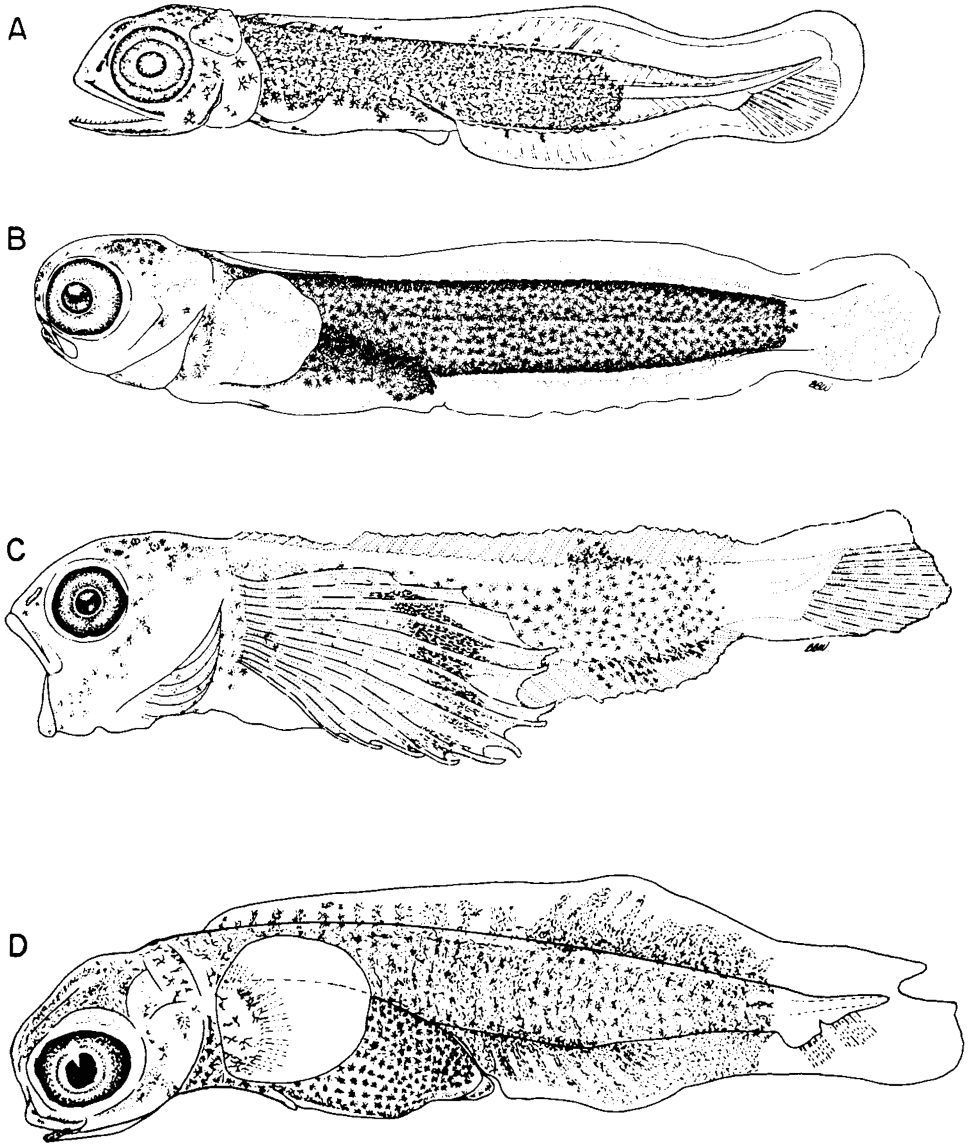


Fig. 231. Larvae of the *Hemitripterus* group (A–C) of cottids of Washington and Richardson (MS) (see Washington et al., this volume) and Agonidae. (A) *Hemitripterus villosus*, ca. 15.5 mm SL (from Kyushin, 1968); (B) *Blepsias cirrhosus*, 11.0 mm SL (from Richardson, 1981a); (C) *Nautichthys oculofasciatus*, 11.7 mm SL (from Richardson and Washington, 1980); (D) *Agonomalus* or *Hypsagonus* sp., 8.2 mm SL (original, courtesy B. Vinter).

benthic juvenile occurs at about 14 to 15 mm SL. *Rhamphocottus* larvae are extremely deep-bodied with a very long snout–anus length.

Larvae are uniformly covered with melanophores except for the caudal peduncle and ventral surface of the gut. *Rhamphocottus* develop small prickle-scales over most of the body by 9 or 10 mm. Larvae develop only one preopercular spine in contrast to the usual four possessed by most cottid larvae. Parietal, nuchal, supracleithral, posttemporal and postocular spines occur during the larval period.

Hemilepidotus-Scorpaenichthys (Fig. 226).—Larvae of this group hatch at 4 to 6 mm NL. Transformation to the neustonic or pelagic juvenile phase occurs at about 13 to 20 mm. Larvae are

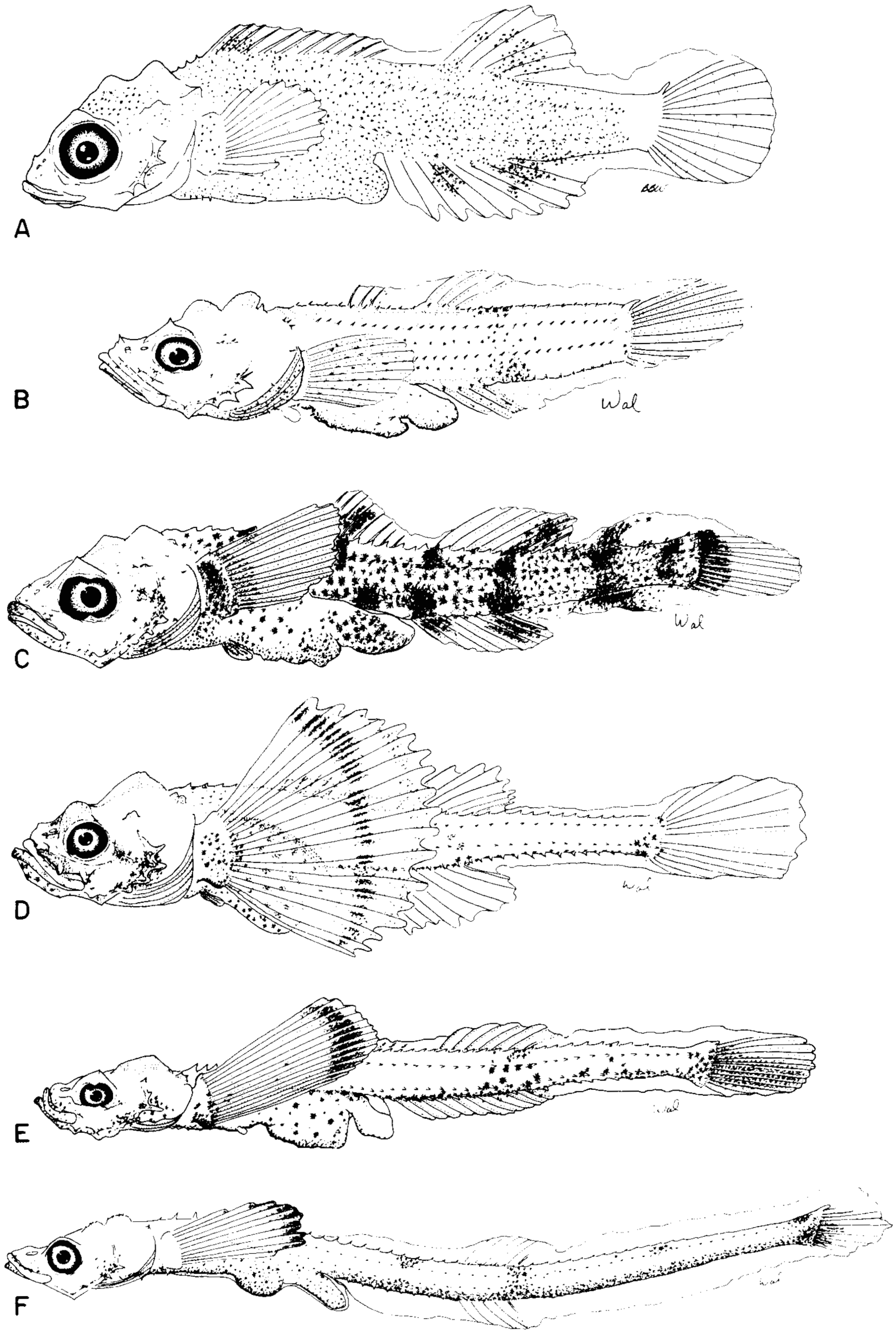


Fig. 232. Larvae of Agonidae (all original). (A) *Hypsagonus quadricornis*, 11.5 mm SL; (B) *Bothragonus swani*, 6.3 mm SL; (C) *Xeneretmus latifrons*, 9.6 mm SL; (D) *Stellerina xyosterna*, 10.2 mm SL; (E) *Ocella verrucosa*, 10.1 mm SL; (F) *Aspidophoroides monopterygius*, 14.3 mm SL.

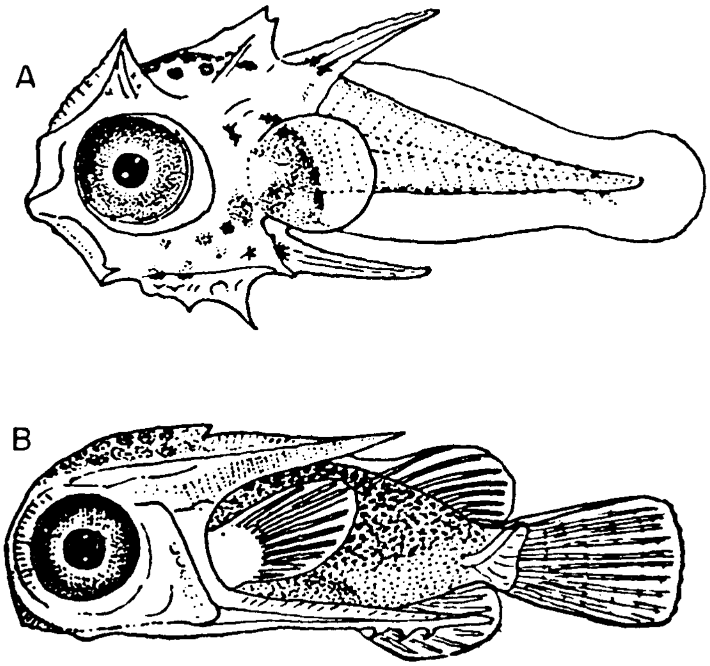


Fig. 233. Larvae of Dactylopteridae. (A) *Dactylopterus volitans*, 2.4 mm (from Padoa, 1956e); (B) *Dactylopterus volitans*, 7.5 mm (ibid.).

long and slender at hatching with moderately long guts (44 to 60%) and rounded snouts. They become increasingly deep-bodied with development.

Larvae are relatively heavily pigmented with melanophores over the head and gut. *Scorpaenichthys* larvae have dense pigment covering the body except for the caudal peduncle while *Hemilepidotus* spp. have postanal pigment concentrated on the dorsal and ventral body midlines. Lateral melanophores develop above and below the notochord in *Hemilepidotus*.

Hemilepidotus and *Scorpaenichthys* larvae develop four prominent preopercular spines. *Hemilepidotus* possess numerous head spines while *Scorpaenichthys* develop bony bumps in corresponding areas. Larvae of this group develop unique pitted dermal bones on the head. In addition, the uppermost pectoral radial is tiny and fuses to the scapula in larval *Scorpaenichthys* and nearly so in *Hemilepidotus*.

Myoxocephalus group (Figs. 227 and 228).—This is the least well-defined and most diverse cottid group containing 13 genera. Where known, size at hatching varies from 2.9 to 10 mm. Transformation to the benthic juvenile stage varies from 7.6 to 20 mm.

Members of this group are generally slender-bodied with pointed snouts; however, *Enophrys* is stout-bodied, and *Orthonopias* has a blunt, rounded snout.

Pigmentation is variable. Heavy pigment on the dorsal surface of the gut, on the nape and along postanal ventral midline is characteristic of many members of this group. Several genera possess heavy melanistic pigmentation on the lateral body surface (e.g. *Radulinus*, some *Myoxocephalus*). Head pigment may be present.

Larvae of this group develop four preopercular spines and a distinctive bony preopercular shelf. Parietal, nuchal, supracleithral, posttemporal and occasionally, postocular spines develop in late-stage larvae.

Artedius group (Fig. 229, Table 107).—This group contains 3 genera, *Artedius* (in part), *Clinocottus* and *Oligocottus* and the larvae have been described by Washington (1981). Larvae hatch at 3 to 5 mm and transform to benthic juveniles at approximately 10 to 13 mm. Larvae are stubby-bodied with a slightly humped appearance at the nape. Snouts are rounded and guts trail distinctively below the ventral body midline. Several species of *Artedius* develop dorsal gut diverticula while *Clinocottus acuticeps* develops long hindgut diverticula.

Larvae are relatively lightly pigmented and characterized by pigment on the nape, over the gut and along the postanal ventral midline. Head pigment is present in some species.

Larvae develop a unique preopercular spine pattern with 6 to 24 spines. Parietal and supracleithral spines are variable in this group and may form in clusters, individually or not at all.

Leptocottus group (Fig. 229).—This group includes the genera *Leptocottus* and *Cottus*. Hatching occurs at 4 to 5 mm and transformation ranges from 8 to 12 mm. Larvae are relatively slender-bodied with rounded snouts and moderately short guts. Pigmentation is usually light with melanophores on the nape, over the gut and widely spaced along the postanal ventral midline. Head pigment may be present.

Where known, these larvae develop four weak preopercular spines; however, other head spines are lacking.

Psychrolutes group (Fig. 230).—This group includes two genera *Psychrolutes* and *Gilbertidia*. Larvae hatch at a relatively large size, about 6 to 7 mm. They transform and settle from the plankton at about 18 to 20 mm SL. Larvae are generally tadpole shaped with large rounded heads tapering toward the tail. Larvae possess an outer layer of loose flabby skin.

Melanistic pigment occurs on the head, nape, gut and characteristically on the pectoral fins. Postanal ventral midline melanophores are absent; however, pigment is added laterally with development.

Head and preopercular spines are absent.

Malacocottus group (Fig. 230).—This group includes *Malacocottus* and *Dasycottus*. Size at hatching is not known. Larvae of this group are similar to those of the *Psychrolutes* group with large, blunt heads tapering to the tail. An outer bubble or layer of skin is present in both genera and is particularly pronounced in *Malacocottus*.

Pigmentation is present on the head, nape and over the entire gut. Pigment occurs laterally on the anterior third of the tail in *Malacocottus* larvae. As in the *Psychrolutes* group, the pectoral fins are characteristically pigmented.

Larvae develop four preopercular spines with a fifth accessory spine present in *Malacocottus*.

Hemitripterus group (Fig. 231).—This group includes the genera: *Hemitripterus*, *Blepsias* and *Nautichthys*. Hatching occurs at a relatively large size, 7 to 13 mm NL. Newly-hatched larvae have elongate, slender bodies which become deeper with development. *Nautichthys* larvae have distinctively long, pigmented pectoral fins.

Pigmentation is relatively heavy with melanophores covering the head, dorsal surface of the gut and over the lateral body surface except for the caudal peduncle. *Nautichthys* and *Hemitripterus* larvae possess distinctive pigment bands extending onto the dorsal and ventral finfolds that are not found in other cottid larvae.

Larvae develop four prominent preopercular spines and a strong frontoparietal spiny ridge. This group is characterized by delayed ossification in the larval period and a unique "honeycomb" pattern of ossification on the head. *Hemitripterus* larvae develop large bony prickles, similar to the prickle-scales found in agonids.

Agonidae (Figs. 231 and 232).—At least one early life history stage of 9 of the 49 nominal species is known. Agonids hatch at 5.5 to 8.0 mm NL. Development is a gradual transformation to the juvenile form attained at 20 to 30 mm.

Agonid larvae are generally long and slender with relatively long guts. Extremes of form range from short stout genera such as *Agonomalus* and *Bothragonus* to the extremely attenuated forms such as *Ocella* and *Aspidophoroides*. Larvae have distinctively large, fan-shaped pectoral fins.

Pigmentation varies in the family. Melanistic pigment may be present on the head, nape, scattered over the gut and frequently in bands on the postanal lateral surface of the body. The pectoral fins are distinctively pigmented often with distal bands of melanistic pigment. In some species (e.g. *Agonomalus*, *Hypsagonus*) pigmentation extends onto the dorsal and ventral finfolds.

Larvae are characterized by spiny heads with large frontoparietal spiny ridges, postocular spines, and usually four large preopercular spines. Tiny rows of spines form in small larvae and help distinguish agonid larvae. These rows correspond to the plates (scales) of adults.

(B.B.W.) Gulf Coast Research Laboratory, East Beach Drive, Ocean Springs, Mississippi 39564; (W.A.L.) School of Natural Resources, Department of Fisheries, Humboldt State University, Arcata, California 95521; (H.G.M.) National Marine Fisheries Service, Southwest Fisheries Center, Post Office Box 271, La Jolla, California 92038; (W.J.R.) National Marine Fisheries Service, Southeast Fisheries Center, 75 Virginia Beach Drive, Miami, Florida 33149.