Pleuronectiformes: Development

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PLEURONECTIFORM fishes have both eyes on one side of the head in juveniles and adults. The eyes are symmetrical in larvae, and migration of either the left or right eye occurs during metamorphosis. In some flatfish groups the eyes are on the left side (sinistral) while in others they are on the right side (dextral); relatively few species are indiscriminate. In some flatfishes the ocular nerve of the migrating eye usually lies dorsal to the other nerve in the optic chiasma; in other groups the nerve of the migrating eye is dorsal or ventral in the chiasma with about equal frequency. In most groups the nasal organ of the blind side also migrates to a position near the dorsal midline. Features of the dentition and cranial osteology may also show asymmetry. Flatfishes are highly compressed with the underside of the body usually unpigmented. The lateral line may be lacking on the blind side; the pectoral fin is often shorter on the blind side and has fewer rays; the pelvic fin on the blind side is often shorter, smaller and differently placed with respect to the ventral midline compared with the pelvic fin on the ocular side; squamation may be different on the two sides of the body. The dorsal and anal fins are long-based; the dorsal extends anteriad to at least the eye in all flatfishes except *Psettodes* and the anal fin extends well forward of the first haemal spine. The caudal fin is typically rounded or truncate with few or no secondary rays. Pleuronectiforms are benthic carnivores, occurring worldwide, primarily in shallow to moderate depths, with some representatives in brackish and fresh water habitats. Nelson (1976) notes a total of 520 species.

The classification presented below is based on the works of Regan (1910, 1929) and Norman (1934, 1966) with modifications by Hubbs (1945), Amaoka (1969), Hensley (1977), and Futch (1977). Our removal of *Perissias* from the Paralichthyidae and placement in the Bothidae are based on previously unpublished information. Those genera marked with an asterisk are misplaced in this classification and are discussed in this paper and in Hensley and Ahlstrom (this volume).

Order Pleuronectiformes
- Suborder Psettodoidei
  - Family Psettodidae (Indo-Pacific, West Africa)
    - *Psettodes*
- Suborder Pleuronectoidei
  - Family Citharidae
    - Subfamily Brachypleurinae (Indo-Pacific)
      - *Brachypleura,* Lepidoblepharon*
    - Subfamily Citharinae (Indo-Pacific, Mediterranean, West Africa)
      - *Citharoides, Eucitharus*
  - Family Scophthalmidae (North Atlantic, Mediterranean, Black Sea)
    - *Lepidorhombus, Phrynorhombus, Scophthalmus, Zeugopterus*
  - Family Paralichthyidae (Western and Eastern Atlantic, Eastern Pacific, Indo-Pacific)
    - *Ancylopsetta, Cephalopsetta, Citharichthys, Cyclop-*

Fig. 341. Eggs of Pleuronectiformes. Captions in each illustration indicate the species and diameter of the egg in mm. *Scophthalmus maeoticus maeoticus*, from Dekhnik, 1973; *Paralichthys olivaceus*, from Mito, 1963; Bothidae, from Mito, 1963; *Limanda aspera*, from Pertseva-Ostroumova, 1954; *Hippoglossoides dubius*, from Pertseva-Ostroumova, 1961; *Microstomus pacificus*, original, CalCOFI; *Pleuronichthys cornutus*, from Mito, 1963; *Pelotretis flavilatus*, from Robertson, 1975a; *Peltorhamphus novaezeelandiae*, from Robertson, 1975a; *Trinectes maculatus*, from Hildebrand and Cable, 1938; *Pegusa lascaris nasuta*, from Dekhnik, 1973; *Cynoglossus robustus*, from Fujita and Uchida, 1957.

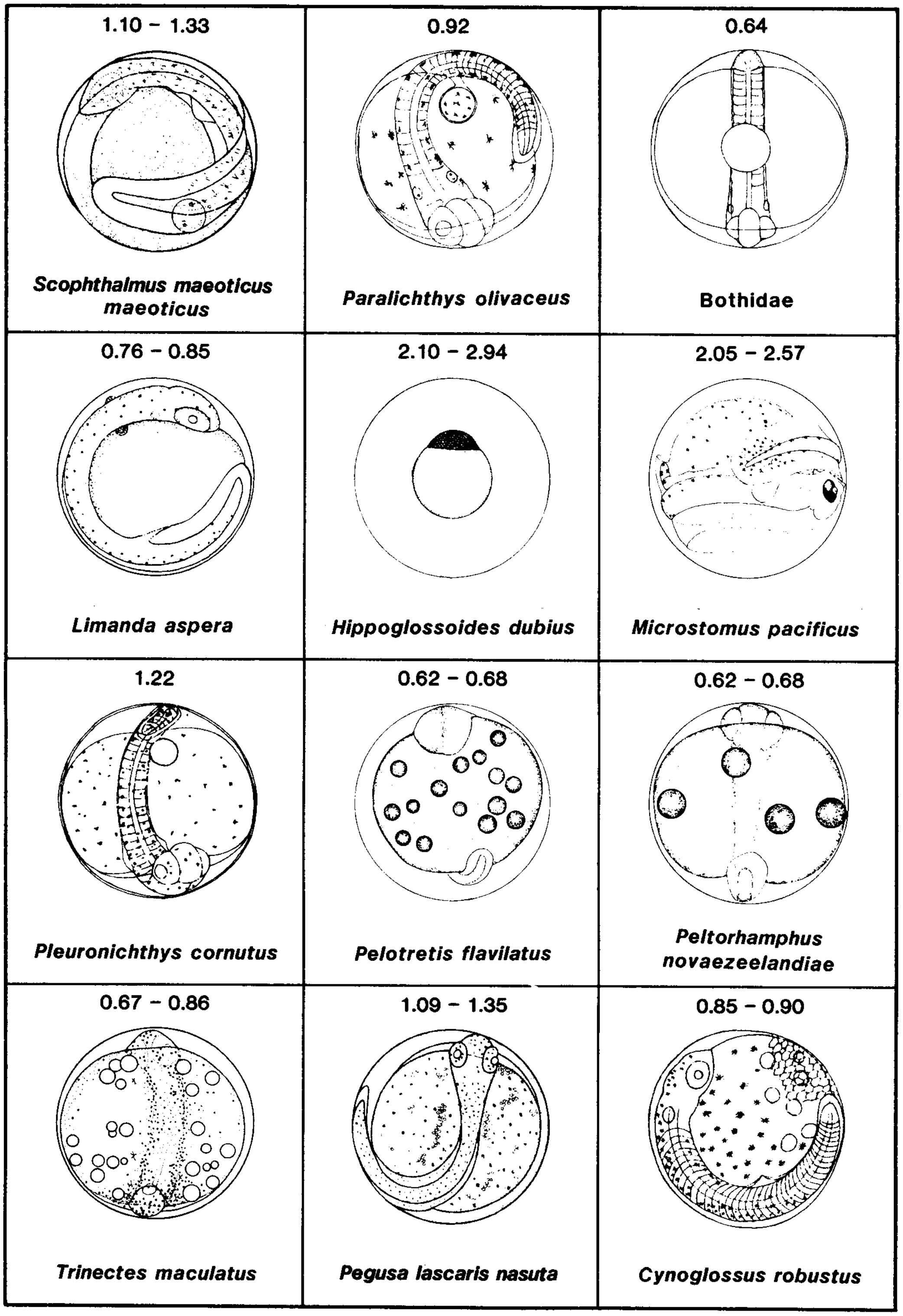
1.10 – 1.33
Scophthalmus maeoticus maeoticus
0.92
Paralichthys olivaceus
0.64
Bothidae
0.76 – 0.85
Limanda aspera
2.10 – 2.94
Hippoglossoides dubius
2.05 – 2.57
Microstomus pacificus
1.22
Pleuronichthys cornutus
0.62 – 0.68
Pelotretis flavilatus
0.62 – 0.68
Peltorhamphus novaezeelandiae
0.67 – 0.86
Trinectes maculatus
1.09 – 1.35
Pegusa lascaris nasuta
0.85 – 0.90
Cynoglossus robustus

TABLE 170. CHARACTERS OF EGGS OF PLEURONECTINAE SPECIES WHICH LACK OIL GLOBULES.

Species	Region[1]	Type of egg (pelagic or demersal)	Egg size (mm)	Chorion	References
Cleisthenes herzensteini	WNP	P	0.84–1.03	—	Pertseva-Ostroumova, 1961
Embassichthys bathybius	ENP	P	3.0	smooth	Richardson, 1981b
Eopsetta grigorjewi	WNP	P	1.10–1.20	striations	Yusa, 1961; Fujita, 1965
E. jordani	ENP	P	1.21–1.25	smooth	Alderdice and Forrester, 1971
Glyptocephalus cynoglossus	NA	P	1.07–1.25	striations	Cunningham, 1887; Ehrenbaum, 1905–1909
G. stelleri	WNP	P	1.20–1.61	thick, reticulate	Pertseva-Ostroumova, 1961; Dekhnik, 1959
G. zachirus	ENP	P	1.9–2.15	striations	Original
Hippoglossoides dubius	WNP	P	2.10–2.94	smooth	Pertseva-Ostroumova, 1961
H. elassodon	NP	P	2.45–3.75	smooth	Thompson and Van Cleve, 1936; Pertseva-Ostroumova, 1961
H. platessoides	WNA	P	1.38–2.64	smooth	Russell, 1976 (summary)
H. robustus	WNP	P	2.04–2.69	smooth, thin	Pertseva-Ostroumova, 1961
Hippoglossus hippoglossus	NA	P	3.0–3.8	smooth, thick	Tåning, 1936; Pertseva-Ostroumova, 1961
H. stenolepis	NP	P	2.9–3.8	minute honey-comb structure	Thompson and Van Cleve, 1936
Isopsetta isolepis	ENP	P	0.90–1.10	smooth	Richardson et al., 1980
Kareius bicoloratus	WNP	P	1.00–1.15	reticulate	Pertseva-Ostroumova, 1961
Lepidopsetta bilineata	NP	D	1.02–1.09	sticky-orange	Pertseva-Ostroumova, 1961
L. mochigarei	WNP	D	0.87–0.95	thick, gluey	Pertseva-Ostroumova, 1961
Limanda aspera	NP	P	0.76–0.85	smooth	Pertseva-Ostroumova, 1954
L. ferruginea	WNA	P	0.79–1.01	striations	Miller, 1958; Colton and Marak, 1969
L. limanda	ENA	P	0.66–1.20	—	Russell, 1976 (summary)
L. punctatissima	WNP	P	0.66–0.87	smooth	Pertseva-Ostroumova, 1961
L. proboscidea	WNP	P	0.72–0.87	smooth	Pertseva-Ostroumova, 1961
L. schrenki	WNP	D	0.73–0.83	adhesive	Yusa, 1960a
L. schrenki (as *Pseudopleuronectes yokohamae*)	WNP	D	0.74–0.83	adhesive	Pertseva-Ostroumova, 1961
L. yokohamae	WNP	D	0.81–0.84	adhesive	Yusa, 1960a, b
Liopsetta glacialis	NP	P	1.20–1.60	thin	Pertseva-Ostroumova, 1961
L. obscura	WNP	D	0.78–0.94	thick, sticky	Pertseva-Ostroumova, 1961
L. pinnifasciata	WNP	P	1.43–1.66	thin, folds	Pertseva-Ostroumova, 1961
Lyopsetta exilis	ENP	P	1.47–1.68	smooth	Original; Ahlstrom and Moser, 1975
Microstomus kitt	WNA	P	1.13–1.45	striations	Russell, 1976; Dekhnik, 1959
M. pacificus	ENP	P	2.05–2.57	smooth	Original; Ahlstrom and Moser, 1975
Parophrys vetulus	ENP	P	0.89–0.93	striations	Budd, 1940; Original
Platichthys flesus	ENA	P	0.80–1.13	—	Russell, 1976 (summary)
P. f. luscus	B	P	1.05–1.35	smooth	Dekhnik, 1973
P. stellatus	NP	P	0.89–1.01	smooth, thin	Orcutt, 1950; Yusa, 1957
Pleuronectes pallasii	NP	P	1.67–2.21	—	Pertseva-Ostroumova, 1961
P. platessa	ENA	P	1.66–2.17	—	Russell, 1976 (summary)
Pleuronichthys coenosus	ENP	P	1.20–1.56	polygonal pattern	Sumida et al., 1979; Budd, 1940
P. decurrens	ENP	P	1.84–2.08	polygonal pattern	Sumida et al., 1979; Budd, 1940
P. verticalis	ENP	P	1.00–1.16	polygonal pattern	Sumida et al., 1979; Budd, 1940
Psettichthys melanostictus	ENP	P	ca. 1.0	—	Hickman, 1959
Pseudopleuronectes americanus	WNA	D	0.71–0.96	adhesive	Breder, 1923
P. herzensteini	WNP	P	0.80–1.0	smooth	Pertseva-Ostroumova, 1961
Reinhardtius hippoglossoides	NA/NP	P	4.00–4.50	—	Jensen, 1935
Tanakius kitaharai	WNP	P	1.20–1.30	striations	Fujita, 1965
Verasper variegatus	WNP	P	1.60–1.64	smooth	Takita et al., 1967; Mito, 1963

[1] B = Black Sea, ENA = eastern North Atlantic, ENP = eastern North Pacific, I = India, NA = North Atlantic, NP = North Pacific, WNA = western North Atlantic, WNP = western North Pacific.

setta, Etropus, Gastropsetta, Hippoglossina, Lioglossina, Paralichthys, Pseudorhombus, Syacium, Tarphops, Tephrinectes, Thysanopsetta,* Verecundum, Xystreurys*

Family Bothidae

Subfamily Taeniopsettinae (Western Atlantic, Eastern Pacific, Indo-Pacific)

Engyophrys, Perissias, Taeniopsetta, Trichopsetta

Subfamily Bothinae (Indian, Pacific, Atlantic, Mediterranean, Southern oceans)

Arnoglossus, Asterorhombus, Bothus, Chascanopsetta, Crossorhombus, Engyprosopon, Grammatobothus, Japonolaeops, Kamoharaia, Laeops, Lophonectes, Monolene, Mancopsetta, Neo-*

TABLE 171. CHARACTERS OF PLEURONECTIFORM EGGS WITH A SINGLE OIL GLOBULE.

Taxon	Region[1]	Egg size (mm)	Oil globule size (mm)	Chorion	Size at hatching (mm)	References
Pleuronectidae						
Hypsopsetta guttulata	ENP	0.78–0.89	0.12–0.14	smooth	1.7–2.3	Sumida et al., 1979; Eldridge, 1975
Pleuronichthys cornutus	WNP	1.03–1.25		polygonal pattern	2.8–3.8	Mito, 1963; Takita and Fujita, 1964
P. ritteri	ENP	0.94–1.08	0.08–0.14	polygonal pattern	2.1	Sumida et al., 1979
Scophthalmidae						
Lepidorhombus whiffiagonis	ENA	1.02–1.22	0.25–0.30	striations	ca. 4.0	McIntosh, 1892; Holt, 1893
Phrynorhombus norvegicus	ENA	0.72–0.92	0.09–0.16	rugose	2.5–2.8	Ehrenbaum, 1905–1909; Hefford, 1910
P. regius	ENA	0.90–0.99	0.16–0.18	–	2.4	Holt, 1897
Scophthalmus aquosus	WNA	0.90–1.38	0.15–0.30	striations	ca. 2.0	Martin and Drewry, 1978 (summary)
S. maeoticus	B	1.10–1.33	0.17–0.23	–	3.5 TL	Dekhnik, 1973
S. maximus	ENA	0.90–1.20	0.15–0.22	rugose	2.1–3.0	Holt, 1892; Jones, 1972
S. rhombus	B	1.20–1.50	0.16–0.25	striations	3.8	Jones, 1972
Zeugopterus punctatus	ENA	0.92–1.07	0.17–0.20	–	2.5–2.9	Hefford, 1910
Paralichthyidae						
Hippoglossina oblonga	WNA	0.91–1.12	0.17	smooth	2.7–3.2	Miller and Marak, 1962
H. stomata	ENP	1.22–1.38	0.20–0.26	smooth	3.7	Sumida et al., 1979
Paralichthys californicus	ENP	0.74–0.82	0.10–0.19	smooth	ca. 2.0	Original
P. dentatus	WNA	0.90–1.10	0.18–0.31	–	2.4–2.8	Smith and Fahay, 1970
P. olivaceus	WNP	0.83–1.03	0.13–0.21	smooth	2.6–2.8	Mito, 1963
Pseudorhombus cinnamoneus	WNP	0.77–0.89	0.12–0.14	–	1.8–2.0	Mito, 1963
Citharichthys arctifrons	WNA	0.70–0.82	–	smooth	ca. 2.0	Richardson and Joseph, 1973
Bothidae						
Arnoglossus capensis	ESA	0.72	0.12	smooth	2.2	Brownell, 1979
A. kessleri	B	0.59–0.70	0.10–0.13	smooth	1.8–1.9	Dekhnik, 1973
A. laterna	ENA	0.60–0.76	0.11–0.15	smooth	2.6	Russell, 1976 (summary)
A. scapha	NZ	0.78–0.88	0.11–0.12	smooth	–	Robertson, 1975a
A. thori	ENA	0.67–0.74	0.12	smooth	1.6–2.0	Russell, 1976 (summary)

[1] ESA = eastern South Atlantic; NZ = New Zealand; key to other regions as in Table 170.

laeops, Parabothus, Pelecanichthys, Psettina, Tosarhombus

Family Pleuronectidae

Subfamily Pleuronectinae (Atlantic, Mediterranean, Pacific, Arctic)

Acanthopsetta, Atheresthes, Cleisthenes, Clidoderma, Dexistes, Embassichthys, Eopsetta, Glyptocephalus, Hippoglossoides, Hippoglossus, Hypsopsetta, Isopsetta, Lepidopsetta, Limanda, Liopsetta, Lyopsetta, Microstomus, Parophrys, Platichthys, Pleuronectes, Pleuronichthys, Psettichthys, Pseudopleuronectes, Reinhardtius, Tanakius, Verasper

Subfamily Poecilopsettinae (Indo-Pacific, Atlantic)

Marleyella, Nematops, Poecilopsetta

Subfamily Paralichthodinae (Indian Ocean off South Africa)

Paralichthodes

Subfamily Samarinae (Indo-Pacific)

Samaris, Samariscus

Subfamily Rhombosoleinae (New Zealand, Southern Australia, South America)

Ammotretis, Azygopus, Colistium, Oncopterus, Pelotretis, Peltorhamphus, Psammodiscus, Rhombosolea

Suborder Soleoidei

Family Soleidae

Subfamily Soleinae (Worldwide, tropical to temperate) Norman (1966) recognized 22 genera

Subfamily Achirinae (American coasts, some fresh water) Norman (1966) recognized 9 genera

Family Cynoglossidae

Subfamily Symphurinae (Tropical-Subtropical American coasts, Mediterranean, West Africa, Indo-Pacific)

Symphurus

Subfamily Cynoglossinae (Indo-Pacific, Mediterranean, West Africa, Japan, some fresh water)

Cynoglossus, Paraplagusia

A profuse literature on the life history stages of flatfishes has accumulated since the early work of Cunningham (1887, 1889, 1890, 1891) who described numerous series reared from eggs collected from running ripe females. Other European workers (Holt, 1893; McIntosh and Prince, 1890; Petersen, 1904, 1905, 1906, 1909; Schmidt, 1904; Kyle, 1913) identified early life history series of additional species so that, by the time of Ehrenbaum's (1905–1909) summary, ontogenetic stages of a major portion of the eastern North Atlantic flatfish fauna were known. Padoa (1956k) summarized ontogenetic information on Medi-

TABLE 172. CHARACTERS OF PLEURONECTIFORM EGGS WITH MULTIPLE OIL GLOBULES.

	Region[1]	Egg size (mm)	Number of oil globules	Yolk	Chorion	References
Achirinae						
Achirus lineatus	WNA	0.71–0.76	12–14	homogeneous	smooth, thin	Houde et al., 1970
Trinectes maculatus	WNA	0.67–0.86	15–34	homogeneous	smooth	Hildebrand and Cable, 1938
Soleinae						
Aesopia cornuta	WNP	1.45–1.60	many; scattered	homogeneous	polygonal mesh	Mito, 1963
Austroglossus microlepis	ESA	0.88	12–20	homogeneous	smooth	Brownell, 1979
Buglossidium luteum	ENA	0.64–0.94	12–21; scattered	peripheral	smooth	Holt, 1891; Hefford, 1910
Dicologoglossa cuneata	ENA	0.70–0.84	60–80; scattered	peripheral segmentation		Lagardere, 1980
Microchirus ocellatus	ENA	0.90–1.10	30–40; scattered	peripheral segmentation	smooth	Palomera and Rubies, 1977
M. variegatus	ENA	1.28–1.42	to 50+; scattered	peripheral segmentation	smooth	Cunningham, 1889
Pegusa impar	M	1.06				Padoa, 1956k
P. lascaris lascaris	ENA	1.28–1.38	to 50+	peripheral segmentation		Holt, 1891; Hefford, 1910
P. lascaris nasuta	B	1.36–1.38	many; clumped	homogeneous	polygonal mesh	Dekhnik, 1973
Solea solea	ENA	0.98–1.58	many; highly clumped	peripheral segmentation	smooth	Cunningham, 1889; Fabre-Domergue and Biétrix, 1905
Synaptura kleini	ESA	1.34	many; clumped	homogeneous	smooth	Brownell, 1979
Zebrias japonicus	WNP	1.75	many; scattered	homogeneous	smooth	Mito, 1963
Z. zebra	WNP	1.60	many; scattered	homogeneous		Mito, 1963
Symphurinae						
Symphurus atricauda	ENP	0.71–0.78	10–23	homogeneous	smooth, colored	Original
Cynoglossinae						
Cynoglossus capensis	ESA	0.75	2–16	homogeneous	smooth	Brownell, 1979
C. robustus	WNP	0.85–0.90	5–15	homogeneous	fine hexagonal network	Fujita and Uchida, 1957
C. (Areliscus) trigrammus	WNP	1.19–1.23	30–50	homogeneous	smooth	Fujita and Takita, 1965
Cynoglossidae no. 5	WNP	0.71	14	homogeneous	smooth	Mito, 1963
Cynoglossidae sp. A	I	0.84	13–15	homogeneous	smooth	Vijayaraghavan, 1957
Cynoglossidae sp. B	I	0.82	18–22; clustered	homogeneous	smooth	Vijayaraghavan, 1957
Cynoglossus I	I	0.60	16–30	homogeneous	smooth	Nair, 1952a
Cynoglossidae (as *Solea ovata*)	I	0.61–0.71	17–25	homogeneous	smooth	John, 1951b
Rhombosoleinae						
Ammotretis rostratus	NZ	ca. 0.8	8–11	homogeneous	smooth	Thomson, 1906
Colistium guntheri	NZ	1.0–1.08	14–26	homogeneous		Robertson, 1975a
C. nudipinnis	NZ	ca. 1.5	21–28	homogeneous		Robertson, 1975a
Pelotretis flavilatus	NZ	0.85–0.95	8–18	homogeneous	smooth	Robertson, 1975a
Peltorhamphus novaezeelandiae	NZ	0.62–0.68	2–6	homogeneous	smooth	Robertson, 1975a
P. tenuis	NZ	0.58–0.68	2–4	homogeneous	smooth	Robertson, 1975a
Rhombosolea leporina	NZ	0.58–0.70	2–7	homogeneous	smooth	Robertson, 1975a
R. plebeia	NZ	0.58–0.72	2–13	homogeneous	smooth	Robertson, 1975a; Robertson and Raj, 1971
Bothinae						
Mancopsetta maculata antarctica	S	2.45–3.00	20+	homogeneous	smooth	Efremenko et al., 1981

[1] M = Mediterranean, S = southern oceans; key to other regions as in Table 170.

terranean flatfishes and more recently Russell (1976) provided an extensive review of previous European contributions. Knowledge of ontogenetic stages of western Atlantic flatfishes is summarized by Martin and Drewry (1978) and Fahay (1983). Early life histories of North Pacific flatfishes are treated comprehensively by Pertseva-Ostroumova (1961). Japanese and Indian workers have provided a long list of contributions to flatfish life history studies and Amaoka (1969, 1979), Hensley (1977) and Futch (1977) employed ontogenetic characters in assessing phylogenetic relationships. The individual contributions to flatfish ontogeny are too numerous to summarize concisely and are cited in the section that follows.

DEVELOPMENT

Eggs

Eggs are known for most species in Pleuronectidae and Scophthalmidae and for only a few to moderate numbers of

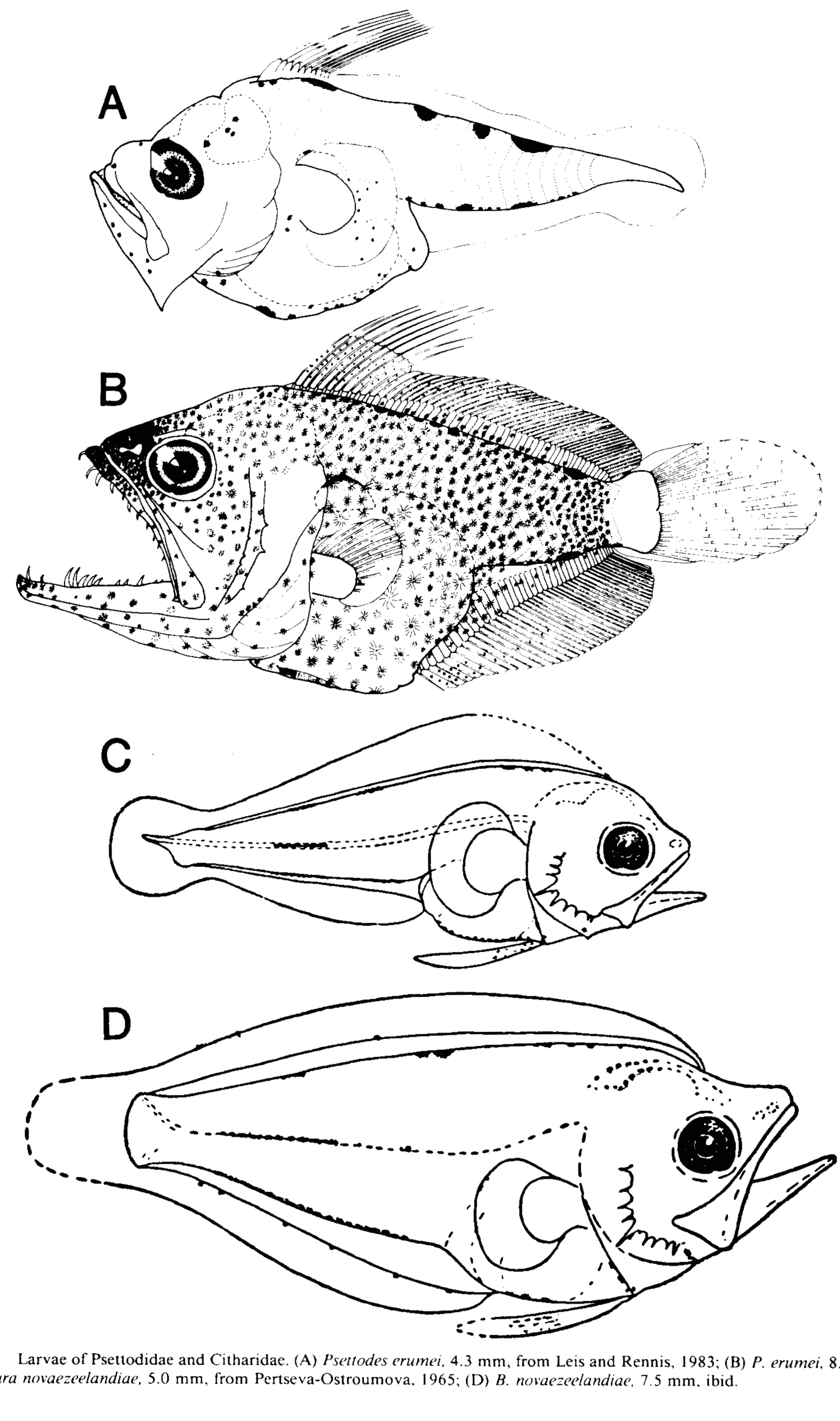

Fig. 342. Larvae of Psettodidae and Citharidae. (A) *Psettodes erumei*, 4.3 mm, from Leis and Rennis, 1983; (B) *P. erumei*, 8.7 mm, ibid; (C) *Brachypleura novaezeelandiae*, 5.0 mm, from Pertseva-Ostroumova, 1965; (D) *B. novaezeelandiae*, 7.5 mm, ibid.

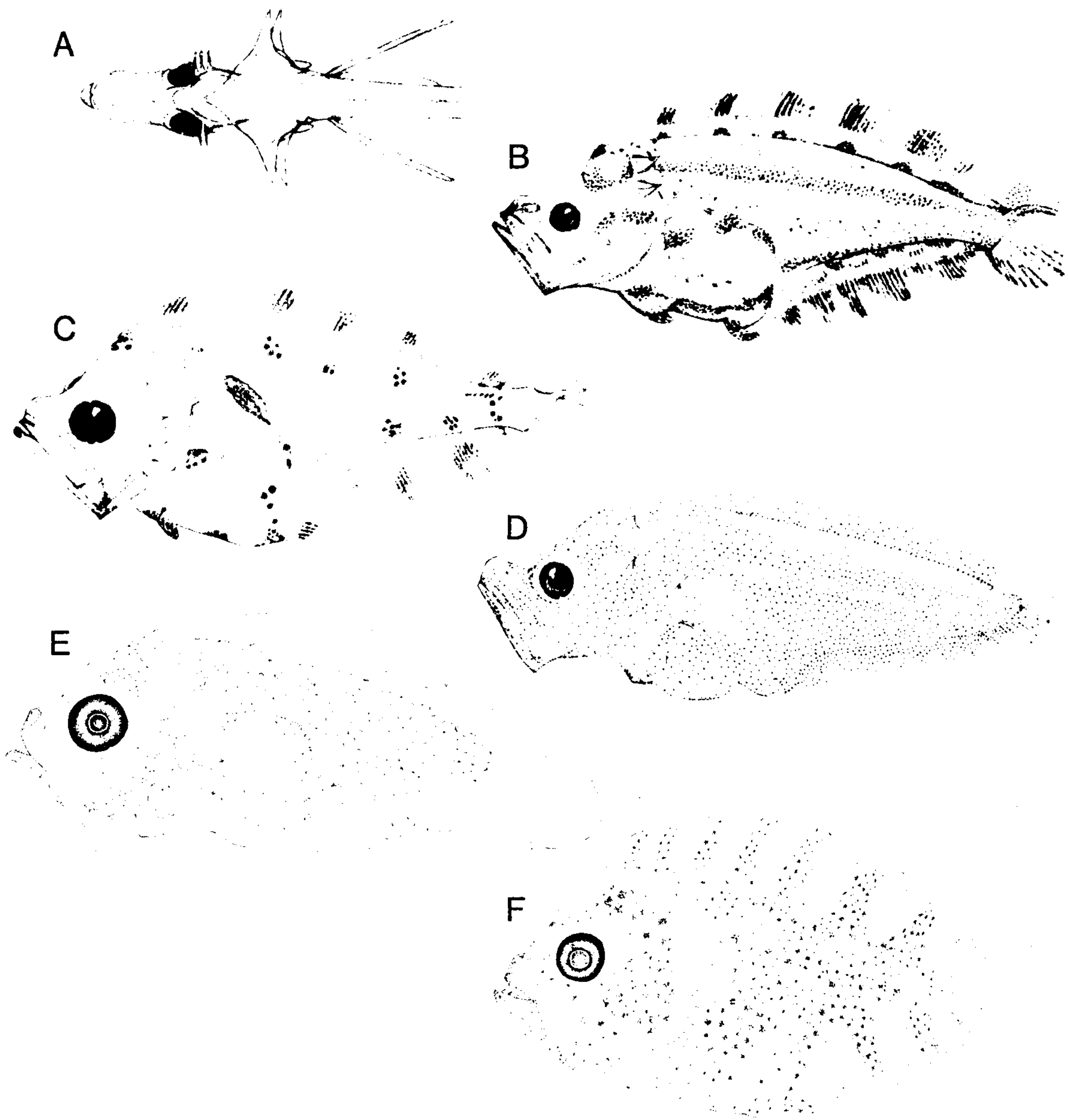

Fig. 343. Larvae of Scophthalmidae. (A) *Zeugopterus punctatus*, 8.9 mm, dorsal view, from Petersen, 1909; (B) *Z. punctatus*, 9.0 mm, ibid; (C) *Lepidorhombus boscii*, 9.7 mm, ibid; (D) *Phrynorhombus regius*, 8.0 mm, ibid; (E) *Scophthalmus maximus*, 7.4 mm, from Jones, 1972; (F) *S. rhombus*, 8.0 mm, ibid.

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Fig. 344. Larvae of Paralichthyidae. (A) *Paralichthys californicus*, 7.0 mm, original, CalCOFI; (B) As above, dorsal view; (C) *Xystreurys liolepis*, 6.7 mm, original, CalCOFI; (D) As above, dorsal view; (E) *Hippoglossina stomata*, 8.6 mm, from Sumida et al., 1979; (F) *Pseudorhombus pentophthalmus*, 9.2 mm, from Okiyama, 1974a; (G) *Tarphops oligolepis*, 9.2 mm, ibid.

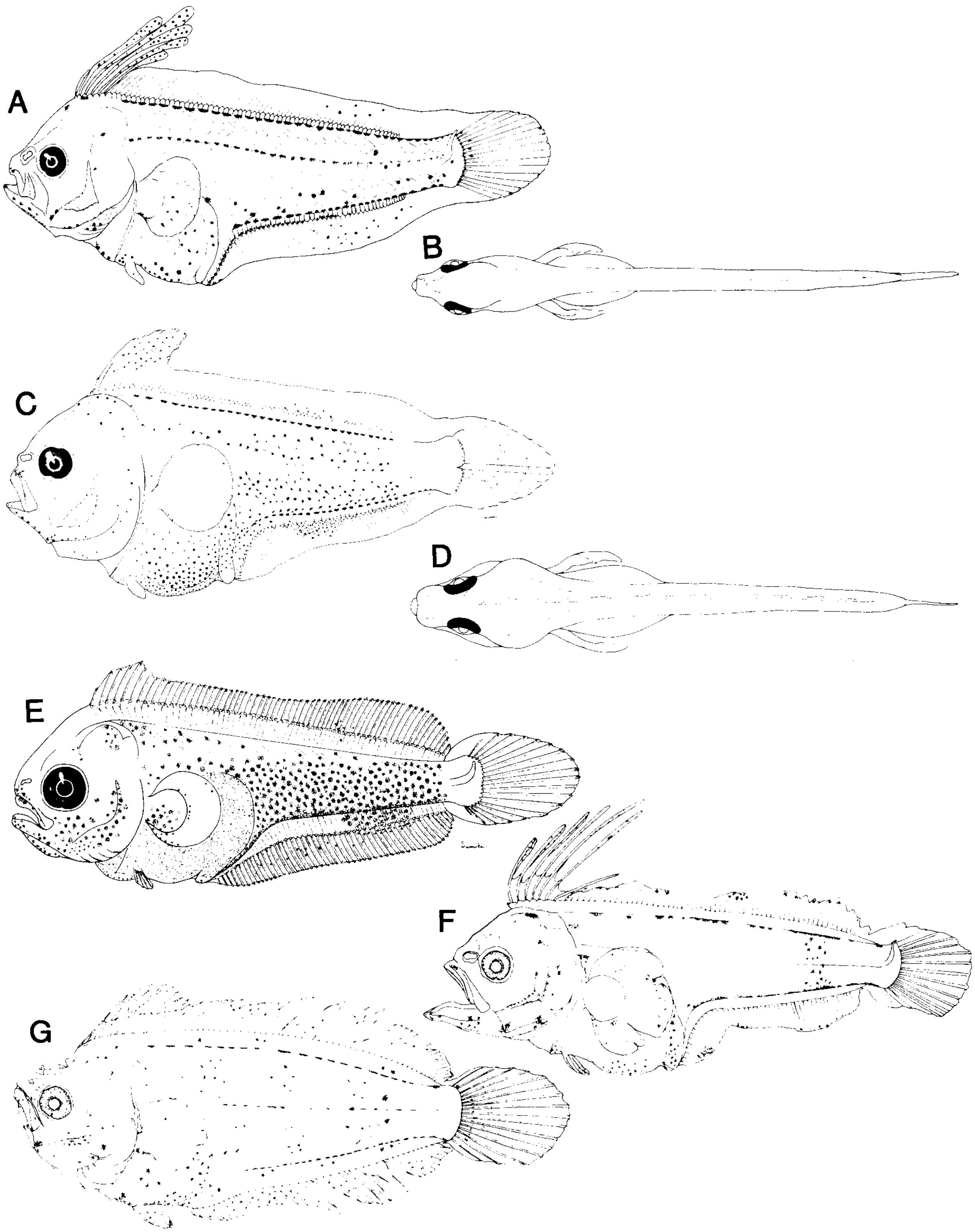
A
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TABLE 173. SUMMARY OF ONTOGENETIC CHARACTERS OF PLEURONECTIFORMS. (Line indicates data unavailable or presented elsewhere in column.)

	Eggs				Larvae		
Taxon	Egg size (mm)	Oil globule: Single/ Multiple/ Absent	Yolk: Homogeneous/ Segmented	Chorion: Smooth/ Striated/ Polygonal	Size at hatching (mm)	Size at metamorphosis (mm)	Elongate dorsal rays: Present (no.)/Absent
Psettodidae	—	—	—	—	—	9–10	10
Citharidae	—	—	—	—	—	—	—
Brachypleura	—	—	—	—	—	7–8	ca. 6
Scophthalmidae	0.72–1.5	S	H	St	2.0–4.0	8–>20	A
Paralichthyidae	<0.70–1.38	S	H	S	1.8–3.7	—	—
Paralichthys group	—	—	—	—	—	7.5–15	4–5
Pseudorhombus group	—	—	—	—	—	8.7–12.5	5–9
Cyclopsetta group	—	—	—	—	—	9–>35	**
Bothidae	0.59–0.88	S	H	S	1.8–2.6	—	—
Taeniopsettinae	—	—	—	—	—	19–60	1
Bothinae	—	—	—	—	—	15–120	1
Pleuronectidae	—	—	—	—	—	—	—
Pleuronectinae	0.66–4.5	A*	H	S, P, St	1.7–16.0	4.4–65	A
Poecilopsettinae	—	—	—	—	—	ca. 30	A
Samarinae	—	—	—	—	—	ca. 30	1
Rhombosoleinae	0.58–1.5	M	H	S	ca. 1.8	—	—
Soleidae	0.64–1.75	M	H, S	S, P	1.6–4.1	—	—
Soleinae	—	—	—	—	—	3.4–18	A
Achirinae	—	—	—	—	—	3–5.5	***
Cynoglossidae	0.60–1.23	M	H	S, P	1.3–3.2	—	—
Cynoglossinae	—	—	—	—	—	ca. 4–18	2
Symphurinae	—	—	—	—	—	ca. 12–32	usually 4–5

* Single oil globule present in 3 species.
** 0–2 in *Etropus*; 0, 2, 3 in *Citharichthys*; 5–8 in *Syacium*; 8–11 in *Cyclopsetta*.
*** Third ray elongated in *Achirus*.
**** 0, 1, or 2 in *Citharichthys*; 2 or 3 in *Cyclopsetta* and *Syacium*; 0 or 1 in *Etropus*.
***** *S. ligulata* develops elongate third and fourth rays.
****** Protruding in *Chascanopsetta*, *Pelecanichthys*, and *Kamoharaia*.

species in other groups, including Soleidae, Cynoglossidae, Paralichthyidae, and Bothidae.

With a few exceptions, the eggs of flatfishes are pelagic, round, have homogeneous yolk, a narrow perivitelline space, and an unsculptured chorion (Fig. 341). The eggs of all flatfishes are spawned separately. The characters of eggs showing greatest differences among flatfishes are 1) egg size, and 2) the presence or absence of an oil globule(s) (Tables 170–172).

Of the approximately 60 species of pleuronectine flatfishes of the North Pacific and North Atlantic, eggs are known for at least 45 (Table 170). Six species are known to have demersal eggs; these are round or occasionally off-round and have a sticky, adhesive chorion that permits clustering or adhesion to bottom objects. Egg diameters range from 0.66 to 4.5 mm within the subfamily. The yolk is homogeneous in all pleuronectine eggs. The perivitelline space is narrow to moderate, except for eggs of *Hippoglossoides*, which have a wide perivitelline space, usually 25–30% of the egg diameter on either side of the yolk mass. The chorion has the appearance of being smooth on eggs of most species, but closer inspection reveals striations or reticulations on the chorion of some kinds. The chorion of *Pleuronichthys* eggs has a striking hexagonal pattern. The eggs of pleuronectine flatfishes, except for three species, lack an oil globule. The state of embryonic development achieved in the egg is related to egg size, more specifically to yolk size. Larvae hatching from small eggs lack eye pigment, a functional mouth and pectoral fins; those hatching from larger eggs are much more advanced, with pigmented eyes, a functional mouth and pectorals. Embryos in middle- and late-stage eggs are pigmented, with patterns varying between genera and species. Among species, yolk pigment can range from unpigmented, to some pigment on yolk adjacent to the embryo, to heavily pigmented. Pigment can also be present on finfolds of late-stage eggs of some flatfishes.

Eggs of Scophthalmidae, Paralichthyidae and Bothidae have a single, small to moderate-sized oil globule, are pelagic, round, have a narrow to moderate perivitelline space, and homogeneous yolk (Fig. 341, Table 171). In late-stage eggs and newly hatched larvae the single oil globule usually is in the rear of the yolk mass.

Eggs are known for 8 of the 10 species of scophthalmid flatfishes. They range in size from 0.72 to 1.50 mm. The chorion is striated or rugose in six species and this may apply to all. Embryos develop considerable pigment over the head and body and often in finfolds; pigment over the yolk mass and oil globule can range from none, or sparse, to intense.

Eggs are known for only a few species in the family Paralichthyidae. These range in size from 0.70–1.38 mm; chorions are unsculptured. Except for a few species of *Arnoglossus*, eggs of bothid flatfishes are practically unknown. Mito (1963) lists 10 kinds of bothid eggs off Japan, unidentified to genus; 8 of these have diameters under 1.0 mm. Eggs of his Bothidae No. 9 are slightly off-round and three different eggs have a conspicuous wart-like appendage. Much work remains to be done in identifying eggs of fishes of these families, preferably through rearing eggs from known parents.

Eggs with multiple oil globules are typical of the families

TABLE 173. EXTENDED.

Larvae								
Elongate pelvic rays: Present/Absent	Gut: Normal/ Protruding/ Trailing	Preopercular spines: Present/ Absent	Otic region spines: Present/ Absent	Frontal region spines: Present/ Absent	Urohyal spines: Present/Absent	Basipterygial spines: Present/ Absent	Cleithral spines: Present/ Absent	Body spines: Present/Absent
A	N	P	A	A	A	A	A	A
—	—	—	—	—	—	—	—	—
P	N	P	A	A	A	A	A	A
A	N	P, A	P, A	P, A	A	A	A	A
—	—	—	—	—	—	—	—	—
A	N	P	A, P	A	A	A	A	A
A	N	P	A, P	A	A	A	A	A
****	N	P	P, A	A	A	A	A	A
—	—	—	—	—	—	—	—	—
A	N	A	P	A	P	P	P	A
A	******	A	A	A	P, A	P, A	P, A	P, A
—	—	—	—	—	—	—	—	—
A	N	A, P	A, P	A, P	A	A	A	A
A	N	A	A	A	A	A	A	A
A	P	A	A	A	A	A	A	A
—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—
A	N, P	A	A	A	A	A	A	A
A	N, P	A, P	A, P	A, P	A	A	A	P, A
—	—	—	—	—	—	—	—	—
A	P	A	A	A	A	A	A	A
A, *****	P, T	A	A	A	A	A	A	A

Soleidae, Cynoglossidae, the pleuronectid subfamily Rhombosoleinae, and *Mancopsetta,* previously considered a bothid (Fig. 341, Table 172). Eggs have been described for about a dozen kinds of soleids ranging in size from 0.64–1.75 mm. Eggs are round, or occasionally slightly off-round. Oil globules are usually numerous but vary in number, size and distribution within the yolk. They can be highly clumped, as in *Solea solea,* or scattered throughout the yolk, as in *Microchirus variegatus.* In eggs of the latter, oil globules were observed to range in size from 0.015–0.12 mm, whereas they are much smaller and more uniform in size in *Solea solea* or *Pegusa lascaris.* Eggs of the two achirine soleids described from the western Atlantic have a relatively low number of oil globules. Perivitelline space is narrow to negligible in soleid eggs. The yolk is peripherally segmented in eggs of the four species known from the eastern North Atlantic. Yolk is more completely segmented in the egg designated as Synapturinae No. 1 by Mito (1963). Yolk can remain unsegmented, however, as for example in *Achirus lineatus* and *Trinectes maculatus.* Although the chorion of soleid eggs is usually smooth and unsculptured, Mito (1963) found eggs of *Aesopia cornuta* to have a pattern of large hexagonal meshes, 0.18–0.24 mm wide, covering the chorion, and Dekhnik (1973) shows fine polygonal sculpturing on the chorion of *P. lascaris.*

Eggs of the few cynoglossid species known (Table 172) are small, have homogeneous yolk without secondary segmentation, a narrow perivitelline space and either an unsculptured chorion or one with small polygonal meshes. Oil globules range in number between 5–50, and can be variously distributed in the yolk.

Robertson (1975a) described eggs of seven species of Rhombosoleinae, belonging to four genera (Table 172). Egg diameters range from 0.58 to 1.5 mm. Oil globules in described eggs range in number from 2–28. Yolk is homogeneous, the perivitelline space is narrow, and the chorion is smooth.

Efremenko et al. (1981) described the ovarian and planktonic eggs of *Mancopsetta maculata antarctica* and showed that they are large (2.45–2.75 mm) and have multiple oil globules (>20). This finding provides evidence that *Mancopsetta* does not belong in the Bothidae.

Larvae

In addition to such features as meristics, fin arrangement, and osteology of the fin supports and axial skeleton (which develop gradually during ontogeny and are essential for identification of flatfish larvae) the larval stage itself provides many characters useful in identification and systematic analysis. Larval characters are summarized in Table 173 and below.

Psettodidae (Fig. 342).—Aboussouan's (1972c) description of preflexion larvae of *Psettodes bennetti* was based on five specimens, 4.4–5.7 mm in length. Leis and Rennis (1983) describe a series of five larval specimens of *Psettodes erumei,* 3.0–8.7 mm in length. The smallest specimen has a large yolk sac, the 6.0-mm larva is in mid-flexion and the largest specimen is undergoing eye migration. Larvae have: a deep, relatively thick body; large head with massive jaws that extend well beyond the rear margin of the eye and bear large, early-forming curved teeth; large eye; small preopercular spines; and 10 early-forming elongate dorsal rays. Dorsal and anal fin rays are all present at 6.0 mm but rays do not appear in paired fins until about 8.0 mm. Preflexion larvae have a series of large melanophores along the dorsal midline, large melanophores alternating with smaller ones

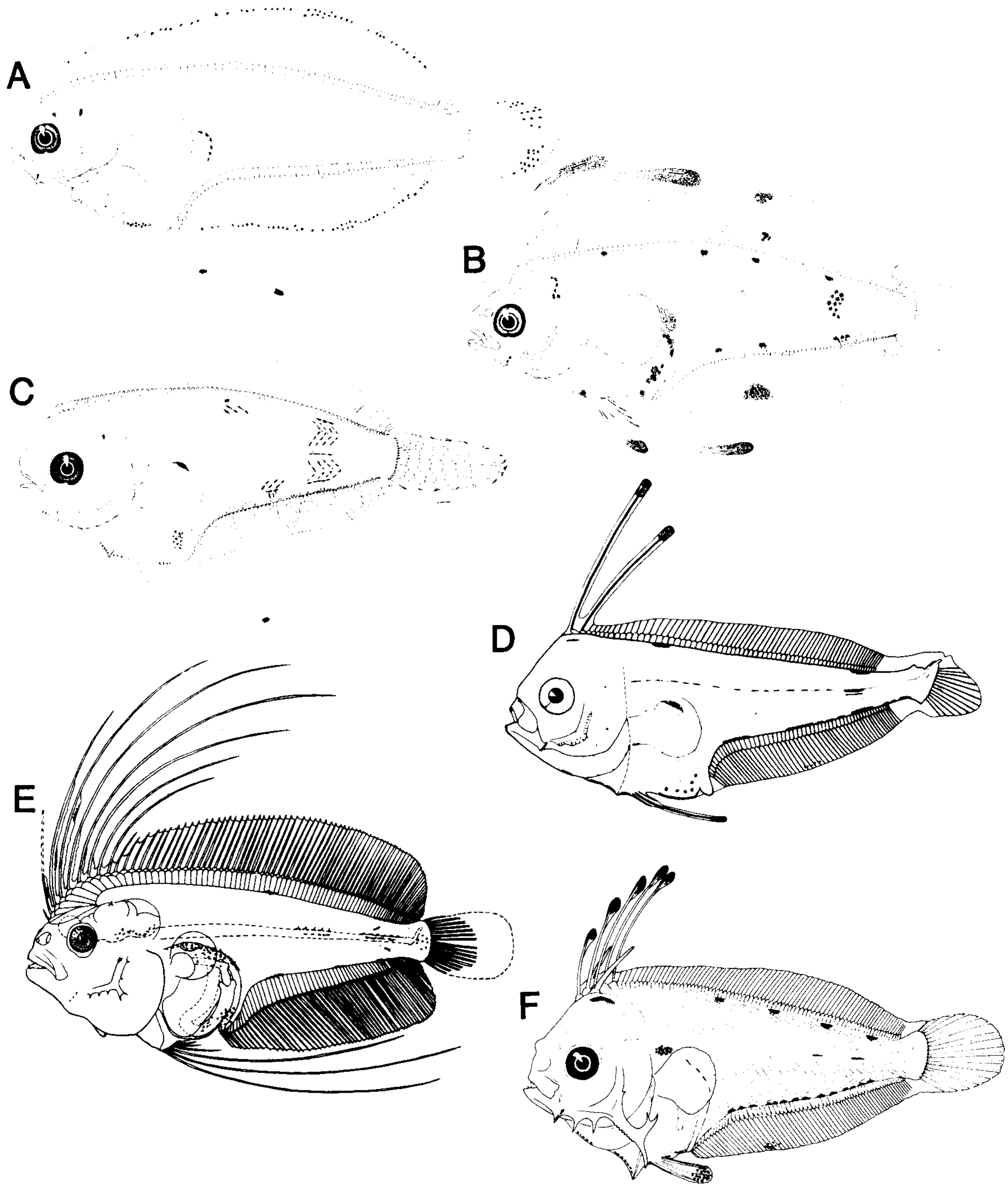


Fig. 345. Larvae of Paralichthyidae. (A) *Citharichthys stigmaeus*, 14.8 mm, from Ahlstrom and Moser, 1975; (B) *C. sordidus*, 14.5 mm, ibid; (C) *C. platophrys*, 8.6 mm, original, CalCOFI; (D) *Etropus crossotus*, 6.0 mm, from Tucker, 1982; (E) *Cyclopsetta chittendeni*, 13.0 mm, from Evseenko, 1982a; (F) *Syacium ovale*, 6.5 mm, original, CalCOFI.

TABLE 174. NUMBERS OF RAYS IN DORSAL CREST AND SIZE AT DEVELOPMENTAL EVENTS IN PARALICHTHYIDAE.

Species	Number of elongate dorsal fin rays	Size at hatching (mm)	Size at flexion (mm)	Size at transformation (mm)	References
Hippoglossina stomata	6	3.7	6.2–8.8	9.1–>11.7	Sumida et al., 1979
H. oblonga	~6	2.7–3.2	6.3–7.7	10–14	Leonard, 1971
Paralichthys californicus	5	2.0	6.0–7.3	7.5–9.4	Original, Ahlstrom and Moser, 1975
P. dentatus	4–8	2.4–2.8	7–9.5	~9.5	Smith and Fahay, 1970
P. olivaceus	5–6	2.6–2.8	7.1–8.7	10.2–>14.2	Okiyama, 1967
Xystreurys liolepis	6	2.0	6.0–6.7	7.5–>8.7	Original
Pseudorhombus elevatus	9	—	5.5–6.4	~10	Devi, 1969
P. pentophthalmus	7	—	7.1–7.6	8.7–12.2	Okiyama, 1974a; Minami, 1981a
Tarphops oligolepis	8	—	—	9.2–12.5	Okiyama, 1974a
Citharichthys arctifrons	3	<2.3	~5–8	13–15	Richardson and Joseph, 1973
C. cornutus	3	<2.2	5.8–8.9	~18	Tucker, 1982
C. gymnorhinus	3	—	5.3–7.7	~18	Tucker, 1982
C. platophrys	3	<2.0	5.3–6.1	11.2–18.5	Original
C. sordidus	2	~2.0	10.4–11.4	20–>39	Ahlstrom, 1965; original; Ahlstrom and Moser, 1975
C. spilopterus	2	—	5.7–6.8	9–12	Tucker, 1982
C. stigmaeus	0	~2.0	9.2–10.2	24.0–>35.5	Ahlstrom, 1965; original; Ahlstrom and Moser, 1975
Etropus crossotus	2	<2.3	4.9–9.5	~11	Tucker, 1982
E. microstomus	0	<2.3	5–7	10–12	Richardson and Joseph, 1973
Cyclopsetta chittendeni	8–9	—	~7.5	>13.0	Evseenko, 1982a
C. fimbriata	~9	~1.5	6.9	14.0	Gutherz, 1970; Evseenko, 1982a
C. querna	8–11	—	—	>32	Ahlstrom, 1972a
Syacium guineensis	7	<2.1	<6.5	>13.9	Aboussouan, 1968b
S. gunteri	5–8	<1.8	—	—	Evseenko, 1982a
S. micrurum	5–8	<1.8	—	—	Evseenko, 1982a
S. ovale	5–8	~1.6	4.1–4.8	~14–~20	Ahlstrom, 1972a; original
S. papillosum	5–8	<2.3	5.5–6.0	15–13	Futch and Hoff, 1971; Evseenko, 1982a

along the ventral midline, and small melanophores on the trunk, tail, ventral gut, pectoral fin, brain and lower jaw. During flexion the entire body except for the caudal fin base becomes solidly pigmented, a darker band forms forward of the caudal peduncle, and the snout becomes heavily pigmented.

Citharidae (Fig. 342).—Larvae of this family are known from five specimens (4.0–8.0 mm) of *Brachypleura novaezeelandiae* described by Pertseva-Ostroumova (1965). Notochord flexion occurs between 5.0 and 7.0 mm and transformation at about 8.0 mm. Larvae have a moderately deep, thick body and a large head with large jaws and eyes and about 10 large preopercular spines; the sixth dorsal ray is elongate and the rays anterior to it are assumed to be elongate, although damaged in all available specimens; pelvic fins are elongate, extending beyond the anus; pigment consists of a series of melanophores along the dorsum, a series along the horizontal septum, and a postanal series along the ventrum, melanophores below the gut, and on the pelvic fin.

Scophthalmidae (Fig. 343).—Larvae are known for 9 of the 10 species of this family. Petersen (1909) described 5 of the 7 species occurring in the eastern North Atlantic; Jones (1972) provided excellent illustrations of the 2 species of eastern Atlantic *Scophthalmus* and Bigelow and Welsh (1925) described larvae of *S. aquosus*, the only western Atlantic representative of the family. Newly hatched larvae are 2.0–4.0 mm in length (Table 171); size at notochord flexion for most species is 6.0–8.0 mm. Metamorphosis can begin by 8 or 9 mm and be completed by 13 mm (*S. aquosus*, *Phrynorhombus norvegicus*, *Zeugopterus punctatus*) or delayed to over 20 mm (*S. maximus*, *S. rhombus*). Larvae are deep- and thick-bodied, especially at the gut, have a large head and jaws and moderate to large eyes. Scophthalmid larvae develop extensive head spination. Three species (*Z. punctatus*, *P. regius*, *Lepidorhombus whiffiagonis*) develop paired otic spines. In *Z. punctatus*, spines also develop at the lateral aspect of the midbrain and on the opercle. Larvae of *P. norvegicus* develop spines along the lower jaw, on the opercle and preopercle, and at the shoulder (posttemporal region) while *L. boscii* has preopercular spines and a shoulder cluster. *S. maximus* and *S. rhombus* have a supraocular spiny ridge, numerous spines on the opercle and preopercle and a shoulder cluster. Pigmentation is heavy on the head and body in most species. *Z. punctatus* has a series of finfold bars and *L. boscii* develops these and also incomplete bars on the body. Late larvae of all species develop bars on the dorsal and anal fins.

Paralichthyidae (Figs. 344, 345).—Three subgroups are recognized in this family on the basis of adult characters: *Paralichthys* and relatives (*Ancylopsetta*, *Gastropsetta*, *Hippoglossina*, *Lioglossina*, *Verecundum*, *Xystreurys*); *Pseudorhombus* and relatives (*Cephalopsetta*, *Tarphops*); and *Cyclopsetta* and relatives (*Citharichthys*, *Etropus*, *Syacium*).

In the first group larvae are known for species of *Paralichthys* and *Hippoglossina* and for *Xystreurys liolepis* and in the second group larvae are known for *Pseudorhombus* and *Tarphops*. In

TABLE 175. MERISTIC AND LARVAL CHARACTERS OF BOTHIDAE.

Taxon	Larvae described[1]	Number of vertebrae	Urohyal spines[2]	Basipterygial spines	Cleithral spines	Otic spines	Scale spines	2nd dorsal ray[3]	Length at transformation (mm)	References
Taeniopsettinae										
Engyophrys	+	10 + 27–31 = 37–41	++	++	++	+	0	M	~19	Hensley, 1977
Taeniopsetta	+	10 + 30–32 = 40–42	++	++	++	+	0	S	~60	Amaoka, 1970
Trichopsetta	+	10–11 + 30–33 = 40–43	++	++	++	+	0	S	~28	Futch, 1977
Perissias	–	10 + 29–30 = 39–40								
Bothinae										
Arnoglossus	+	10–12 + 27–36 = 37–48	0	0	0	0	+	M, L	21–46	Kyle, 1913; Pertseva-Ostroumova, 1965; Amaoka, 1973, 1974
Bothus	+	10 + 25–32 = 35–42	0	0	0	0	0	M, L	9–42	Kyle, 1913
Chascanopsetta	+	16–18 + 37–44 = 53–59	0	0	0	0	0	M	78–120	Bruun, 1937; Nielsen, 1963b; Amaoka, 1971; Pertseva-Ostroumova, 1971
Crossorhombus	+	10 + 24–27 = 34–37	0	+	0	0	+	M, L	15–20	Ochiai and Amaoka, 1963
Engyprosopon	+	10 + 23–27 = 33–37	++	++	0, ++	0	0	M	16–18	Pertseva-Ostroumova, 1965
Grammatobothus	+	10 + 27–28 = 37–38	+	+	0	0	0	M	~15	
Kamoharaia	+	13–14 + 37–39 = 50–53	0	0	0	0	0	M	~91	Nielsen, 1963c
Laeops	+	10–12 + 35–42 = 46–53	0	0	0	0	0	L	51–80	Balakrishnan, 1963; Amaoka, 1972a; Hubbs and Chu, 1934
Lophonectes	+	10 + 32–33 = 42–43	0	+	0	0	0	M	~20	Original
Monolene	+	10 + 28–38 = 38–48	0	0	0	0	0	L	~30	Futch, 1971
Pelecanichthys	+	17 + 40 = 57	0	0	0	0	0	M	>90	Struhsaker, pers. comm.
Psettina	+	10 + 29–30 = 35–40	+	+	0	0	+	M	16–20	Pertseva-Ostroumova, 1965; Amaoka, 1976
Asterorhombus	–	10 + 26–27 = 36–37								
Japonolaeops	–	11 + 41–44 = 52–53								
Mancopsetta	–	13–16 + 38–50 = 52–66								
Neolaeops	–	13 + 38 = 51								
Parabothus	–	10 + 31–36 = 41–46								
Tosarhombus	–	10 + 28–30 = 38–40								

[1] + = yes; – = no. [2] 0 = absent; + = present; ++ = strong.
[3] S = short; M = moderate; L = long.

these two subgroups hatching, notochord flexion and metamorphosis occur at a small size (Table 174). Larvae of these groups are noted for a dorsal crest consisting of elongate early forming rays, beginning with the second dorsal ray (Table 174). Larvae of the *Paralichthys* group are moderate in body depth, with a deep head and moderate-size jaws. Body thickness is moderate except that *Paralichthys* is more laterally compressed than in other genera reported (Fig. 344). The gut mass is large. Preopercular spination consists of an anterior and posterior series in *Paralichthys*, *Pseudorhombus* and *Tarphops* and an anterior series only in *Hippoglossina*. Larvae of *Paralichthys dentatus* have one to several minute sphenotic spines (Smith and Fahay, 1970) and *P. olivaceus* develops a spine cluster on the sphenotic, one spine on the epiotic, and 1–2 spines on each bone in the opercular series. Larvae of *Pseudorhombus pentophthalmus* have a single sphenotic spine, and some on the opercular bones (Okiyama, 1974a); Devi (1969) shows two rows of sphenotic spines in *P. elevatus*.

Yolk-sac larve of the *Paralichthys* and *Pseudorhombus* groups develop moderate to heavy pigmentation with some on the finfolds. Later-stage larvae have pigment over the brain, on the lower head and jaw region and below and lateral to the gut. Most species have a melanophore series along the dorsum and ventrum. Lateral pigment may consist of a series along the horizontal septum (*Paralichthys, Tarphops*), a wide-spread zone of melanophores (*Xystreurys, Hippoglossina*) or a posterior bar (*Pseudorhombus pentophthalmus*). Most species have a series of internal melanophores above the spinal column and some melanophores on the posterior region of the finfold and developing dorsal and anal fins.

Larvae of the *Cyclopsetta* assemblage are similar morphologically to those of the *Paralichthys* and *Pseudorhombus* assemblages, but differ in spination and fin ray development. The rays forming the dorsal crest are typically longer and stand out more abruptly compared with *Paralichthys* and associated genera. The fin ray complement of the crest, along with other characters, divides the assemblage into two generic pairs: *Citharichthys-Etropus* and *Cyclopsetta-Syacium*. Species of the former group have either two or three elongate rays, except for two species which lack a crest altogether (Table 174). Species of *Syacium* have 5–8 elongate dorsal rays and 8–11 occur in *Cyclopsetta*. The left pelvic fin forms before the right and may develop elongate rays in some species. The first two pelvic rays are elongate in *Citharichthys sordidus* and *C. platophrys*, the second ray only is elongate in *C. cornutus*, *C. gymnorhinus*, *C. spilopterus* and *Etropus crossotus*; *C. arctifrons*, *C. stigmaeus* and *E. micros-*

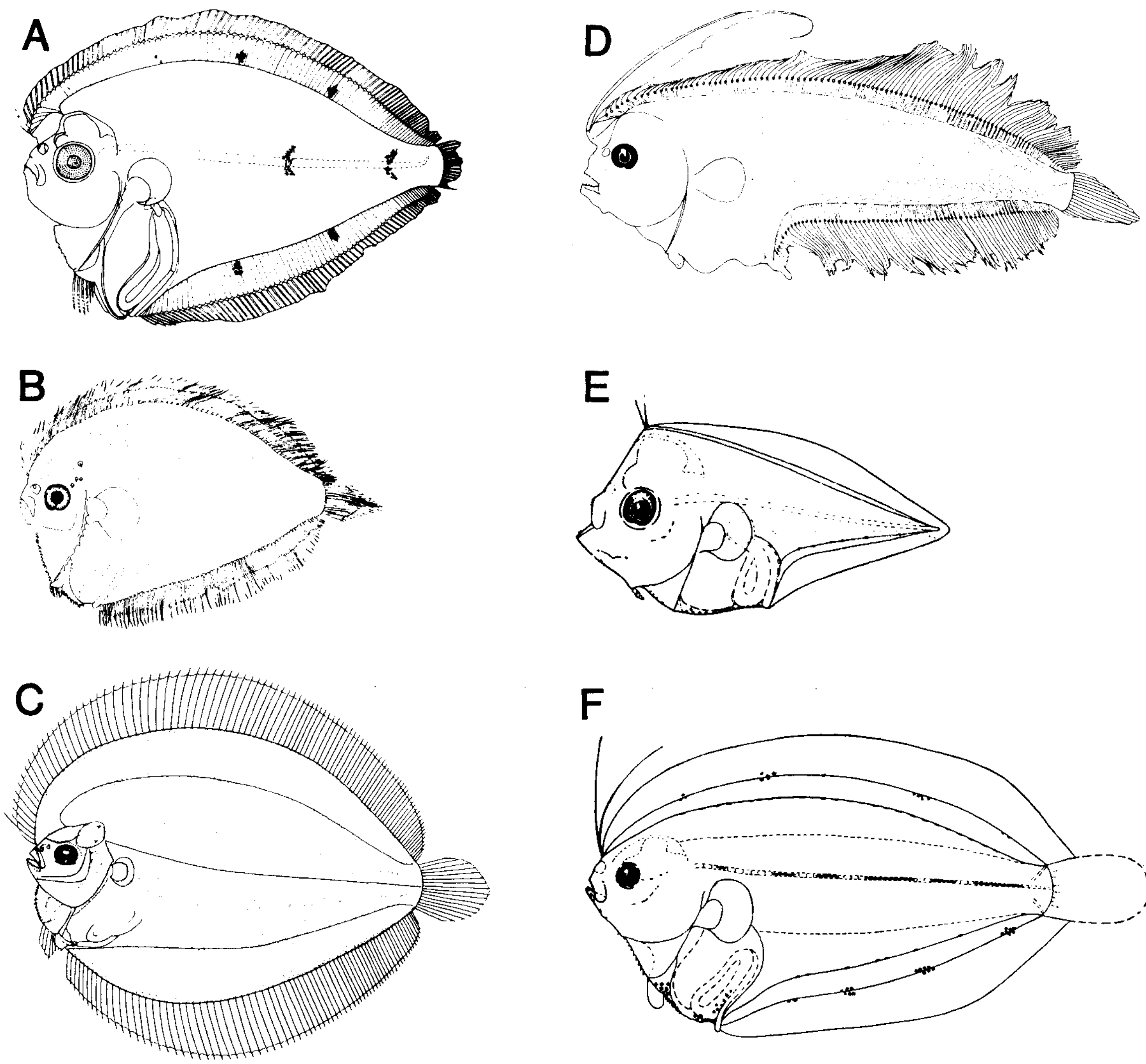


Fig. 346. Larvae of Bothidae. (A) *Trichopsetta ventralis*, 21.9 mm, from Evseenko, 1982a; (B) *Engyophrys senta*, 12.3 mm, from Hensley, 1977; (C) *Taeniopsetta ocellata*, 59.0 mm, from Amaoka, 1970; (D) *Monolene sessilicauda*, 14.3 mm, redrawn from Futch, 1971; (E) *Psettina hainanensis*, 4.2 mm, from Pertseva-Ostroumova, 1965; (F) *P. hainanensis*, 18.1 mm, ibid.

tomus lack elongate pelvic rays. The first three pelvic rays become markedly elongate in *Cyclopsetta* and the entire left fin becomes moderately elongate in *Syacium*.

Etropus and *Citharichthys* (except for *C. arctifrons*) develop one or more rows of small preopercular spines. According to Tucker (1982), small frontal-sphenotic spines are present in some species of *Citharichthys* and *Etropus* (6–8 spines on each side in *C. cornutus*, up to 6 in *C. gymnorhinus*, 1–2 in *C. spilopterus*, and 3–4 in *E. crossotus*). *Syacium* and *Cyclopsetta* develop a series of large preopercular spines at the margin of the bone and, in some species, an irregular anterior series. The spine at the angle of the primary series becomes antler-like in preflexion larvae of *Syacium* and in postflexion larvae of *Cyclopsetta*. Early preflexion larvae of *Syacium* develop single elongate sphenotic spines which remain prominent during the remainder of the larval period. Sphenotic spines in *Cyclopsetta* are early-forming but short.

Larvae of both subgroups of the *Cyclopsetta* assemblage typically have pigment above the brain, on the lower head region, below the gut, lateral to the posterior region of the gut, and above the gas bladder. Early preflexion larvae of most species have a series of small postanal melanophores and a bar or a

TABLE 176. SIZE DATA FOR PLEURONECTINAE LARVAE.

	Size at hatching (mm)	Size at notochord flexion (mm)	Size at transformation (mm)	References
Acanthopsetta nadeshnyi	<3.0	8.4–9.9	ca. 20–?	Pertseva-Ostroumova, 1961
Atheresthes evermanni	<8.4	ca. 11.5–15	—	Pertseva-Ostroumova, 1961
A. stomias	—	—	32.9–?	Pertseva-Ostroumova, 1961
Cleisthenes herzensteini	2.2–2.6	7.0–7.9	8.1–11.4	Okiyama and Takahashi, 1976; Dekhnik, 1959
Embassichthys bathybius	ca. 9.0	—	16.2–?	Richardson, 1981b
Eopsetta grigorjewi	2.5–3.0	7.2–8.9	11.4	Okiyama and Takahashi, 1976
E. jordani	2.8	—	—	Alderdice and Forrester, 1971
Glyptocephalus cynoglossus	3.5–5.6	15–21	25–?	Petersen, 1904
G. stelleri	4.1–5.2	15–17	19–48	Okiyama, 1963; Dekhnik, 1959; Pertseva-Ostroumova, 1961
G. zachirus	ca. 6	15.3–24.0	49–72	Original; Ahlstrom and Moser, 1975
Hippoglossoides dubius	3.0–3.4 TL	<12.4	18.1	Okiyama and Takahashi, 1976
H. elassodon	5.4–6.6 TL	9.0–10.2	—	Dekhnik, 1959; Pertseva-Ostroumova, 1961
H. platessoides	4.0–6.0	9.5–17.5	18–30	Petersen, 1904; Russell, 1976; Nichols, 1971; Colton and Marak, 1969
H. robustus	ca. 4.0	ca. 11–?	>28.6	Pertseva-Ostroumova, 1961
Hippoglossus hippoglossus	6.5–7.0	16–18	22–34	Schmidt, 1904; Russell, 1976 (summary)
H. stenolepis	7.8–8.5	13.6–17.8	14.7–24.1	Thompson and Van Cleve, 1936; Pertseva-Ostroumova, 1961
Hypsopsetta guttulata	1.7–2.3	4.0–5.2	4.4–>8.8	Sumida et al., 1979
Isopsetta isolepis	2.7–2.9	9.1–14.0	15–>21.9	Richardson et al., 1980
Kareius bicoloratus	ca. 3.0	ca. 4.0–9.0	ca. 14–?	Pertseva-Ostroumova, 1961
Lepidopsetta bilineata	3.4–3.8	ca. 8.4–9.9	>17.7	Pertseva-Ostroumova, 1961
L. mochigarei	3.95–4.48	ca. 8.9	—	Yusa, 1958; Okiyama and Takahashi, 1976
Limanda aspera	2.2–2.8	7.5–9.5	ca. 10–?	Dekhnik, 1959; Pertseva-Ostroumova, 1961
L. ferruginea	2.0–3.5	5.9–ca. 10	ca. 14	Bigelow and Welsh, 1925; Miller, 1958
L. limanda	2.7–4.0	7–8.7	12–20	Russell, 1976 (summary)
L. punctatissima	1.79–2.21	—	8.1–>9.6	Pertseva-Ostroumova, 1961
L. schrenki	ca. 2.4	—	—	Hikita, 1952
L. schrenki (as *Pseudopleuronectes yokohamae*)	ca. 2.4	<7.4	12.0–?	Pertseva-Ostroumova, 1961
L. yokohamae	3.5–3.8	ca. 7.0	ca. 7.5–10.0	Yusa, et al., 1971; Minami, 1981a
Liopsetta glacialis	3.7	—	—	Pertseva-Ostroumova, 1961
L. obscura	2.5–3.5	~6.6	>9.0	Pertseva-Ostroumova, 1961; Kurata, 1956
L. pinnifasciata	3.15–3.93	8.11–8.45	>8.5	Pertseva-Ostroumova, 1961
L. putnami	3.1–3.6	6.0–7.1	7.3	Laroche, 1981
Lyopsetta exilis	ca. 5.6	9.0–10.9	15.7–24.7	Original; Ahlstrom and Moser, 1975
Microstomus achne	—	8.8	—	Okiyama and Takahashi, 1976
M. kitt	4.84	12–15	18–28	Petersen, 1904
M. pacificus	ca. 6.0	ca. 10–15	ca. 20–>45	Original; Ahlstrom and Moser, 1975
Parophrys vetulus	2.3–2.8	8.8–10.5	ca. 20	Original; Budd, 1940; Ahlstrom and Moser, 1975
Platichthys flesus	2.25	5.9–7.1	9–12	Nichols, 1971; Russell, 1976 (summary)
P. stellatus	1.9–2.1	5.5–6.0	—	Orcutt, 1950; Yusa, 1957; Pertseva-Ostroumova, 1961
P. pallasii (as *Platessa quadrituberculata*)	5.6	8.9	ca. 10.0–?	Pertseva-Ostroumova, 1961
P. platessa	6.0–7.5	8.9–10.2	10.5–14	Nichols, 1971; Russell, 1976 (summary)
Pleuronichthys coenosus	3.9	6.2–8.5	8.2–>11.4	Sumida et al., 1979; Budd, 1940
P. cornutus	2.65–2.8	>3.6	7.25–13.0	Takita and Fujita, 1964; Minami, 1982a
P. decurrens	4.9–5.5	7.8–11.0	10.5–>21.0	Sumida et al., 1979; Budd, 1940
P. ritteri	2.1	4.3–5.6	6.0–>10.0	Sumida et al., 1979
P. verticalis	2.4	5.0–7.2	7.3–>11.0	Sumida et al., 1979; Ahlstrom and Moser, 1975; Budd, 1940
Psettichthys melanostictus	<3.0	ca. 8.0	>22.6	Hickman, 1959
Pseudopleuronectes americanus	2.3–3.5	5.0–7.1	6.8	Breder, 1923; Laroche, 1981
P. herzensteini	2.6–2.9	ca. 6.0–8.5	ca. 10.4–?	Dekhnik, 1959
Reinhardtius hippoglossoides	10–16	25–27	45–65	Jensen, 1935
Tanakius kitaharai	ca. 3.0	—	18.9–ca. 20	Okiyama and Takahashi, 1976
Verasper variegatus	3.8	ca. 9–12.4	ca. 16.4–?	Takita et al., 1967; Pertseva-Ostroumova, 1961; Uchida, 1933

short lateral pigment series posteriad on the tail. In some species of *Citharichthys* the ventral series coalesces into a more sparse series of larger spots and a similar series develops along the dorsum (e.g., *C. arctiforns, C. cornutus, C. sordidus*). In other species, series along the dorsum and ventrum are abbreviated or absent and only the tail bar may be present (e.g., *C. gymnorhinus, C. platophrys*) or absent (*C. spilopterus*). *Etropus* larvae have dorsal and ventral series and either a short lateral series (*E. crossotus*) or a long one (*C. microstomus*). *Cyclopsetta* and *Syacium* have dorsal and ventral series and a short lateral series posteriad on the tail. Fin pigment is principally on the spatulate tips of the elongate dorsal and pelvic fin rays. Late-

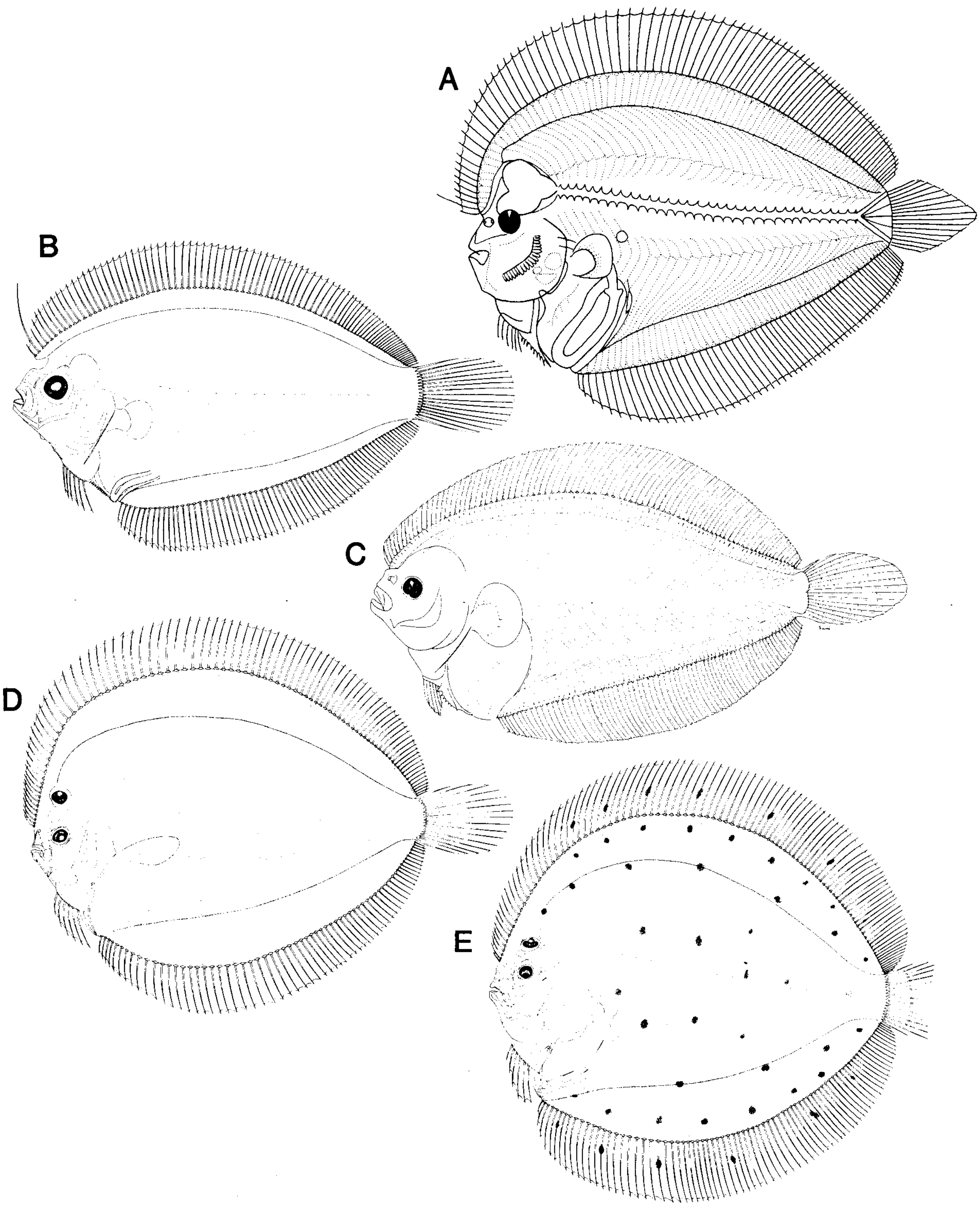


Fig. 347. Larvae and transforming specimens of Bothidae. (A) *Crossorhombus kobensis*, 16.0 mm, from Amaoka, 1979; (B) *Engyprosopon xenandrus*, ca. 20.0 mm; (C) *Lophonectes gallus*, 18.5 mm, original, K 138/74, New Zealand; (D) *Bothus thompsoni*, ca. 36.0 mm; (E) *B. mancus*, ca. 30.0 mm. B, D, and E from P. Struhsaker, unpublished.

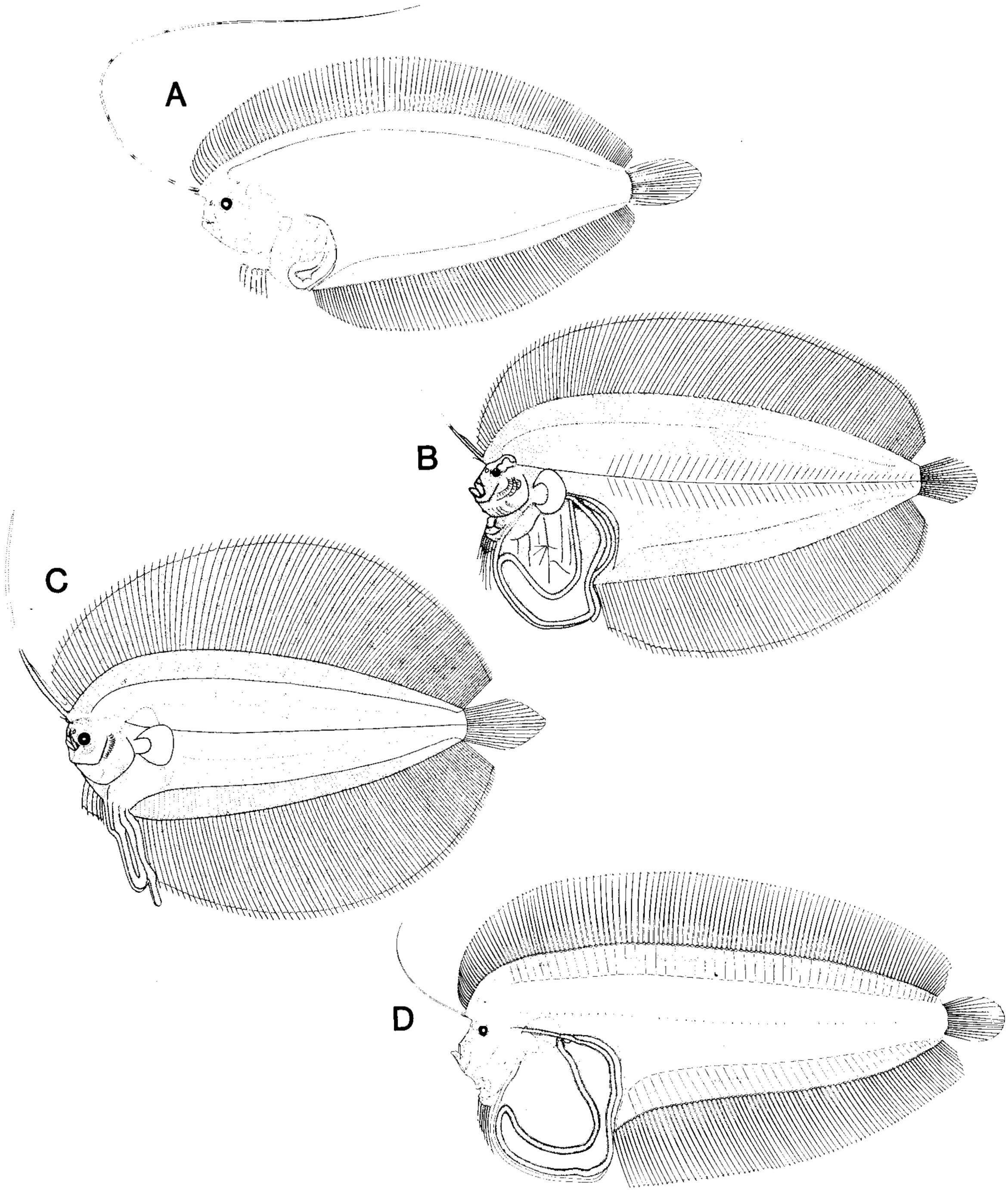


Fig. 348. Larvae of Bothidae. (A) *Arnoglossus debilis*, ca. 59.0 mm, from P. Struhsaker, unpublished; (B) *Chascanopsetta lugubris*, 120.0 mm, from Amaoka, 1971; (C) *Laeops kitaharae*, 79.0 mm, from Amaoka, 1972; (D) *Pelecanichthys* sp., ca. 95.0 mm, from P. Struhasker, unpublished.

TABLE 177. SIZE DATA FOR LARVAE OF ACHIRINAE AND SOLEINAE.

Taxon	Size at hatching (mm)	Size at flexion (mm)	Size at transformation (mm)	References
Achirinae				
Achirus lineatus	1.6	ca. 2.5–3	3.0–5.5	Houde et al., 1970
Trinectes maculatus	1.7–1.9	ca. 3–4	ca. 5	Hildebrand and Cable, 1938
Soleinae				
Aesopia cornuta	4.1	—	9.2–?	Mito, 1963
Austroglossus microlepis	1.7	5.5–6.6	8.5–ca. 16	O'Toole, 1977; Brownell, 1979
Bathysolea profundicola	—	—	4.32	Aboussouan, 1972c
Buglossidium luteum	1.8–2.3	ca. 6–8	ca. 6–10	Holt, 1891; Ehrenbaum, 1897
Dicologoglossa cuneata	1.3	ca. 6.3–6.5	7–7.5	Lagardere, 1980; Lagardere and Aboussouan, 1981
Euryglossa pan	<2.66	<4.6	3.4–6.5	Jones and Menon, 1951
Heteromycteris capensis	1.7	?–6.5	ca. 6.2–?	Brownell, 1979
H. japonicus	—	ca. 4.55	5.0–7.0	Minami, 1981b
Microchirus boscanion	—	—	7.2	Aboussouan, 1972c
M. frechkopi	—	—	5.68	Aboussouan, 1972c
M. ocellatus	2.0	4.6–5.1	6.8–>8.2	Palomera and Rubies, 1977
M. variegatus	2.4–2.9	6.1–>7.1	ca. 7–12 (18)	Cunningham, 1890; Petersen, 1909
Pegusa cadenati	—	—	7.0	Aboussouan, 1972c
P. impar	—	—	8.5–>12	Padoa, 1956k
P. lascaris lascaris	<3.5	5.3–8.1	9.5–>11.2	Clark, 1914
P. lascaris nasuta	2.1–2.5	—	—	Dekhnik, 1973; Padoa, 1956k
Solea cuneata	—	—	7.0	Aboussouan, 1972c
S. heinii	<2.2	>2.7–3.2	—	Balakrishnan and Devi, 1974
S. hexophthalma	—	—	8.0	Aboussouan, 1972c
S. ovata	—	ca. 3–4	4.5–?	Balakrishnan, 1963
S. solea	2.5–3.8	5.5–?	ca. 7–14.6	Russell, 1976 (summary)
Synaptura kleini	3.0	?–6.5	ca. 7–9	Brownell, 1979
Zebrias japonicus	4.1 TL	—	—	Mito, 1963
Z. zebra	4.0 TL	—	—	Mito, 1963

stage larvae of most species develop chevron-shaped bars on the epaxial and hypaxial myosepta. Metamorphosing specimens of *Cyclopsetta* have series of large ocelli on the dorsal and anal fins. *Dorsopsetta norma* described by Nielsen (1963b) on the basis of two metamorphosing specimens is apparently a species of *Cyclopsetta.*

Bothidae (Figs. 346–348).—Two bothid subfamilies are recognized, Taeniopsettinae and Bothinae. Bothid larvae are thin-bodied to diaphanous, sparsely pigmented, and all develop an elongate second dorsal ray (Table 175). Also, spines may appear on the urohyal, basipterygia, cleithra and epiotics in a pattern which is generally consistent for subfamilies and genera (Table 175). Bothid larvae reach a relatively large size before metamorphosis. Early larval stages are often poorly represented in collections.

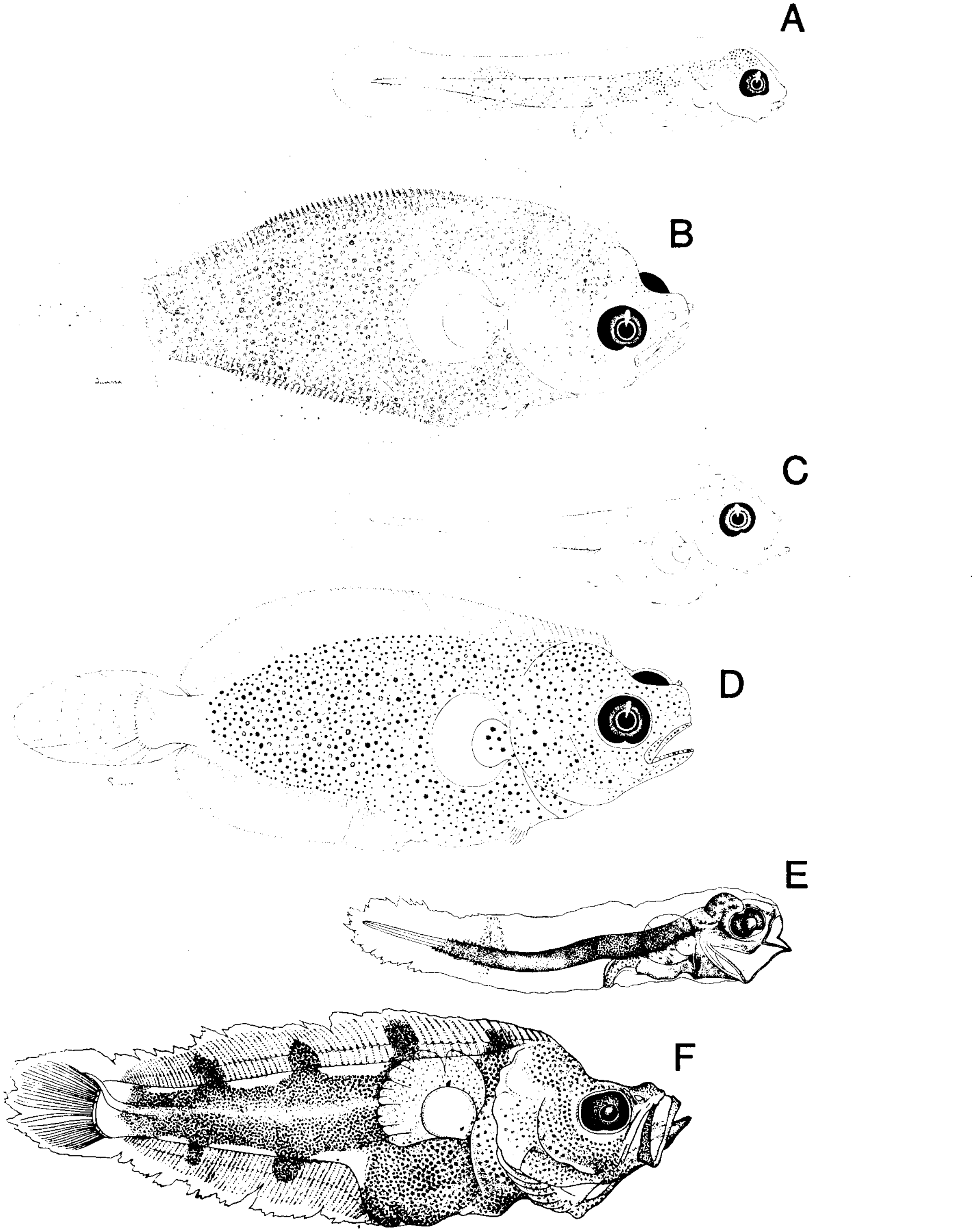
Larval series are known for all taeniopsettine genera, except *Perissias.* Larvae of *Trichopsetta* and *Engyophrys* are ovate while those of *Taeniopsetta* are round (Fig. 346). All have a complete complement of head spines (Table 175). The second dorsal fin ray is slightly or moderately elongate. *Taeniopsetta* lacks melanophores, but live larvae have four reddish-orange spots along the bases of the dorsal and anal fins, and orange, reddish and yellow blotches and bands on the body and head. *Trichopsetta* has three series of melanistic blotches along the dorsal and anal pterygiophores and along the body axis (left side). *Engyophrys* lacks melanophores.

Larvae of Bothinae have an ovate, round, or elongate shape Figs. 347, 348) and lack epiotic spines. *Engyprosopon* has numerous urohyal and basipterygial spines and some species have numerous spines on the cleithrum. *Psettina* and *Grammatobothus* have urohyal and basipterygial spines, and early larvae of the former have a hook-like projection on the lower jaw (Fig. 346). *Crossorhombus* and *Lophonectes* have basipterygial spines only and all other known bothid larvae lack head spines. *Crossorhombus* larvae have a series of scale spines along the bases of the dorsal and anal fins, one scale per ray, and species of *Psettina* and *Arnoglossus* also develop such scale spines. In the species of *Arnoglossus* described by Kyle (1913), patches of scale spines develop on the median and ventral regions of the abdomen. The second dorsal ray is usually moderately elongate but can be greatly elongate and ornamented, as in *Arnoglossus.*

Pigmentation is sparse in most bothine larvae and lacking in some species. Exceptions are found in species of *Arnoglossus* and *Psettina* which usually have melanophores above the brain, ventrally on the gut, above the gas bladder, in series along the dorsal and ventral midlines, and along the horizontal septum; in some species a complete or partial bar is present posteriad on the tail. Preflexion larvae of *Bothus* have a melanistic blotch near the tip of the notochord; later larval stages are unpigmented, except that transforming specimens of some species, *B. myriaster* (Amaoka, 1964) and *B. mancus* (Fig. 347), become heavily spotted over the body and fins. *Laeops* has melanistic blotches forming an irregular pattern over the body and median fins.

Monolene shares some adult characters with taeniopsettines but larval characters place it with the bothines. Larvae are elongate, lack head spines, have an elongate ornamented second dorsal ray, and melanistic pigment above the gut, on the right side of the brain and on the dorsal fin membrane (Fig. 346).

Pleuronectidae (Figs. 349–355).—Of the five pleuronectid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subfamilies recognized (see introduction), the Pleuronectinae is the largest with 26 genera, representing ⅔ of the genera in the family. Three contributions that summarize egg and larval information for pleuronectine flatfishes from the eastern North Atlantic and Mediterranean are Ehrenbaum (1905–1909), Padoa (1956k), and Nichols (1971). Bigelow and Welsh (1925), Bigelow and Schroeder (1953), Martin and Drewry (1978), and Fahay (1983) give information on eggs and larvae of western Atlantic pleuronectine flatfishes. The most comprehensive work dealing with early life history stages of flatfishes from the western North Pacific is Pertseva-Ostroumova (1961).

Yolk-sac larvae of pleuronectine flatfishes can be as small as 1.7 mm (*Hypsopsetta guttulata*) or as large as 10–16 mm (*Reinhardtius hippoglossoides*) and size at hatching is a primary character for identifying yolk-sac larvae (Table 176). The pigment pattern can be quite distinctive, as for example in the genus *Pleuronichthys*, but in many pleuronectines the body pigment migrates during the yolk-sac stage, and is variable from specimen to specimen of the same species. The yolk sac itself can lack pigment (as in *Parophrys vetulus*, *Hippoglossus stenolepis* or *Eopsetta jordani*), can be moderately pigmented (as in *Lyopsetta exilis*, *Lepidopsetta bilineata* or *Psettichthys melanostictus*) or can be heavily pigmented (as in *Pleuronichthys decurrens* or *Verasper variegatus*). Similarly the finfold can lack pigment or be variously pigmented and useful in identification.

Early preflexion pleuronectine larvae are slender; the head is of moderate size; snout-anus length can be as much as 50% NL (as in four species of *Pleuronichthys* larvae, Sumida et al., 1979) but usually is shorter (i.e., 35–45% NL). The gut is initially straight but develops a coil soon after the completion of yolk absorption. Greatest body depth after the gut becomes looped is either at the anus or slightly anterior to it. Body shape of preflexion larvae is quite similar from species to species. There are few distinctive characters unique to the larval period of pleuronectine flatfishes. Only a few kinds of pleuronectine larvae develop head spination. Preopercular spines form in larvae of *Atheresthes*, *Glyptocephalus*, *Tanakius* and *Eopsetta*; otic spines develop on larvae of *Microstomus* (at least on 2 species), *Hypsopsetta*, and *Pleuronichthys* (1 species); *Atheresthes* has a spinous supraocular crest. Head spination develops during the preflexion stage, but usually is best developed on flexion or early postflexion larvae.

The caudal fin begins forming either slightly before or together with the dorsal and anal fins. The first caudal supporting bones to form as cartilage are the hypurals. Usually several caudal rays (2 + 2 or 3 + 3) are formed before flexion begins. In late flexion and early postflexion larvae, the end of the notochord can project beyond the hypural plates. The complete complement of caudal rays is usually laid down during the flexion period.

The dorsal and anal fins form in the finfold at some distance from the main part of the body. The intervening space becomes filled with the pterygiophores that support the dorsal and anal fin rays, causing an increase in body depth. In both dorsal and anal fins the rays begin forming at the anterior ends of the fins and the differentiation proceeds posteriad. The first few rays in both fins are reduced in size and the terminal ray is often minute. Pelvic fin buds usually form during the flexion stage but pelvic rays usually are not developed until the postflexion stage. As in all flatfishes, formation of pectoral fin rays is delayed to the end of the transformation stage.

The vertebral processes ossify before the centra. In the caudal group of vertebrae, ossification of haemal and neural processes proceeds posteriad. Ossification of abdominal neural processes can follow several patterns, but usually proceeds anteriad. The last neural and haemal processes to ossify are the truncate spines of the 2 or 3 vertebrae anterior to the urostyle. Centra ossify initially at the bases of neural and haemal processes and ossification proceeds peripherally until a complete ring is formed. On first formation only the middle portion of a vertebral centrum is ossified, hence the space between adjacent centra may be as wide as the ossified portions of the centra. The ural centra are the first to ossify in some pleuronectines or they can ossify at the same time as other centra. The last centra to form are those of the 2 (or 3) vertebrae anterior to the urostyle.

All pleuronectine larvae that have been described have body pigment. The pigment pattern changes with growth, often markedly. Also, there is often considerable variation in pigmentation of larvae of similar sizes of the same species. Notwithstanding, body and finfold pigment constitutes a primary character for identification of flatfish larvae during the preflexion stage.

To show the variety of pigment patterns found on preflexion stage pleuronectine larvae, preflexion larvae of 17 species from the North Pacific are illustrated (Figs. 349–351). Heavily pigmented larvae are in the genera *Pleuronichthys*, *Hypsopsetta*, and *Verasper* (Fig. 349). The posterior portion of the tail is unpigmented or pigment is confined to marginal spots along the notochord. The unpigmented tail area is more extensive in some species than in others. Finfold pigment is very useful in identifying these larvae to species taken in conjunction with larval size and extent of tail pigment.

In the other 14 kinds of larvae representing as many genera, tail pigment appears in a number of patterns. The larvae illustrated in Figs. 350 and 351 are arranged in the order of increasing complexity. In the simplest pattern pigment is concentrated along the ventral midline with only moderate dorsal or lateral pigment, as in *Hippoglossus stenolepis* or *Reinhardtius hippoglossoides*. Although *Parophrys vetulus* and *Lyopsetta exilis* have more ventral margin pigment than dorsal, it is almost continuous on both margins. *Platichthys stellatus* has more diffused pigment over the tail portion of the body, but it is not in a pattern. The most unusual pigment is found in *Atherestes*. There are two conspicuous dorsal patches as opposed to almost no ventral pigment. Pigment on *Eopsetta jordani* is limited to a mid-tail band and a terminal notochord patch. A more common pattern is encountered in *Isopsetta*, which has two pigment bands across the tail together with the terminal notochord pigment. A basically similar pattern is found in *Lepidopsetta bilineata*. *Psettichthys* is unusual in having alternating dorsal and ventral blotches. *Hippoglossoides elassodon* has three tail pigment areas (i.e., opposing dorsal and ventral pigment patches) together with terminal notochord pigment. This is also the basic pattern in *Microstomus*. *Embassichthys* increases opposing tail patches to

Fig. 349. Larvae and transforming specimens of Pleuronectidae. (A) *Pleuronichthys coenosus*, 3.7 mm, from Sumida et al., 1979; (B) *P. coenosus*, 8.9 mm, ibid; (C) *Hypsopsetta guttulata*, 2.6 mm, ibid; (D) *H. guttulata*, 6.6 mm, ibid; (E) *Verasper variegatus*, 5.6 mm, from Pertseva-Ostroumova, 1961 after Uchida, 1933; (F) *V. variegatus*, 12.4 mm, ibid.

four plus terminal notochord pigment (Richardson, 1981b); *Glyptocephalus zachirus* has pigment bands which alternate with ventral patches, plus the terminal notochord pigment.

At least four other genera of pleuronectine flatfishes occur in the eastern North Pacific. The preflexion stage larvae of *Pleuronectes pallasii, Liopsetta glacialis*, and *Limanda aspera* lack melanistic bands (Pertseva-Ostroumova, 1961). Larvae are unknown for the fourth genus, *Clidoderma*.

Larvae are known for species representing six additional genera in the western North Pacific. According to Pertseva-Ostroumova (1961), preflexion larvae of *Acanthopsetta nadeshnyi* and *Kareius bicoloratus* lack bands; those of *Cleisthenes herzensteini* (see also Okiyama and Takahashi, 1976), *Pseudopleuronectes herzensteini* and *P. yokohamae* (see also Dekhnik, 1959; Yusa, 1960a, b; Yusa et al., 1971) have two tail pigment bands plus terminal notochord pigment. Preflexion larvae of *Verasper variegatus* (Fig. 349) are as heavily pigmented as those of *Pleuronichthys* (Takita et al., 1967; Uchida, 1933). The pigment pattern on preflexion larvae of *Tanakius kitaharai* is very similar to that on larvae of *Glyptocephalus stelleri* (Okiyama and Takahashi, 1976). Larvae have not been described for the monotypic genus *Dexistes*.

In species with banded preflexion larvae, the bands usually persist into later larval stages; those with diffuse or linear pigment patterns generally do not develop bands in later stages, although pigment may become associated with myosepta (Figs. 352, 353). Virtually all late postflexion and metamorphic pleuronectines develop a distinct pattern of bars or blotches on the body and median fins, which persists into the juvenile stage (Fig. 354).

Of the four other pleuronectid subfamilies, larvae have not been described for Paralichthodinae, while some information is available on the Samarinae, Poecilopsettinae, and Rhombosoleinae. Pertseva-Ostroumova (1965) described two larval specimens (6.4, 8.7 mm) of *Samaris cristatus* and Struhsaker (pers. comm.) has described large pelagic larvae of *Samariscus* sp. and *Poecilopsetta hawaiiensis* (Fig. 355). Larvae of *S. cristatus* are deep-bodied in the gut region, have a relatively large head and jaws and a pigment pattern consisting of melanophore patches along the dorsum and ventrum, along the outer margins of the pterygiophore zones, and along the dorsal and anal fins; the ventral region of the gut is pigmented. A series of *Samariscus triocellatus*, 7.3–19.0 mm (provided by Dr. T. A. Clarke, Univ. of Hawaii), is similar to *Samaris cristatus* in having a slender body and wide pterygiophore zones but the gut coil is elongate, protrudes beyond the ventral profile, and the fourth dorsal ray is elongate. The left eye has begun to migrate at 7.3 mm and is at the dorsal midline by 12.0 mm. Larvae of *Samariscus corallinus* are similar but attain a larger size (ca. 26 mm). Both species lack pigment. Late postflexion larvae of *Poecilopsetta* have a body form similar to samarines (slender body with wide pterygiophore zones) but have a different gut structure, no elongate dorsal ray, and have a striking pigment pattern consisting of dorsal and ventral myoseptal series and large blotches over the pterygiophore zones, dorsal and anal fins, and gut (Fig. 355). A 29-mm late postflexion larva from the North Atlantic has a pigment pattern identical to Hawaiian specimens.

Reared yolk-sac and early preflexion larvae of rhombosoleine species have been illustrated and briefly described: *Ammotretis rostratus* (Thomson, 1906); *Rhombosolea plebeia* (Anderton, 1907); *Colistium guntheri, Pelotretis flavilatus*, and *Peltorhamphus novaezeelandiae* (Thomson and Anderton, 1921). The oil globules remain evenly dispersed throughout the yolk-sac period. Heavy melanistic pigmentation develops on the head, body, yolk sac, and finfold. Late yolk-sac larvae of *C. guntheri* develop an unusual lobate projection of the dorsal finfold, which extends well anterior to the head. A similar structure appears in yolk-sac larvae of the soleid, *Pegusa lascaris* (Holt, 1891). Rapson (1940) described and illustrated with photographs a reared series of *Pelotretis flavilatus*. Flexion-stage larvae of this species are deep-bodied and similar in appearance to paralichthyids, although they lack elongate dorsal fin rays (Fig. 355). Pigmentation consists of dorsal and ventral midline series, series above and below the spinal column, a linear patch below the gut, and embedded melanophores in the otic region. Postflexion larvae become mottled with large blotches on the body and fins. Crossland (1981) briefly described and illustrated pre- and postflexion stages of a similar larva which he identified as *Peltorhamphus latus* and stated that Rapson's (1940) series was a species of *Peltorhamphus*. Crossland's (1982) illustration of a flexion-stage *Pelotretis flavilatus* has heavy pigmentation, a protruding gut mass and looks very much like a soleid.

Soleidae (Fig. 356).—Two subfamilies, Soleinae and Achirinae, are recognized in the family. In the Soleinae, life history stages are well known for the eastern North Atlantic species, *Solea solea, Microchirus variegatus, Buglossidium luteum* and *Pegusa lascaris* (references summarized in Ehrenbaum, 1905–1909 and Russell, 1976). A comprehensive volume on the development of *S. solea* was produced by Fabre-Domergue and Biétrix (1905). Padoa (1956k) summarized information on eggs and larvae of soles from the Mediterranean, and Aboussouan (1972c) briefly

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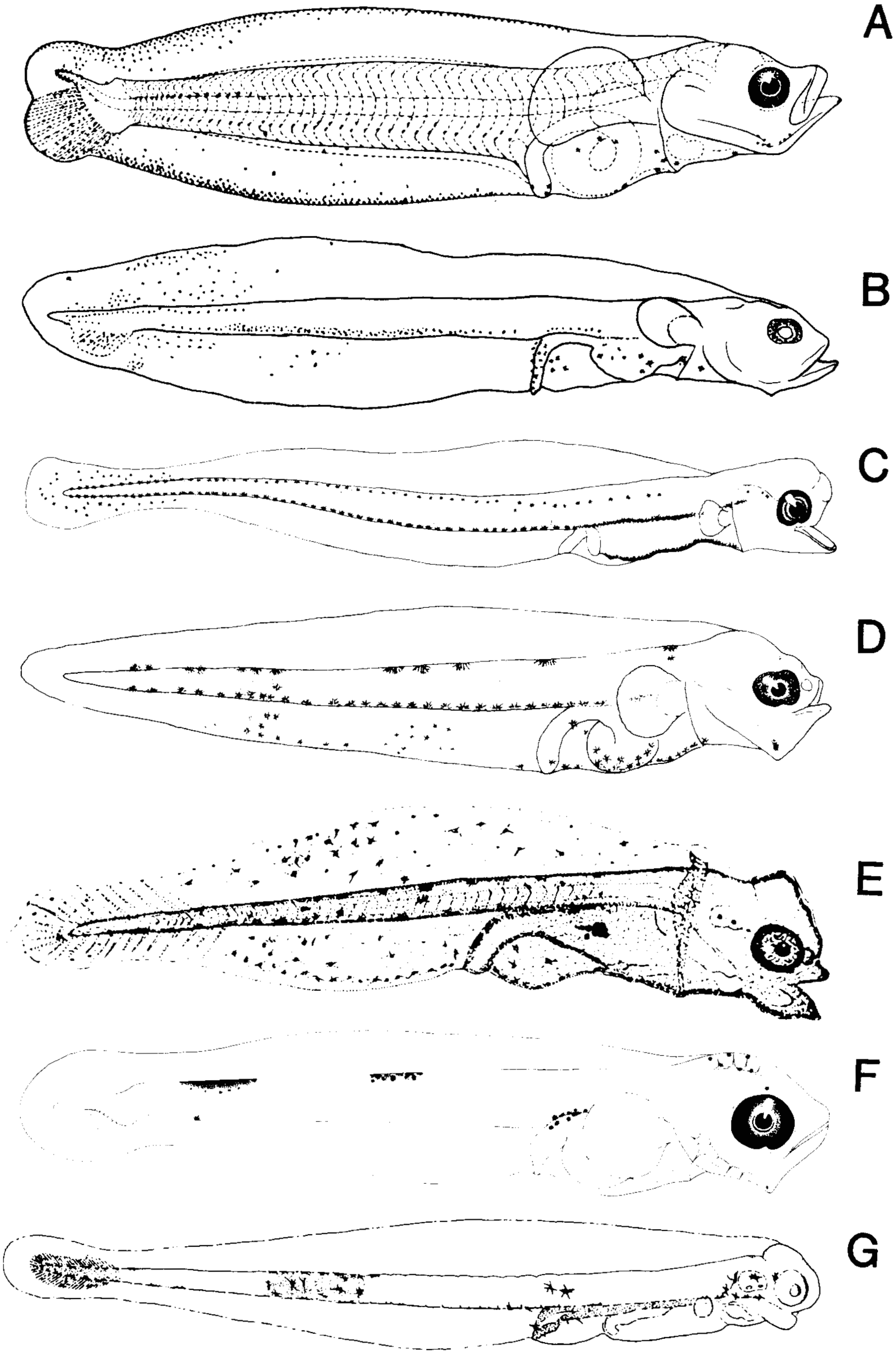
Fig. 350. Larvae of Pleuronectidae. (A) *Hippoglossus stenolepis*, 15.0 mm, from Pertseva-Ostroumova, 1961; (B) *Reinhardtius hippoglossoides*, 17.0 mm, from Jensen, 1935; (C) *Lyopsetta exilis*, 5.9 mm from Ahlstrom and Moser, 1975; (D) *Parophrys vetulus*, 4.3 mm, ibid; (E) *Platichthys stellatus*, 2.6 mm, from Orcutt, 1950; (F) *Atheresthes stomias*, 10.5 mm, original; (G) *Eopsetta jordani*, 6.2 mm, from Alderdice and Forrester, 1971.

Fig. 351. Larvae of Pleuronectidae. (A) *Isopsetta isolepis*, 9.5 mm, original, CalCOFI 7205, Sta. 40.38; (B) *Lepidopsetta bilineata*, 4.6 mm, from Pertseva-Ostroumova, 1965; (C) *Psettichthys melanostictus*, 6.7 mm, original, CalCOFI 5807 Sta. 40.38; (D) *Hippoglossoides elassodon*, 9.2 mm, from Pertseva-Ostroumova, 1961; (E) *Microstomus pacificus*, 7.0 mm, redrawn from Ahlstrom and Moser, 1975; (F) *Embassichthys bathybius*, 18.5 mm, original, CalCOFI 4905, Sta. 29.83; (G) *Glyptocephalus zachirus*, 22.8 mm, redrawn from Ahlstrom and Moser, 1975.

Fig. 352. Larvae of Pleuronectidae. (A) *Lyopsetta exilis*, 14.7 mm, original, CalCOFI 7805, Sta. 100.29; (B) *Parophrys vetulus*, 16.0 mm, redrawn from Ahlstrom and Moser, 1975; (C) *Isopsetta isolepis*, 14.2 mm, original, CalCOFI 7205, Sta. 40.38, (D) *Eopsetta grigorjewi*, 10.0 mm, from Okiyama and Takahashi, 1976; (E) *Psettichthys melanostictus*, 9.4 mm, original, CalCOFI.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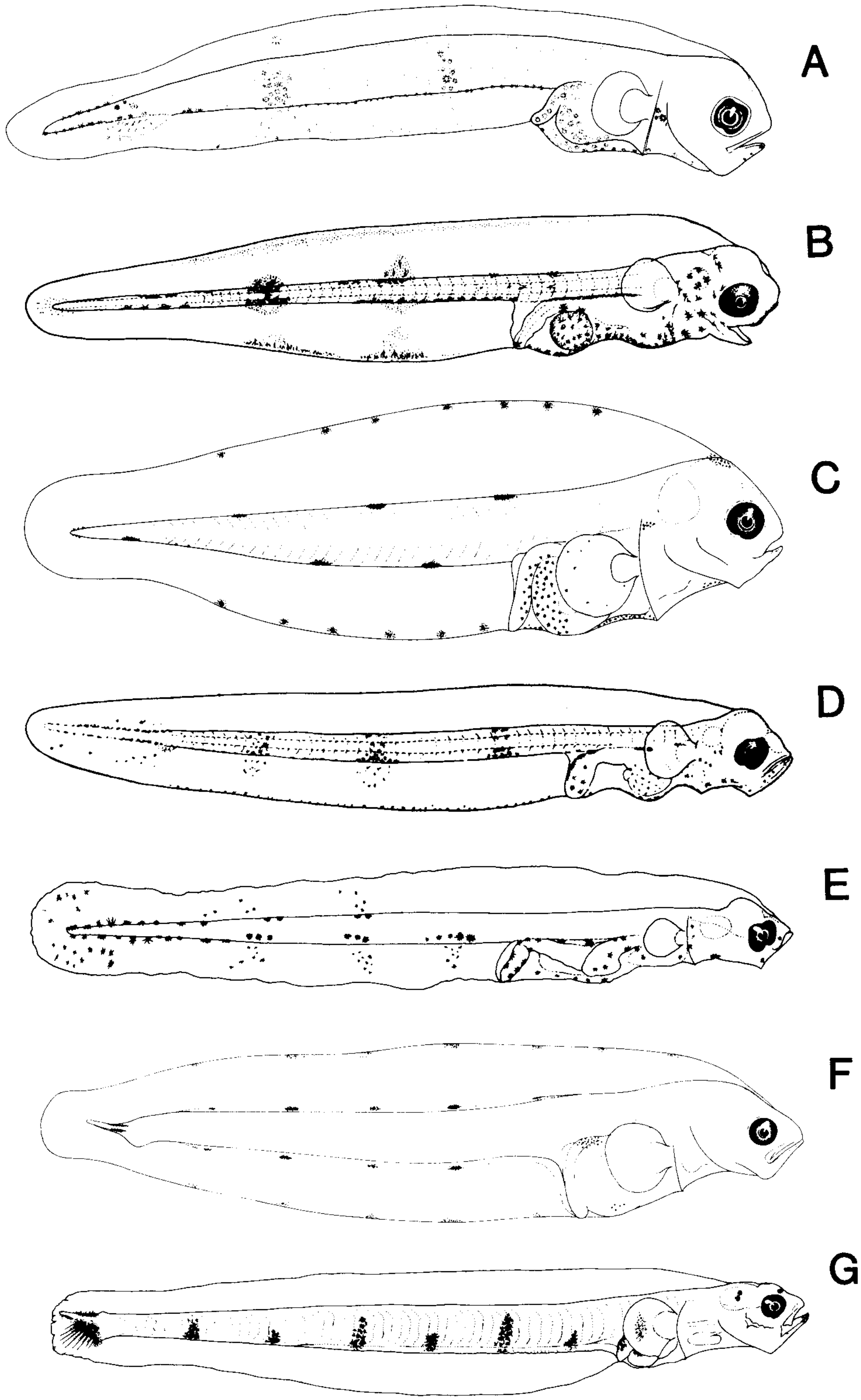
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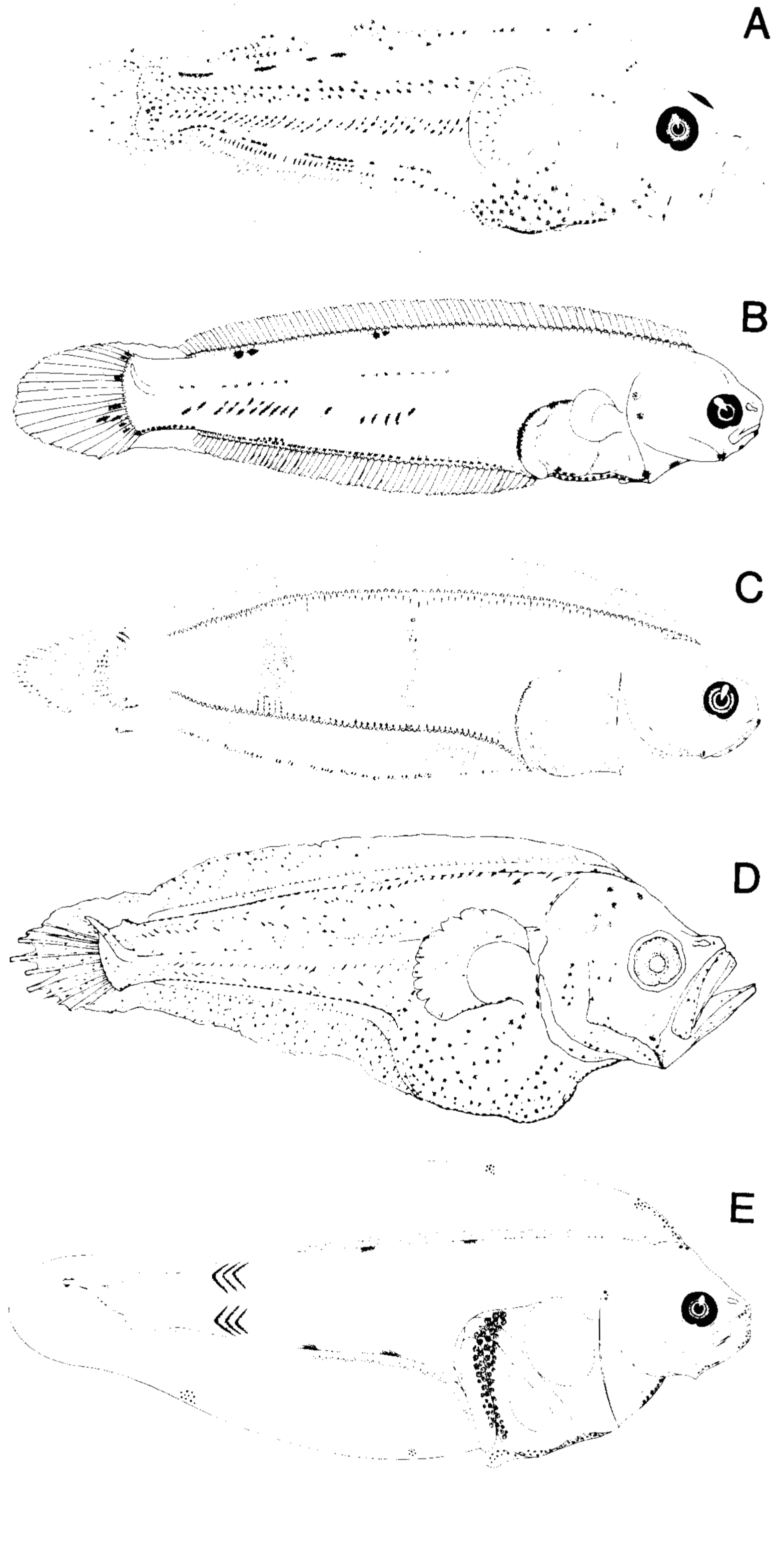
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TABLE 178. SIZE DATA AND NUMBER OF ELONGATE DORSAL RAYS FOR LARVAE OF SYMPHURINAE AND CYNOGLOSSINAE.

Taxon	Number of elongate dorsal rays	Size at hatching (mm)	Size at flexion (mm)	Size at transformation (mm)	References
Symphurinae					
Symphurus atricauda	5	1.9	9.4–10.8	19–24.2	Original
S. lacteus	4–5	—	6–<10	18	Kyle, 1913
S. ligulata	5	—	<10.5	32	Kyle, 1913
S. orientalis	5	—	>4.4–<9.3	>12.3	Pertseva-Ostroumova, 1965
S. plagiusa	4–5	<1.3	<6.2	<13	Hildebrand and Cable, 1930; Olney and Grant, 1976
Cynoglossinae					
Cynoglossus abbreviatus (as *Areliscus trigrammus*	2	3.2	—	—	Fujita and Takita, 1965
C. arel (as *C. oligolepis*)	2	—	—	—	Pertseva-Ostroumova, 1965
C. bilineatus	2	—	>4.0	6–8	Vijayaraghavan, 1957; Pertseva-Ostroumova, 1965
C. brevis	—	—	—	ca. 4.0	Balakrishnan and Devi, 1974
C. capensis	2–4	1.2	ca. 9.9	10–15	Brownell, 1979
C. cynoglossus	2	≤1.6	ca. 4.1	<4.7	Balakrishnan and Devi, 1974
C. kopsi (as *C. sibogae*)	2	—	7.6	—	Pertseva-Ostroumova, 1965
C. lida	2	<2.1	>4.6	—	Balakrishnan and Devi, 1974
C. lingua	—	—	—	17.7–?	Jones and Menon, 1951
C. macrostomus (as *C. semifasciatus*)	2	<2.5	4.2	ca. 5	Seshappa and Bhimachar, 1955
C. monopus	2	—	5–7	7.0	Balakrishnan, 1963
C. puncticeps	2	<1.4	ca. 4.2–?	ca. 4–5	Balakrishnan and Devi, 1974
C. robustus	2	1.85	—	—	Fujita and Uchida, 1957
C. semifasciatus	2	<2.0	7.2–11	11–12.5	Balakrishnan, 1961
Paraplagusia japonica	2	—	<10.2	ca. 12.2	Minami, 1982b

described several species from off west Africa. Life history series have been described for two achirine species of the western North Atlantic, *Trinectes maculatus* and *Achirus lineatus*. Eggs of achirines are smaller than in most soleines (Table 172) and, accordingly, size at hatching is also smaller; achirines and some soleines undergo notochord flexion and transformation at very small sizes (Table 177). Achirines are deep-bodied, with a large gut that occupies a major portion of the body volume, a large deep head with a distinct dorsal hump; eyes and jaws are large (Fig. 356). Preflexion larvae of *A. lineatus* develop spinous ridges above the eye (frontal bone), at the otic region (parietal and autopterotic bones) and on the preopercle. Also, five rows of papilla-like spines develop on the body. Larvae of *T. maculatus* develop bony ridges on the frontal, parietal and autopterotic bones. *A. lineatus* larvae are unique among described soleids in having an elongate third dorsal ray. Early larvae of *A. lineatus* are unpigmented but by late preflexion stage have developed pigment on the head, gut, elongate dorsal ray, dorsal and ventral body margins and blotches on the dorsal and anal fins. Early larvae of *T. maculatus* are heavily pigmented and have three large blotches in the dorsal finfold and two in the ventral finfold. In later larvae these blotches become dusky bars that overlie the nearly solid background pigment.

Soleines have a large head and jaws as in achirines but the eye is relatively smaller and the dorsal hump is less prominent (Fig. 356). Also, soleines are less deep-bodied and the gut occupies a relatively smaller portion of the body mass; in many soleine species the rounded gut mass protrudes well beyond the ventral profile. Pigmentation is highly varied ranging from species of *Aseraggodes* which lack pigment to species such as *Solea solea, Pegusa lascaris, Microchirus variegatus* and *Euryglossa pan* which are solidly covered with melanophores. A typical pattern appearing in many described species consists of a series of melanophores along the dorsum, ventrum and horizontal septum, and melanophores on the head, gas bladder and finfolds (Fig. 356).

Cynoglossidae (Fig. 357).—Two subfamilies, Symphurinae and Cynoglossinae, are recognized in the family. The first larval descriptions of the former are of *Symphurus lacteus, S. ligulata* and *S. pusilla* (Kyle, 1913). Hildebrand and Cable (1930) described a series as *S. plagiusa*, but Olney and Grant (1976) described a different series as *S. plagiusa* and pointed out that Hildebrand and Cable's descriptions must refer to another species. Pertseva-Ostroumova (1965) ascribed a larval series to *S. orientalis* and we have identified eggs and larvae of *S. atricauda*. Larval series or metamorphosing specimens have been ascribed to at least 11 types of cynoglossines; however, most of these are incomplete series and identifications are tentative (Table 178). Most cynoglossids are less than 2.5 mm at hatching;

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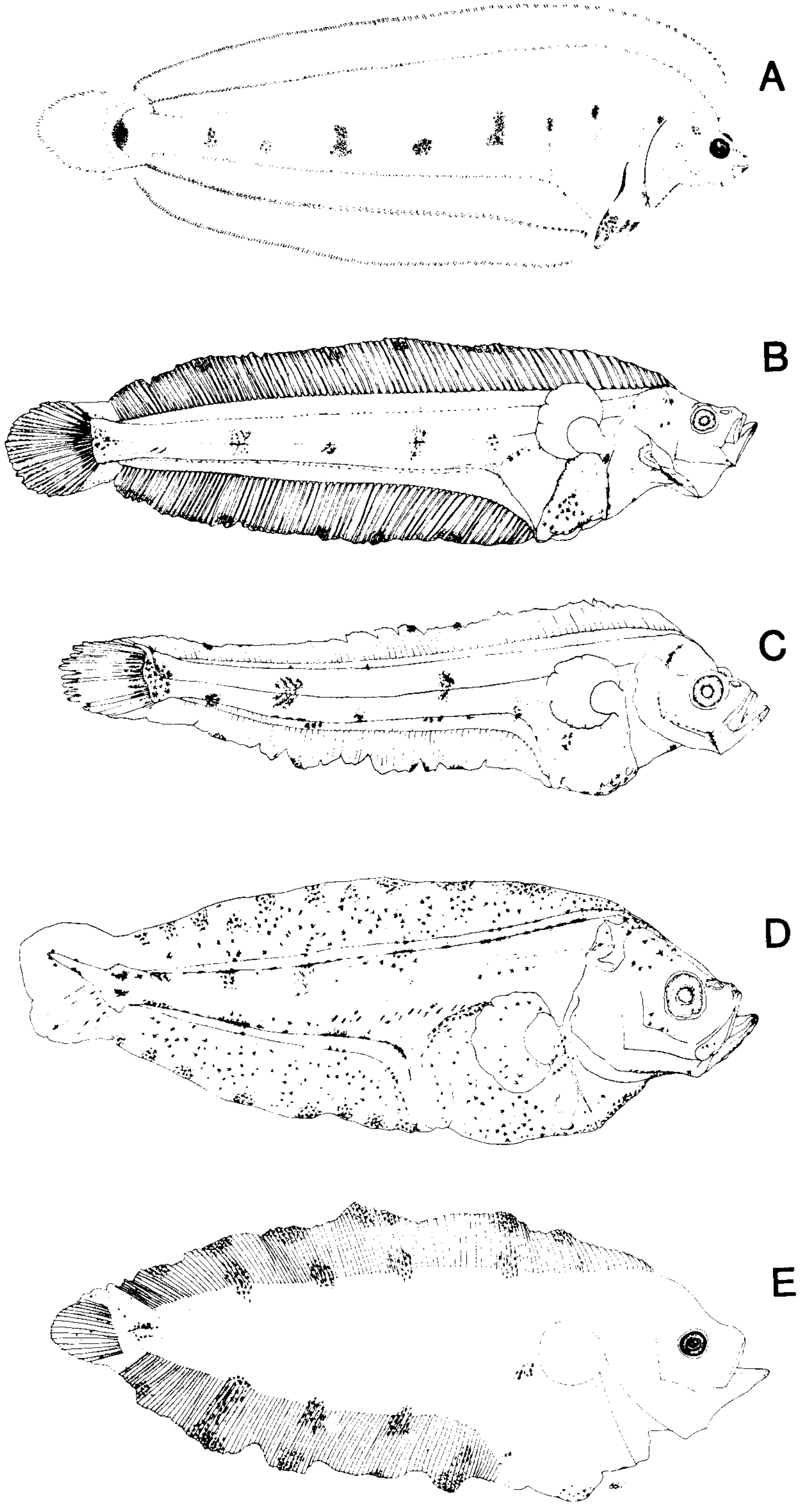
Fig. 353. Larvae of Pleuronectidae. (A) *Glyptocephalus zachirus*, 48.7 mm, redrawn from Ahlstrom and Moser, 1975; (B) *G. stelleri*, 24.6 mm, from Okiyama and Takahashi, 1976; (C) *Tanakius kitaharai*, 15.8 mm, ibid; (D) *Microstomus achne*, 8.8 mm, ibid; (E) *Embassichthys bathybius*, 16.2 mm, from Richardson, 1981b.


A
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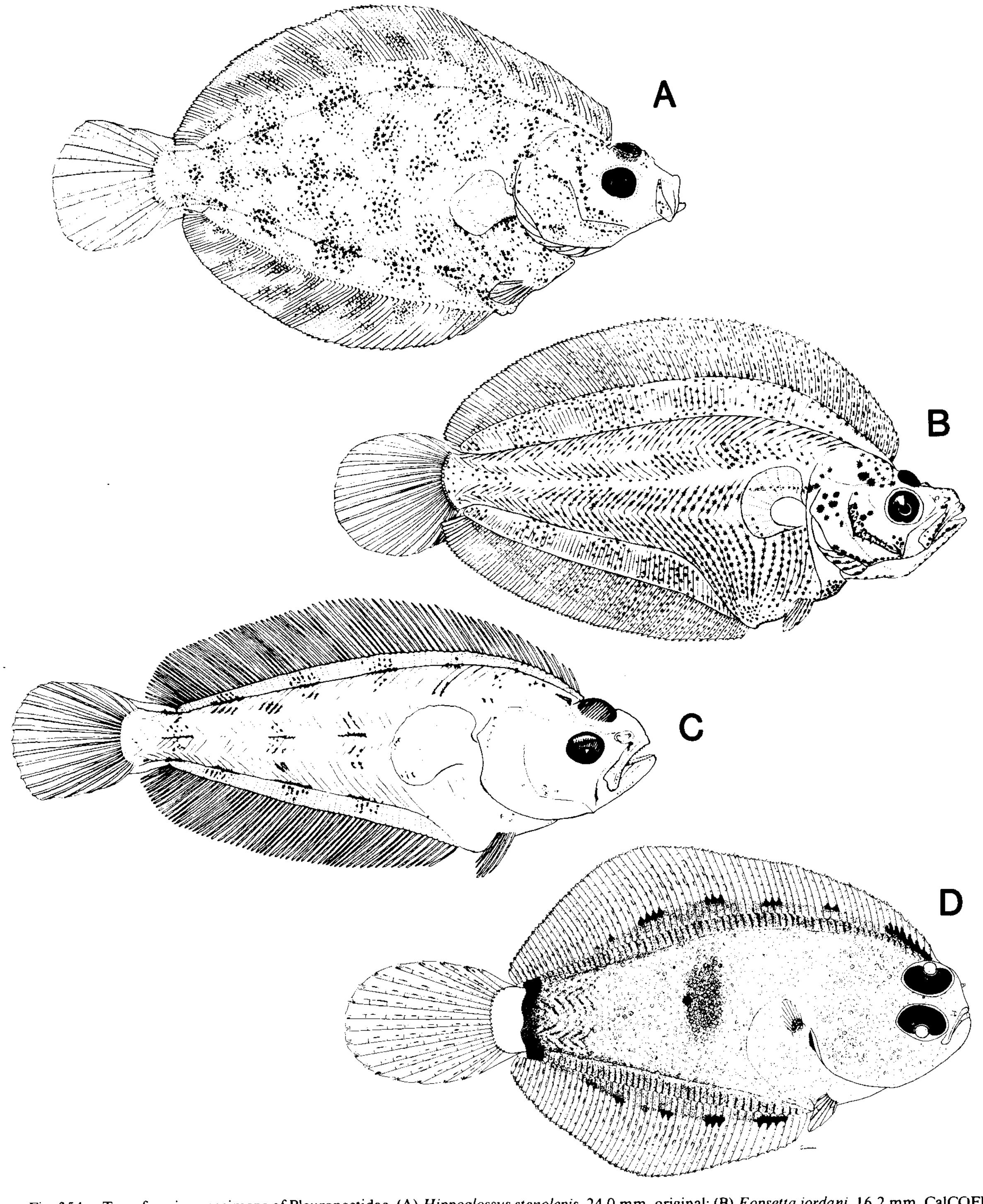

Fig. 354. Transforming specimens of Pleuronectidae. (A) *Hippoglossus stenolepis*, 24.0 mm, original; (B) *Eopsetta jordani*, 16.2 mm, CalCOFI 5104, Sta. 70.55; (C) *Lyopsetta exilis*, 22.0 mm, from Ahlstrom and Moser, 1975; (D) *Pleuronichthys ritteri*, 10.0 mm, from Sumida et al., 1979.

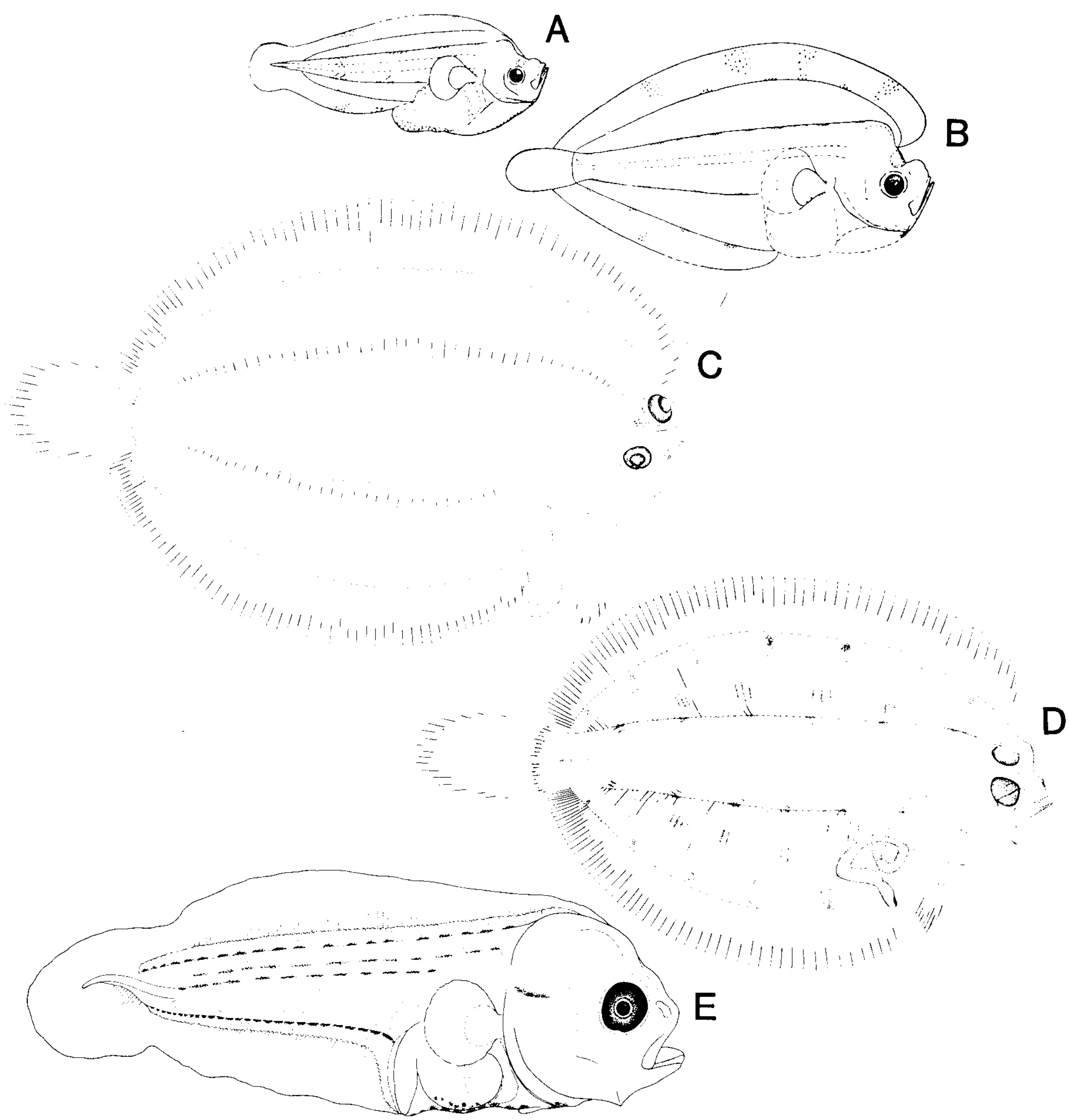

Fig. 355. Larvae and transforming specimens of Pleuronectidae. (A) *Samaris cristatus*, 6.4 mm, from Pertseva-Ostroumova, 1965; (B) *S. cristatus*, 8.7 mm, ibid; (C) *Samariscus* sp., ca. 24.0 mm; (D) *Poecilopsetta hawaiiensis*, ca. 29.0 mm; (E) *Pelotretis flavilatus*, 4.3 mm, redrawn from Rapson, 1940. C and D from P. Struhsaker, unpublished.

an exception is *C. abbreviatus* which has a relatively large egg. Notochord flexion and transformation occur at larger sizes in symphurines compared with cynoglossines and some *Symphurus* have an extended larval stage that exceeds 30 mm in length Table 178). Cynoglossid larvae are similar to those of soleids in having a large deep head and tapering body, but the jaws are relatively smaller in cynoglossids and the body is more attenuate (Fig. 357). The gut mass protrudes beyond the ventral profile and in some species it trails posteriad. In *S. lactea* a conical structure is attached to the trailing gut coil (Kyle, 1913). Cy-

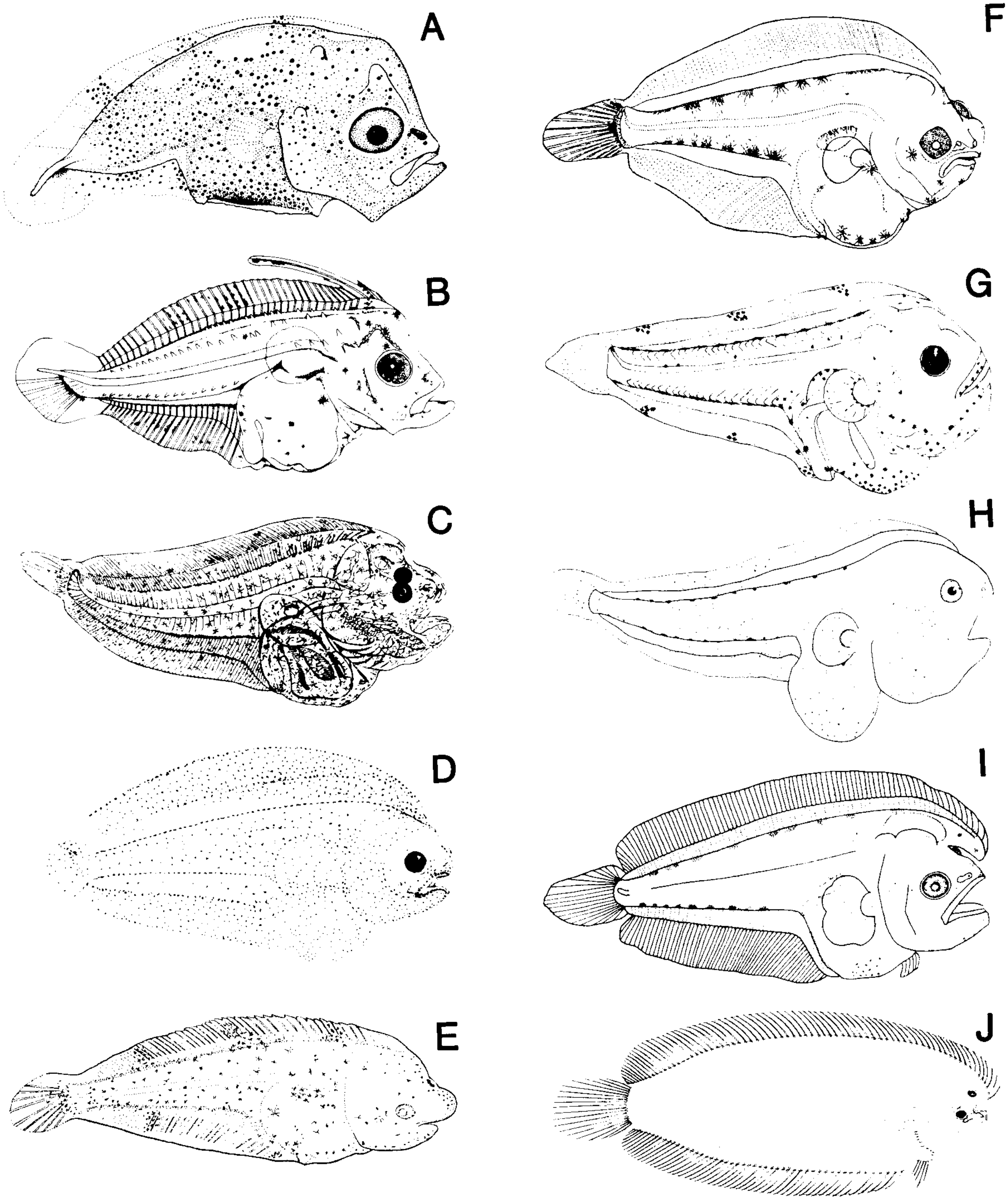

Fig. 356. Larvae and transforming specimens of Soleidae. (A) *Trinectes maculatus,* 2.0 mm, from Hildebrand and Cable, 1938; (B) *Achirus lineatus,* 3.1 mm, from Houde et al., 1970; (C) *Solea solea,* 7.5 mm, from Ehrenbaum, 1905–1909; (D) *Microchirus variegatus,* 10.0 mm, from Petersen, 1909; (E) *Euryglossa pan,* 4.6 mm, from Jones and Menon, 1951; (F) *Solea ovata,* 4.7 mm, from Jones and Pantulu, 1958; (G) *Microchirus ocellatus,* 5.1 mm, from Palomera and Rubies, 1977; (H) *Austroglossus microlepis,* 6.6 mm, from O'Toole, 1977; (I) *Heteromycteri japonicus,* 4.9 mm, from Minami, 1981b; (J) *Aseraggodes whitakeri,* ca. 27.0 mm, from P. Struhsaker, unpublished.

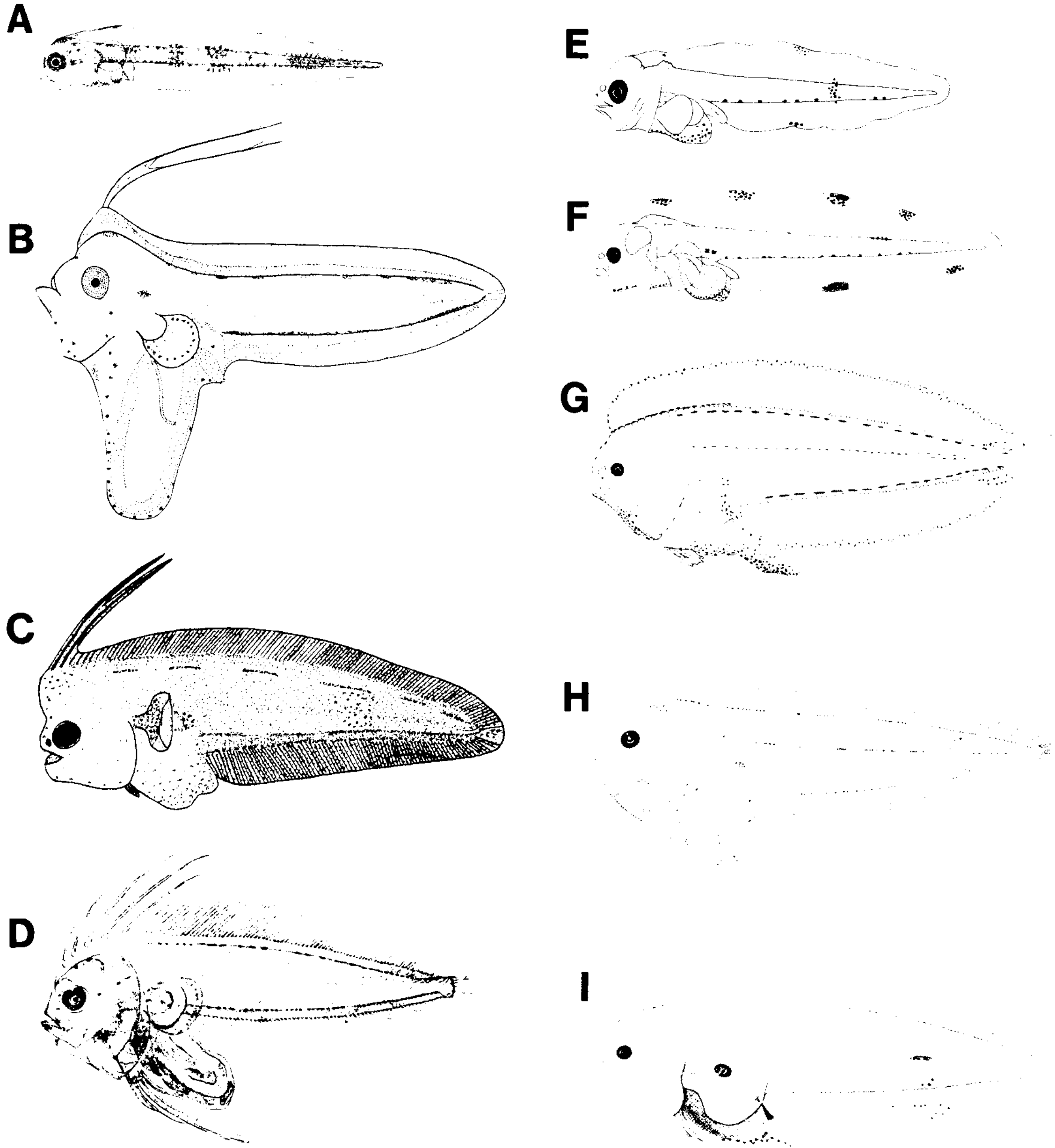

Fig. 357. Larvae of Cynoglossidae. (A) *Cynoglossus abbreviatus*, 5.0 mm, from Fujita and Takita, 1965; (B) *C. monopus*, 7.0 mm, from Balakrishnan, 1963; (C) *C. macrostomus*, 4.5 mm, from Seshappa and Bhimachar, 1955; (D) *Symphurus ligulata*, 10.5 mm, from Kyle, 1913; (E) *S. atricauda*, 4.0 mm, original, CalCOFI; (F) *S. atricauda*, 6.5 mm, original, CalCOFI; (G) *S. atricauda*, 12.8 mm, original, CalCOFI; (H) *S. plagiusa*, 6.2 mm, redrawn by Fahay (1983) from Olney and Grant, 1976; (I) *S. lactea*, 18.0 mm, from Padoa, 1956k.

noglossid larvae develop a crest consisting of elongate anterior dorsal rays, 2 rays in *Cynoglossus* and usually 4 or 5 in *Symphurus*. Pectoral fins are present during the larval period, but do not develop rays and disappear at metamorphosis. One species, *S. ligulata*, develops elongate third and fourth pelvic rays (Kyle, 1913; Padoa, 1956k).

Pigmentation in early larvae of *Cynoglossus* consists of 4–5 opposing blotches along the dorsum and ventrum, pigment on the head, gut and gas bladder. In some species, large blotches in the finfold distal to the dorsal and ventral midline blotches give the larvae a barred appearance. In later stages the midline blotches become more numerous and some species develop a series along the horizontal septum. Early larvae of *Symphurus* have small melanophores along the ventral midline, and in some species, also along the dorsal midline. Most species have a single bar posteriad on the tail and at least one, *S. atricauda*, has large blotches at the finfold margins. The head (particularly ventrally), gut, gas bladder and horizontal septum become pigmented and later-stage larvae have pigment patterns similar to *Cynoglossus* species.

Metamorphic stages

Pleuronectiforms undergo a remarkable metamorphosis during which one of the eyes, the left in dextral and the right in sinistral species, migrates around or through the head to a position dorsal to the non-migrating eye. Metamorphosis occurs over a wide size range among flatfishes, from about 5 mm in achirine soles (Houde et al., 1970) to greater than 120 mm in some bothines (Amaoka, 1971). Capture of specimens of the enormous flatfish larva observed by Barham (1966) from a diving saucer may double the maximum size for flatfish larvae. Most flatfishes metamorphose within the range of 10–25 mm (see preceding sections and Tables 173–178); the size interval over which the process occurs is smaller in species which metamorphose at a small size.

Metamorphosing specimens are relatively rare in plankton collections because 1) the process is transitory, 2) avoidance is increased at larger sizes, and 3) metamorphosing individuals may change habitat. Existing information indicates a variety of mechanisms of eye migration among flatfishes. In groups where the dorsal fin origin in larvae is at the posterior margin of the eye or more rearward (psettodids, citharids, scophthalmids, most paralichthyids, pleuronectids), a depression forms in the interocular region and the eye migrates over the dorsal midline anterior to the fin origin. Subsequently the dorsal fin extends forward to its adult position (except in psettodids). In larvae of bothids and the paralichthyid genera *Cyclopsetta*, *Syacium* and *Citharichthys* (some species), the dorsal fin is attached to the skull anterior to the eye and, during metamorphosis, the eye migrates through a slit which forms between the fin base and the skull. In some metamorphosing soleids the dorsal fin projects forward above the snout and the eye migrates through the space between this protuberance and the skull; subsequently the fin projection fuses to the skull (Houde et al., 1970; Palomera and Rubies, 1977; Minami, 1981b). Seshappa and Bhimachar (1955) described the process of eye migration in a captive specimen of *Cynoglossus macrostomus*. Just before eye migration a fleshy hook-shaped protuberance grew forward from the region of the head anterior to the dorsal fin origin. The right eye migrated through the space between the protuberance and the skull, after which the fleshy appendage fused to the dorsal region of the skull. The entire process took place over a 5-hour period during the night. A similar structure appears on advanced larvae of an unidentified cynoglossid illustrated by John (1951b) and this mechanism of eye migration may be widespread among cynoglossids.

During eye migration in flatfishes a number of other metamorphic events occur: 1) larval spines are lost, 2) elongate rays assume their juvenile proportions, 3) gut protrusions are brought into the body cavity and internal organs are rearranged, 4) gas bladder, if present, is lost, 5) pectoral fins develop rays, except in cynoglossids, some soleids, some bothids and *Mancopsetta*, where (one or both) fins are lost altogether during this period, 6) larval pigment patterns are replaced by juvenile patterns, 7) ossification of the vertebral column and other bony structures is completed, 8) intermuscular bones appear in bothids, and 9) scales form.

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