Trachinoidea: Development and Relationships

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THE blennioid infraorder Trachinoidea, as used here, contains about 140 species in 11 families of morphologically quite diverse, but generally small, primarily shallow-living temperate and tropical marine demersal or burrowing fishes (Chiasmodontidae is bathypelagic; Cheimarrhichthyidae inhabits fresh water). These families have not always been considered as closely related (e.g., Gosline, 1968, 1971), but we follow Nelson (1976) in considering them together here. Nelson (1976) originally placed 16 families in the Trachinoidea, but subsequently synonymized the Limnichthyidae with Creediidae (Nelson, 1978). Springer (1978) removed Oxudercidae to the Gobiidae. Three other families are treated elsewhere in this volume: Bathymasteridae and Dactyloscopidae with the Blennioidea (Matarese et al., this volume) and Opistognathidae with the Percoidei (G. D. Johnson).

In this brief review, we summarize the present state of knowledge of the early life histories of trachinoid fishes and attempt to determine whether such information contributes to our understanding of their phylogenetic relationships. Unfortunately, early life histories, mostly incomplete, are known for only a small number of species (Table 134). This paucity of early life history data makes generalizations about development tenuous at best, but for purposes of this paper the known taxa are considered representative.

DEVELOPMENT

Eggs

Eggs are unknown for the Percophididae, Trichonotidae, and Leptoscopidae. Only ovarian eggs have been described for the

TABLE 134. SUMMARY OF EARLY LIFE HISTORY INFORMATION AVAILABLE FOR TRACHINOID FISHES.

Family	Number of genera	Approximate number of species	Distribution	Descriptions		Illustrations		Early life history source
				Genera	Species	Genera	Species	
Trichodontidae	2	2	North Pacific	1	1	1	1	Breder and Rosen, 1966; Marliave, 1981
Champsodontidae	1	10	Indo-Pacific	1	1	1	1	Mito, 1962d, 1966
Chiasmodontidae	4	23	Worldwide (temperate and tropical, marine)	1	1	1	1	Ahlstrom, pers. comm.; Lavenberg, pers. comm.
Percophididae	6	17	Atlantic, Indo-Pacific	1	1	1	1	Crossland, 1982
Mugiloididae	3	36	Atlantic, Indian, Pacific (subtropical and tropical)	1	5	1	4	Leis and Rennis, 1983; Mito, 1966; Robertson, 1973, 1975a; Watson, unpubl.
Trichonotidae	2	5	Indo-Pacific	1	2	1	1	Leis and Rennis, 1983
Cheimarrhichthyidae	1	1	New Zealand (freshwater)	0	0	0	0	McDowall, 1973c
Creediidae	7	14	Indo-Pacific	2	2	2	3	Leis, 1982; Leis and Rennis, 1983; Regan, 1916; Watson and Leis, 1974
Trachinidae	1	4–5	Eastern Atlantic, Mediterranean	1	4	1	2	Breder and Rosen, 1966; Dekhnik, 1973; Ehrenbaum, 1905–1909; Marinaro, 1971; Padoa, 1956g; Russell, 1976; Schnakenbeck, 1928; Vodyanitsky and Kazanova, 1954
Uranoscopidae	8	25	Atlantic, Indian, Pacific (shallow temperate and tropical)	3	4	2	3	Dekhnik, 1973; Fritzsche, 1978; Mito, 1966; Robertson, 1974
Leptoscopidae	2	3	Australia, New Zealand (marine)	0	0	0	0	

Cheimarrhichthyidae (McDowall, 1973c). Six of the seven remaining families spawn small to moderate (0.70–2.45 mm diameter), spherical, single pelagic eggs (Table 135). McDowall (1973c) suggested a pelagic spawning mode for Cheimarrhichthyidae as well, unusual for the suggested riparian spawning habitat but consistent with the close relationship, or identity, of Cheimarrhichthyidae with Mugiloididae. All pelagic eggs have oil droplets (most have only one, 0.16–0.26 mm in diameter) and all except some Uranoscopidae have smooth, unsculptured chorions. Incubation periods range from 2 to 6 days and larvae are not well developed at hatching (Trachinidae are somewhat better developed, with pigmented eyes and pelvic buds).

Demersal egg masses (750–1,000 eggs) are produced only by the Trichodontidae (Table 135). These eggs are large (3.52 mm in diameter), slightly flattened, with an unsculptured chorion and no oil droplet. Incubation is estimated at about one year (Marliave, 1981) and larvae are well developed at hatching.

Larvae

Larval stages are unknown for the Cheimarrhichthyidae and Leptoscopidae. The described trachinoid larvae display only a few unifying characteristics: (1) all are pelagic, hatching at ca. 2–15 mm (Table 136); (2) they pass through no specialized stages (except the gargaropteron juvenile stage of the chiasmodontid genus *Kali*); and (3) they metamorphose gradually to the demersal juvenile stage at a small to moderate size (ca. 10–60 mm).

Morphology.—Morphology is quite variable; however, larvae are either relatively long and slender (Fig. 299: Trichodontidae, Chiasmodontidae, Percophididae, Trichonotidae, Creediidae) or rather robust (Fig. 300: Champsodontidae, Mugiloididae, Trachinidae, Uranoscopidae). All the robust larvae and one of the slender types (Trichodontidae) have somewhat rounded heads with relatively short snouts. Preanal length in both types usually is not more than 50% of standard length (60% or more in Creediidae and Trichonotidae) and changes little during development. Head and body spination are extremely variable. Preopercular spination is known for six families: Trichodontidae, Chiasmodontidae, Champsodontidae, Mugiloididae, Creediidae, and Trachinidae. Champsodontid larvae develop a serrate crest on the snout and head during the postflexion period, and chiasmodontid larvae (except *Kali*: R. J. Lavenberg, pers. comm.) develop small body spicules (Fig. 299) just before or during notochord flexion.

Pigmentation.—Pigmentation of trachinoid larvae is quite variable, from nearly absent to quite intense (Table 137). Larval champsodontids, mugiloidids, trichonotids, and creediids remain lightly pigmented throughout development, while larval trichodontids, chiasmodontids, trachinids, and uranoscopids may become rather heavily pigmented. Pigmentation usually increases with increasing larval size; trichonotids and creediids change little in pigmentation with growth.

Head.—Eyes are pigmented at hatching for the demersally-spawned Trichodontidae, and for two of the six families with pelagic eggs (Table 137). Pigmentation is present at hatching, or subsequently develops, over the brain in five families. The degree of pigmentation of other areas of the head is variable.

Gut.—Pigmentation typically is present dorsally over the gut and swim bladder throughout larval development (absent only in creediids and postflexion trichonotids). Other gut pigment is variable.

TABLE 135. CHARACTERISTICS OF TRACHINOID EGGS.

Family	Pelagic (P) or demersal (D)	Single or mass	Egg diameter (mm)	Oil droplets number: size range (mm)	Attachments or ornamentation	Pigmentation	Incubation period	Source
Trichodontidae	D	Mass 750–1,000 eggs	3.52	0	None	Amber	2 mo.–1 yr.	Breder and Rosen, 1966; Marliave, 1981
Champsodontidae	P	Single	1.09–1.19	1: 0.17–0.22	None	Melanophores on embryo and oil droplet		McDowell, 1973c; Mito, 1966
Chiasmodontidae	P	Single	1.08–1.14	1: 0.26	None	Chorion rose to amber		Ahlstrom, pers. comm.
Percophididae	Unknown							
Mugiloididae	P	Single	0.77–1.25	1: 0.16–0.25	None	Melanophores on embryo and oil droplet	5–6 days	Mito, 1966; Robertson, 1973, 1975a
Trichonotidae	Unknown							
Cheimarrhichthyidae	P (assumed)	Single (ovarian)						McDowell, 1973c
Creediidae	P	Single	0.70–1.10	400–600 in 8–12 clusters; coalesce to 3–8: 0.05–0.10	None	Melanophores on embryo	2 days	Leis, 1982; Watson and Leis, 1974
Trachinidae	P	Single	0.94–1.37	1–30, coalesce: 0.19–0.25	None		4–5 days	Breder and Rosen, 1966; Dekhnik, 1973; Marinaro, 1971; Padoa, 1956g; Russell, 1976
Uranoscopidae	P	Single	1.52–2.45	3–27: 0.02–0.15	Polygonal network on chorion in *Uranoscopus*	Melanophores on yolk and embryo		Dekhnik, 1973; Fritzsche, 1978; Mito, 1966; Robertson, 1975a
Leptoscopidae	Unknown							

Trunk and tail.—Most trachinoid larvae display some degree of pigmentation along the ventral margin of the tail (absent in some mugiloidids and preflexion trachinids). Pigmentation (typically rather light) occurs along the dorsal margin of the trunk and tail at some time during larval development in many trachinoids. Internal pigment may develop above and below the vertebral column (e.g., Trichodontidae).

Hypural margin.—Hypural pigment typically is light or absent although its presence as a bar is diagnostic for the Trichodontidae.

Fins.—Fins typically are unpigmented in trachinoid larvae, although for some groups fin pigmentation can be diagnostic (e.g., the caudal and posterior dorsal and anal fin pigment of Trich-

TABLE 136. SIZE (MM SL) OF TRACHINOID LARVAE AT SELECTED DEVELOPMENTAL STAGES.

Family	Hatching	Notochord flexion	Prejuvenile or specialized stages	Juvenile
Trichodontidae	14.5	Before hatching	None	32–60
Champsodontidae	3.4–3.7	4.6–5.0	None	9.6–10.7
Chiasmodontidae	ca. 4	Before ca. 9	ca. 45	ca. 12–45
Percophididae		<16.0		
Mugiloididae	2.2–3.0	3.7–4.8	None	10.0 to ≥12.6
Trichonotidae		5.2–6.3	None	>18.8
Cheimarrhichthyidae				≤25
Creediidae	2.6–3.5	7.0–10.2	None	>11.0, ≤29.2
Trachinidae	3.2	5.0–10.0	None	13–15
Uranoscopidae	≥2.5–4.38		None	≥23
Leptoscopidae	No information			

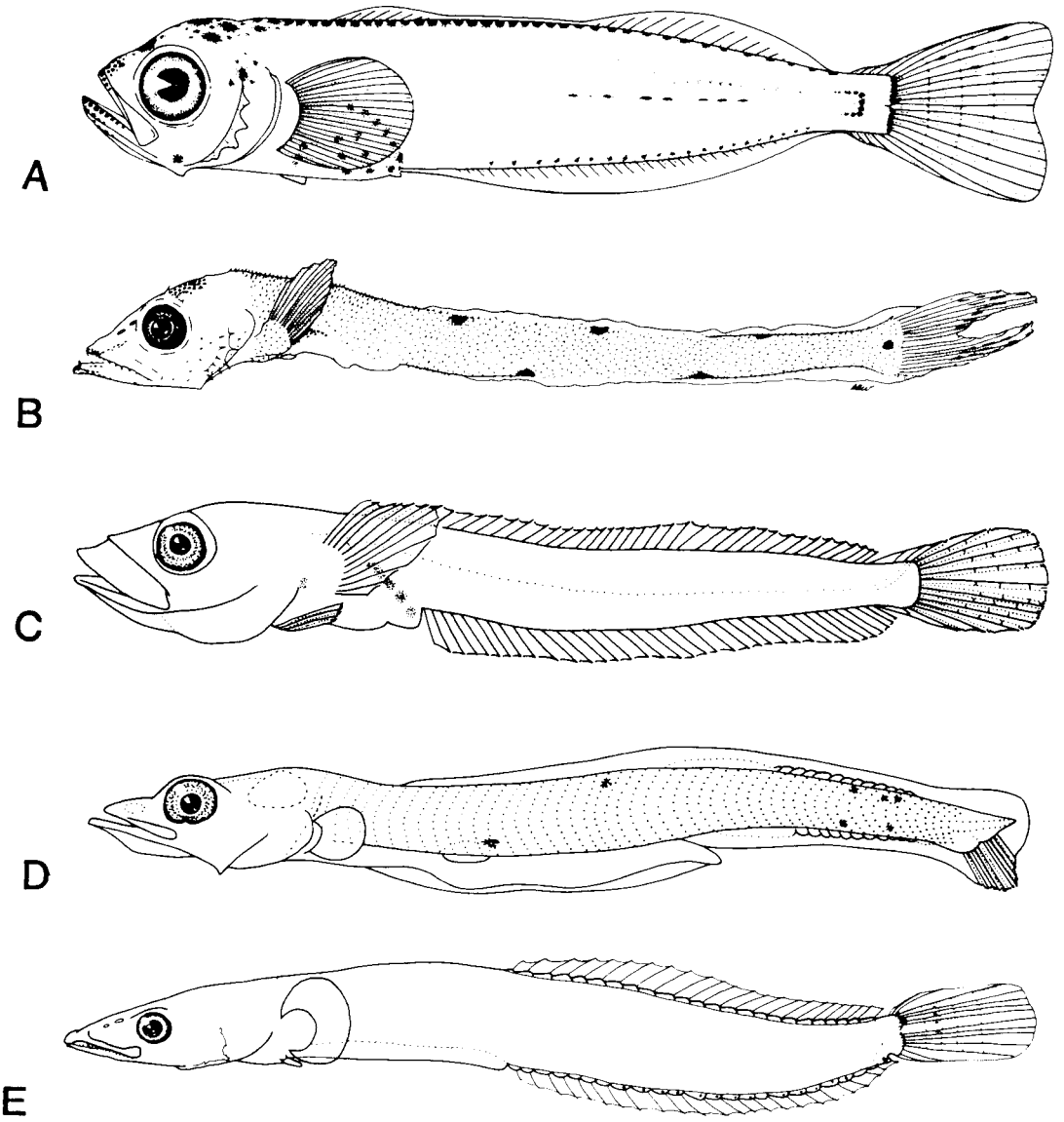

Fig. 299. (A) Trichodontidae: *Trichodon trichodon*, 13.0 mm, from Marliave (1981); (B) Chiasmodontidae: *Pseudoscopelus* sp., 14.0 mm, CalCOFI station 5710-5-130.80 (approximately 24°49'N, 116°49'W); (C) Percophididae: *Hemerocoetes* sp., 16.0 mm, redrawn from Crossland (1982); (D) Trichonotidae: *Trichonotus* sp., 5.9 mm, from Leis and Rennis (1983); and (E) Creediidae: *Limnichthys donaldsoni*, 11.0 mm, from Leis (1982).

onotidae or the early developing heavily pigmented pelvic fins of trachinids).

Meristic characters.—Vertebral and fin ray counts are summarized in Table 138. The sequence of fin ray formation, incompletely described for most families, appears to be quite variable except that the caudal fin is first to begin ossification of rays in all but the trachinids (the caudal is second in this family, following the pelvic fins). Dorsal and anal fin rays are second to form in four families (Mugiloididae, Trichonotidae, Creediidae, Uranoscopidae), while pectoral fin rays are second in two (Trichodontidae and Chiasmodontidae) and pelvic fin rays in one (Champsodontidae).

Special structures.—Special structures are generally lacking in trachinoid larvae. Only the elongate opercular appendage of

TABLE 137. SUMMARY OF PIGMENTATION (MELANIN ONLY) OF LARVAL TRACHINOID FISHES. Key: +, present; 0, absent; ↑, increasing with development; ↓, decreasing with development; 0→+, initially unpigmented, becoming pigmented with development; An, anterior; Po, posterior.

		Head						Gut				Trunk and tail: Ventral margin	
Family	Eye at hatching	Brain	Jaws	Snout	Opercle	Isthmus	Nape	An-terior	Dor-sal	Ven-tral	Lat-eral	Pre-flexion	Flexion
Trichodontidae	+	+↑	+	+	0	0	0→+	0	0	0	+		+
Champsodontidae	+	+	0	+↓	0	0	0→+	0	+	0→+	+	+	+
Chiasmodontidae	0	+	+	0	0	0→+	0	0	+	0	0	+	+
Percophididae		0	0	0	+	0	0	0	+	0	0		
Mugiloididae	0	0, or +↓, or +↑	0	0, or +↓	0	0	0	0, or +	+↑	0, or +	0→+	0, or +	+
Trichonotidae	0	0	0	0	0	0	0	0	+↓	0	0	+ Po	+ Po
Cheimarrhichthyidae[1]													
Creediidae	0	0	0	0	0	0	0	0	0	+	0	+ Po	+ Po
Trachinidae	+	0, or +↑	0, or +↑	0, or +↑	0→+↑	0	0, or +	0	+	0	0→+↑	0, or +	+
Uranoscopidae	0	+↑	0→+	+↑	0→+	0→+	0→+	+	+↑	0→+↑ or +↑	0→+↑ or +↑	+↑, or +↓	+↑, or +↓
Leptoscopidae[1]													

[1] Larvae unknown.

TABLE 138. SELECTED MERISTICS OF TRACHINOID FISHES.

Family	Dorsal fin	Anal fin	Pectoral fin	Pelvic fin	Primary caudal fin rays	Vertebrate	Source
Trichodontidae	X–XVI + 0–I, 13–19	I, 27–31	21–23	I, 5	12–15	12–15 + 34–40 = 47–50	Marliave, 1981; NWAFC, unpubl.
Champsodontidae	V + I, 18–22	I, 17–20	9–13	I, 5		10 + 19–22 = 29–32	de Beaufort and Chapman, 1951; Matsubara et al., 1964; Mito, 1962d
Chiasmodontidae	VI–XIII + 18–28	0–I, 17–28	10–15	I, 5	17	33–44	Johnson and Cohen, 1974; Lavenberg, pers. comm.; Norman, 1929
Percophididae	0–IX + 14–31	0–I, 15–42	20–28	I, 5	15	8–9 + 19–21 = 27–30	Ginsburg, 1955; Iwamoto and Staiger, 1976; Miller and Jorgenson, 1973
Mugiloididae	IV–VII, 19–28	I, 16–26	15–22	I, 5	14–15	10–16 + 18–22 = 28–38	Cantwell, 1964
Trichonotidae	III–VII, 40–46	36–40	12–14	I, 5	13	15 + 40 = 55	Leis and Rennis, 1983; Masuda et al., 1975
Cheimarrhichthyidae	IV–VI, 18–21	I–II, 14–16	14–18	I, 5	12–15	12 + 20–21 = 32–33	McDowall, 1973c
Creediidae	18–40	25–40	11–17	None, or I, 3–5	10	37–59	Leis and Rennis, 1983; Smith, 1961.
Trachinidae	V–VII + 21–32	25–36	15	I, 5	14	11–12 + 23–31 = 34–43	Padoa, 1956g; Russell, 1976
Uranoscopidae	0–V + 12–19	0–I, 12–19	13–24	I, 5	11–14	9–12 + 14–17 = 25–29	Berry and Anderson, 1961; Fritzsche, 1978; Marshall, 1965; Miller and Jorgenson, 1973; Mito, 1966; Scott et al., 1974; Smith, 1961; Wade, 1946
Leptoscopidae	34–35	37		I, 5		10+	Gosline, 1968; Scott et al., 1974

TABLE 137. EXTENDED.

Trunk and tail							Fins						
Ventral margin	Dorsal margin			Lateral									
Post-flexion	Pre-flexion	Flexion	Post-flexion	Pre-flexion	Flexion	Post-flexion	Hypural margin	Dorsal	Anal	Pectoral	Pelvic	Caudal	Source
+		0→+ An	+↑		0	+↑	+	0→+	0	0→+	0	0→+	Marliave, 1981
+	+	+	+	0	0, or +	0, or +	0	+↓	+↓	0	0	+↓	Mito, 1962d, 1966
+	0, or +	0, or +	+	0	0	0	0	0	0	0	0	0	Ahlstrom, pers. comm.; Lavenberg, pers. comm.
0			0			0		0	0	0	0	0	McDowall, 1973c
+, or +↓	+↓ Po	0, or +↓ Po	0	0, or + Po	0, or + Po	0, or + An	0	0	0	0, or +	0, or +	0	Leis and Rennis, 1983; Mito, 1966; Robertson, 1973; Watson, unpubl.
+ Po	+ Po	+ Po	+ Po	+ Po	+ Po	+ Po	0	+ Po	+ Po	0	0	+	Leis and Rennis, 1983
+ Po	+ Po	+ Po	0, or + Po	0	0	+	0→+	+↓ Po	+↓Po	0	0	+	Leis, 1982; Leis and Rennis, 1983; Regan, 1916
+	0, or + An	0, or + An	0, or + An	0	0, or + An	+ An	+	0→+↑	0	0	+	0	Ehrenbaum, 1905–1909; Padoa, 1956g; Russell, 1976
0, or +	+	0	0	+	+ An	+	+	0, or +↓	0, or +↓	0	0	0	Dekhnik, 1973; Mito, 1966; Pearson, 1941

Champsodon, and the body spicules of the chiasmodontids (except *Kali*) are distinctive. *Trachinus vipera* has precocious, enlarged, and heavily pigmented pelvic fins.

RELATIONSHIPS

The trachinoid families summarized here are presumed to be derived from the Percoidei, or in some cases to belong themselves to the Percoidei (e.g., Trichodontidae, Champsodontidae, Chiasmodontidae: Gosline, 1971). Therefore, in the following discussion we consider early life history characters shared with the Percoidei as primitive. Characters shared with other Blennioidei are, somewhat arbitrarily, considered to be derived. Our purpose in classifying characters into these categories is not to develop a new phylogeny of the Trachinoidea based on early life history, since far too little in known to allow such an undertaking, but rather to determine whether such characters support our treatment of the Trachinoidea as a monophyletic group.

Six of the 11 trachinoid families retain the pelagic spawning

TABLE 139. SUMMARY OF EARLY LIFE HISTORY CHARACTERISTICS OF THE TRACHINOIDEA. The percoid condition is assumed to be primitive, while the blennioid condition is assumed to be derived. The percoid condition includes spawning of pelagic eggs which soon hatch to poorly-differentiated larvae, a moderately deep body, myomeres mid-to-upper twenties, development of dorsal and anal fin rays before pectoral and/or pelvic fin rays, and five pelvic fin rays. The blennioid condition includes spawning of non-pelagic eggs with an extended incubation period and hatching of well developed larvae having pigmented eyes, an elongate shape, myomeres thirty or more, development of pectoral and/or pelvic fin rays before dorsal and anal fin rays, and fewer than five pelvic fin rays. It should be understood that spawning mode, incubation period and development at hatching tend to be correlated, as are larval shape and number of myomeres.

	Eggs			Larvae					
Family	Spawning mode	Incubation period	Development at hatching	Larval shape	Number of myomeres	Pectoral pelvic fin ossification	Reduced number of pelvic rays	Pre-opercular spination	Larval pigmentation
Trichodontidae	Derived	Derived	Derived	Derived	Derived	Derived	Primitive	Present	Heavy
Champsodontidae	Primitive		Derived	Primitive	Primitive	Derived	Primitive	Present	Light
Chiasmodontidae	Primitive		Primitive	Derived	Derived	Derived	Primitive	Present	Heavy
Percophididae				Derived	Primitive	Primitive	Primitive	Absent	Light
Mugiloididae	Primitive	Derived	Primitive	Primitive	Primitive	Primitive	Primitive	Present	Light
Trichonotidae				Derived	Derived	Primitive	Primitive	Absent	Light
Cheimarrhichthyidae	Primitive?								
Creediidae	Primitive	Primitive	Primitive	Derived	Derived	Primitive	Derived	Present	Light
Trachinidae	Primitive	Derived	Derived	Primitive	Derived	Derived	Primitive	Present	Heavy
Uranoscopidae	Primitive		Primitive	Primitive	Primitive	Primitive	Primitive	Absent	Heavy
Leptoscopidae									

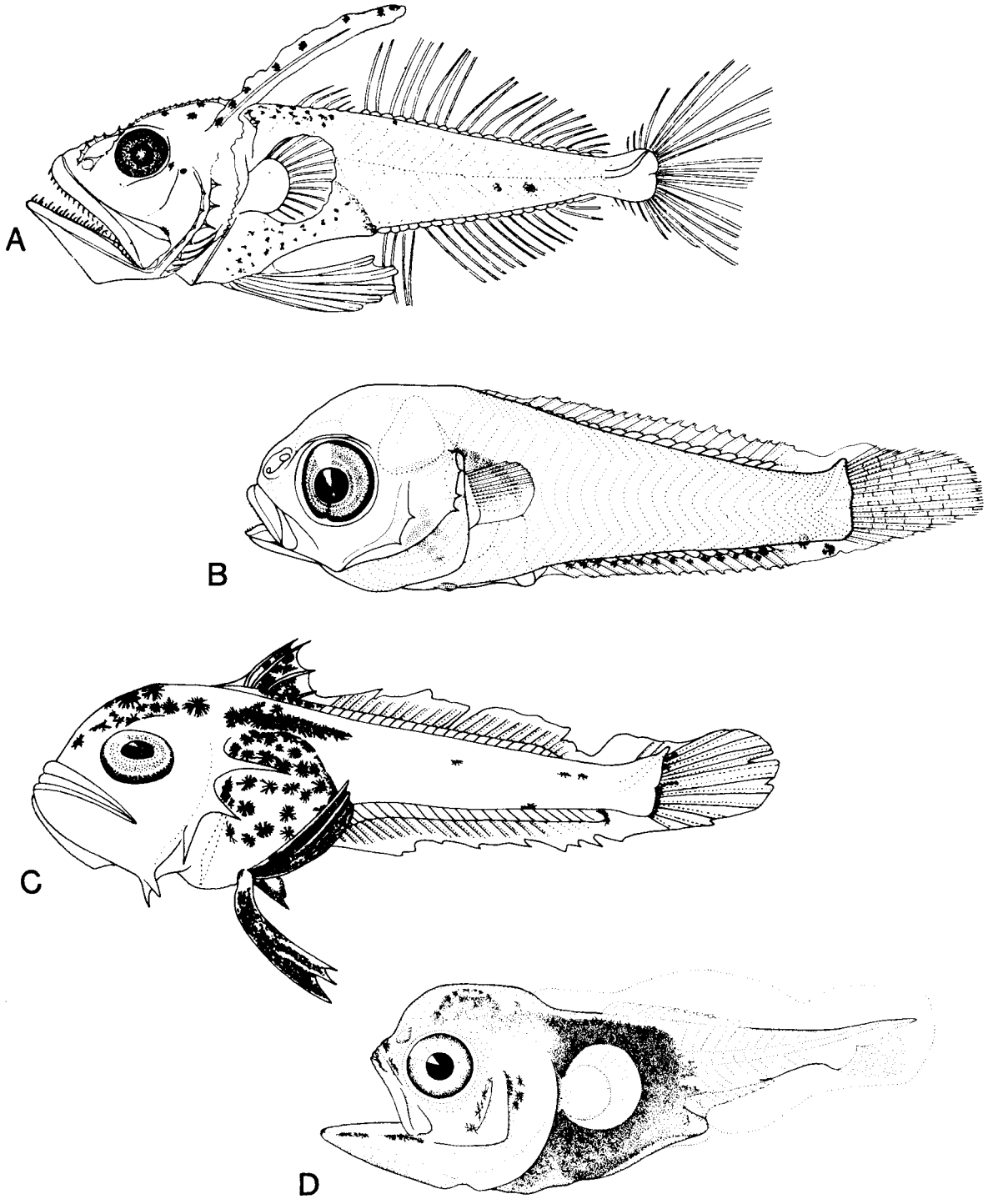

Fig. 300. (A) Champsodontidae: *Champsodon snyderi*, 9.6 mm, from Mito (1962a); (B) Mugiloididae: *Parapercis schauinslandi*, 5.3 mm, Kahe Point, Oahu, Hawaii (approximately 21°16'N, 158°5'W); (C) Trachinidae: *Trachinus vipera*, 7.5 mm, redrawn from Schnakenbeck (1928); and (D) Uranoscopidae: *Astroscopus guttatus*, 4.9 mm, from Pearson (1941).

mode (Tables 135 and 139) typical of the marine percoids, one shares with the other Blennioidei the condition of spawning nonpelagic egg masses. Among the pelagic spawners, four retain the percoid-like condition of early hatching of poorly-differentiated larvae; two share with the demersal spawners the condition of a relatively long incubation and hatching of well developed larvae with pigmented eyes.

The larvae of four families are moderately deep-bodied, a character shared with the majority of percoids. Each of these families (except Trachinidae) contains at least some species with myomeres numbering in the mid-to-upper twenties: typical percoid counts. Five trachinoid families resemble blennioids in having elongate larvae, usually with more than 30 myomeres.

All trachinoid larvae (except some Trachinidae) follow the typical perciform pattern of beginning caudal fin ossification first; larvae of five families follow the percoid pattern of beginning ossification of dorsal and anal fin rays before pectoral and pelvic fin rays. Four families share with the other blennioids the early acquisition of pectoral and/or pelvic fin rays. All trachinoid families share with the other blennioids the jugular placement of pelvic fins, but only one family (not all species) also shares the blennioid condition of fewer than five pelvic fin rays.

Larval pigmentation and preopercular spination of the Trachinoidea (Table 139) are difficult to assess, since both range from absent to highly developed in both the Percoidei and Blennioidei. The distribution of these characters is listed in Table 139 to aid in determining relationships among the Trachinoidea.

Based solely on early life history characters (Table 139), the Uranoscopidae and Mugiloididae (including Cheimarrhichthyidae?) appear to be the most percoid-like members of the Trachinoidea, while Trichodontidae are most like the other Blennioidei. Two points become clear in considering the contribution of early life history to the understanding of trachinoid phylogeny: (1) the Trachinoidea is a very diverse, probably polyphyletic, group; and (2) much more early life history data are needed before any substantial contribution can be made to the understanding of this group.

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