CURRENT KNOWLEDGE OF LARVAE OF SCULPINS (PISCES: COTTIDAE AND ALLIES) IN NORTHEAST PACIFIC GENERA WITH NOTES ON INTERGENERIC RELATIONSHIPS[1]

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ABSTRACT

Current knowledge of cottid larvae in northeast Pacific genera is summarized. Larvae are known for representatives of 25 of the 40 genera reported from Baja California to the Aleutian Islands although two genera, *Gymnocanthus* and *Icelus*, are represented only by species which live in other areas as adults. Included are illustrations of larvae of 29 species representing the 25 genera plus one potentially new northeast Pacific genus, identified only as "Cottoid Type A."

The larvae exhibit a wide diversity of form. Based on shared larval characters, including spine patterns, body shape, and pigmentation, 6 phenetically derived groups of genera are apparent within the 25 genera for which representatives are considered: 1) *Artedius*, *Clinocottus*, *Oligocottus*, *Orthonopias*; 2) *Paricelinus*, *Triglops*, *Icelus*, *Chitonotus*, *Icelinus*; 3) *Dasycottus*, *Psychrolutes*, *Gilbertidia*, ?*Malacocottus*, "Cottoid Type A"; 4) *Scorpaenichthys*, *Hemilepidotus*; 5) *Blepsias*, *Nautichthys*; 6) *Leptocottus*, *Cottus*. Six genera do not fit with any group: *Enophrys*, *Gymnocanthus*, *Myoxocephalus*, *Radulinus*, *Rhamphocottus*, *Hemitripterus*.

If these preliminary larval groupings reflect relationship, as evidence indicates, they tend to support a number of previously implied relationships within the cottids, but there are some important differences. These include the distinctiveness of the *Artedius* (Group 1) line; the separation of *Artedius* and *Icelus*, once considered closely related; the relationship of *Paricelinus*, generally considered a primitive and rather distinct form, with other members of Group 2; the apparent relationship of *Icelus* to other genera in Group 2 and its questionable placement in a separate family; the distinctiveness of *Radulinus*, previously considered to be related to *Chitonotus* and *Icelinus*.

The Cottidae, which in this paper are considered broadly to include sculpinlike fishes of Cottidae, Icelidae, Cottocomephoridae, Comephoridae, Normanichthyidae, Cottunculidae, and Psychrolutidae of the suborder Cottoidei of Greenwood et al. (1966), comprises a diverse group of temperate and boreal fishes. Nelson (1976) estimated that the group may contain over 350 species, three-fourths marine, in about 86 genera. They are generally coastal fishes inhabiting all oceans but the Indian. Greatest species diversity occurs in the North Pacific. The systematics of the group are not well understood (Quast 1965; Nelson 1976).

Until recently, larvae of relatively few cottids had been described. They were a difficult group to identify in ichthyoplankton collections, particularly in the northeast Pacific where 40 genera are reported to occur between Baja California and the Aleutian Islands (Table 1). With the recent work by Richardson and Washington (1980), larvae are now known for representatives of 25 of these 40 cottid genera, although two genera, *Icelus* and *Gymnocanthus*, are represented only by larvae of species that live in other areas as adults.

The purpose of this paper is twofold. It presents for the first time a summary of important cottid larval characters (those characters occurring only during the larval period and most useful in identifying and distinguishing species) based on the larvae of these 25 northeast Pacific genera. (Larvae of these genera that are known for species inhabiting other areas as adults are also considered.) This knowledge, which is a necessary prerequisite for systematic studies using larvae, is presented to provide a foundation to which future work on cottid larvae can be compared and upon which it can be expanded as more larvae become known. The paper also presents a preliminary examination of generic groupings within these northeast Pacific cottid genera based on shared larval characters, i.e., similarity. These phenetic groupings, even though preliminary, are helpful

[1]This paper was presented at the Second International Symposium on The Early Life History of Fish (sponsored by ICES, IAO, ICNAF, IAOB, SCOR) held at Woods Hole, Mass., 2-5 April 1979. An abstract of the paper appeared in the symposium publication.

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TABLE 1.—List of cottid genera occuring in the northeast Pacific Ocean between Baja California and the Aleutian Islands based on Howe and Richardson (text footnote 3) with a summary of illustrations (accessible to author) of larvae known for those genera worldwide. Lengths (millimeters) of larvae are reported as they appeared in the literature: NL = notochord length; SL = standard length; TL = total length; mm = no length definition was given.

Genus and species	Reference	Sizes illustrated
Artediellus —	—	—
Artedius harringtoni	Richardson and Washington 1980	3.0, 4.7, 6.9 mm NL, 7.3, 9.3, 13.6 mm SL
A. lateralis	Budd 1940	4.1 mm SL
	Marliave 1975	4, 8, 11, 14 mm TL
Artedius Type 2	Richardson and Washington 1980	3.0, 4.7, 6.0 mm NL, 7.2, 9.9, 11.8 mm SL
Ascelichthys —	—	—
Asemichthys —	—	—
Blepsias cirrhosus	Blackburn 1973	12.2 mm SL
	Marliave 1975	10, 14, 19, 15.5 mm TL
Chitonotus pugetensis	Richardson and Washington 1980	3.0, 6.3 mm NL, 8.5, 11.5, 15.4, 16.6 mm SL
	Misitano 1980	3.0, 4.8 mm SL
Clinocottus acuticeps	Richardson and Washington 1980	3.7, 3.9, 6.9 mm NL, 7.6, 10.4, 13.8, 16.5 mm SL
C. analis	Eigenmann 1892	ca. 4 mm
	Budd 1940	ca. 4 mm
C. recalvus	Morris 1951	4.6, 5.0, 7.6, 8.3, 9.9, 10.8, 18.0, 24.3 mm TL
Cottus asper	Stein 1972	5.5, 9.0, 10.8 mm TL
	Richardson and Washington 1980	5.2 mm NL, 8.2, 9.9 mm SL
Dasycottus setiger	Blackburn 1973	7.4 mm SL
Enophrys bison	Blackburn 1973	7.5 mm SL
	Marliave 1975	10 mm TL
	Misitano 1978	5.0, 5.4, 5.8, 6.7, 7.1, 7.6 mm SL
	Richardson and Washington 1980	4.8, 7.0 mm NL, 9.1 mm SL
E. bubalis[1]	Cunningham 1891[2]	5.7 mm
	McIntosh and Masterman 1897[2]	Larva (size not given)
	Ehrenbaum 1904[2]	5.8, 10, 11 mm
	Ehrenbaum 1905-9	5.8, 10, 11 mm
	Russell 1976[3]	4.5, 5.7, 6.4, 9.5 mm
E. lilljeborgi[1]	Bruun 1925[4]	5.6, 6.8, 8.7 mm TL
	Rass 1949[5]	6.8 mm
	Russell 1976[6]	4.08, 4.2, 5.7, 7.0 mm
Eurymen —	—	—
Gilbertidia sigalutes	Blackburn 1973	7.9, 9.5 mm SL
	Marliave 1975	7, 13, 15, 25, 34 mm TL
Gymnocanthus herzensteini[1]	Kyushin 1970	5.79, 6.59, 7.55 mm
G. tricuspis[1]	Koefoed 1907	10.7, 12.7, 15.5 mm
	Rass 1949	9 mm
	Khan 1972	12.2, 13.9, 15.9 mm TL
G. ventralis[1]	Ehrenbaum 1905-9	15, 18 mm
Hemilepidotus gilberti[1]	Gorbunova 1964	7.5, 11.4, 17.5 mm
	Hattori 1964	7.1, 11.6, 19.2, 24.8, 32.5 mm
H. hemilepidotus	Gorbunova 1964	7.25, 10.5 mm
	Peden 1978	ca. 20 mm SL
	Richardson and Washington 1980	5.8, 5.9, 9.1 mm NL, 10.7, 11.5, 19.0 mm SL
H. jordani	Gorbunova 1964	6.4, 10.7, 13.0 mm
	Peden 1978	ca. 20 mm SL
H. papilio	Gorbunova 1964	10.7, 13.7 mm
H. spinosus	Follett 1952	12, 21 mm SL
	Peden 1978	ca. 20 mm SL
	Richardson and Washington 1980	5.0, 6.6, 8.9 mm NL, 11.0, 11.8, 19.0 mm SL
H. zapus	Peden 1978	ca. 20 mm SL
Hemitripterus americanus[1]	Warfel and Merriman 1944	ca. 12 mm
	Khan 1972	11.7,[7] 14.5, 18.8 mm TL
	Fuiman 1976	12.6, 15.5, 20 mm TL
H. villosus[8]	Kyushin 1968	14.78, 15.57, 16.52 mm SL
	Okiyama and Sando 1976	11.6, 14.4, 17.4, 20.0 mm
Icelinus spp.[9]	Richardson and Washington 1980	3.3, 8.6 mm NL, 10.9, 13.8, 15.2, 16.5, 12.5, 16.6 mm SL
Icelus bicornis[1]	Ehrenbaum 1905-9[10]	25 mm
	Rass 1949	12.3 mm
Jordania —	—	—
Leiocottus —	—	—
Leptocottus armatus	Jones 1962	ca. 4 mm
	Blackburn 1973	7.6, 8.3, 12.0 mm SL
	Marliave 1975	8, 12, 13 mm TL
	White 1977	4.9 mm NL
	Richardson and Washington 1980	5.1, 8.1 mm NL, 11.1 mm SL
Malacocottus ?M. zonurus Type 1	Richardson and Bond[11]	7.0, 9.8, 14.2, 24.0 mm SL
	Richardson unpubl. data	6.6, 7.0, 8.8, 9.8, 10.4, 14.2, 24.0 mm SL
Myoxocephalus aenaeus[1]	Perlmutter 1939	6 mm
	Khan 1972	5.0, 7.1, 9.7, 11.8 mm TL
	Lund and Marcy 1975	5.4, 6.1, 6.8, 7.5, 8.5, 9.2 mm TL
M. octodecemspinosus[1]	Colton and Marak 1969	6.8, 8.5, 10.5, 15.2 mm TL
	Khan 1972	7.0, 9.5, 10.7, 12.5, 14.5 mm TL
M. polyacanthocephalus	Blackburn 1973	7.7, 10.7 mm SL
M. quadricornis[1] (marine form)	Zvjagina 1963	12.3, 12.8, 13.6, 14.5, 16.2, 32 mm
	Khan 1972	12.8, 14.5, 17.0 mm TL
	Khan and Faber 1974	12.8, 14.4, 17.0 mm TL

TABLE 1.—*Continued.*

Genus and species	Reference	Sizes illustrated
M. scorpius[1]	McIntosh and Prince 1890[12]	Larva (size not given)
	McIntosh and Masterman 1897[12]	Larva (size not given)
	Ehrenbaum 1904[12]	8.24, 8.16, 10, 18 mm
	Ehrenbaum 1905-9	8.2, 10, 18 mm
	Koefoed 1907	9.5 mm
	Rass 1949	7.9, 9.3 mm
	Bigelow and Schroeder 1953	8.2, 10, 18 mm
	Khan 1972	7.6, 8.5, 10.4, 14.0, 17.4 mm TL
	Russell 1976	7.5, 9.5, 10, 14 mm
Nautichthys oculofasciatus	Blackburn 1973	7.5, 13 mm SL
	Marliave 1975	9.5, 13, 17, 26 mm TL
	Richardson and Washington 1980	11.7 mm NL, 16.6 mm SL
Oligocottus maculosus	Stein 1972	4.6-5.2, 6.0, 6.6, 9.2 mm TL
	Stein 1973	4.6-5.2, 6.0, 6.6, 9.2 mm TL
O. snyderi	Stein 1972	4.5-4.75, 5.5 mm TL
Orthonopias triacis	Bolin 1941	ca. 3-4 mm SL
Paricelinus hopliticus	Richardson and Washington 1980	5.6, 6.2 mm NL, 13.8, 18.6, 25.6 mm SL
Phallocottus —	—	—
Porocottus —	—	—
Psychrolutes paradoxus	Blackburn 1973	10.3 mm SL
	Marliave 1975	10.5, 13, 14, 13 mm TL
Radulinus asprellus	Richardson and Washington 1980	4.7, 7.9, 9.6, 10.9 mm NL, 12.6, 14.4 mm SL
R. boleoides	Richardson and Washington 1980	8.7 mm NL
Rhamphocottus richardsoni	Blackburn 1973	6.7, 10 mm SL
	Marliave 1975	10, 11.5, 15 mm TL
	Richardson and Washington 1980	8.4 mm NL, 10.6, 11.7 mm SL
Scorpaenichthys marmoratus	O'Connell 1953	5.85, 6.26, 10, 17, 30, 48 mm
	Richardson and Washington 1980	5.3, 7.5, 8.6 mm NL, 8.7, 10.4, 13.8 mm SL
Sigmistes —	—	—
Stelgistrum —	—	—
Sternias —	—	—
Stlegicottus —	—	—
Synchirus —	—	—
Thyriscus —	—	—
Triglops murrayi[1]	Khan 1972	8.4, 11.6, 18.9, 23.4 mm TL
T. pingeli[8]	Ehrenbaum 1905-9	18 mm
	Koefoed 1907	13, 16.5, 22 mm
	Rass 1949	10 mm
Triglops sp.	Blackburn 1973	8.3, 12 mm SL
	Richardson and Washington 1980	6.9 mm NL, 15.4 mm SL
Zesticelus —	—	—

[1]Not northeast Pacific species.
[2]As *Cottus bubalis*.
[3]As *Taurulus bubalis*.
[4]As *Cottus lilljeborgi*.
[5]As *Acanthocottus lilljeborgi*.
[6]As *Taurulus lilljeborgi*.
[7]Probably *Myoxocephalus scorpius* (Laroche text footnote 6).
[8]Species occurs in northeast Pacific but larvae described from other areas.
[9]Not identified below genus level.
[10]As *Centridermichthys hamatus*.
[11]Text footnote 5.
[12]As *Cottus scorpius*.

in reducing taxonomic problems. The potential usefulness of the larval groups in providing insights into systematic relationships and evolutionary trends within this difficult group of fishes is also discussed. The use of larval forms of fishes to elucidate systematic relationships has been demonstrated in a number of groups, e.g., ceratioids (Bertlesen 1941), myctophids (Moser and Ahlstrom 1970, 1972, 1974), gonostomatids (Ahlstrom 1974), scombroids (Okiyama and Ueyanagi 1978), and serranids (Kendall 1979).

LARVAL CHARACTERS OF COTTIDS

This is a summary of important larval characters in cottids, i.e., those characters occurring only during the larval period which can be of most use in distinguishing species. These characters include preopercular spine pattern, body shape, and pigmentation. Although meristic characters may be of prime utility in identifying cottid larvae, they persist in adults and are not considered truly larval. Meristic characters for northeast Pacific cottids have been discussed by Richardson and Washington (1980) and Howe and Richardson.[3] The purpose of this summary is to point out the kinds of larval characters that are useful for identification and the spectrum in which those characters may be exhibited since cottid larvae manifest a wide diversity of form.

This summary is based on only the representatives of northeast Pacific cottid genera listed in

[3]Howe, K. D., and S. L. Richardson. 1978. Taxonomic review and meristic variation in marine sculpins (Osteichthys: Cottidae) of the northeast Pacific Ocean. Final rep., NOAA NMFS Contract No. 03-78-MO2-120, 1 January 1978 to 30 September 1978, 142 p. Northwest and Alaska Fisheries Center, National Marine Fisheries Service, NOAA, 2725 Montlake Boulevard East, Seattle, WA 98112.

Table 1. Species from areas outside the northeast Pacific are included when larvae are known because of the taxonomic information their larvae may provide. Generic level designations are used throughout the text for continuity and emphasis although larvae of all species (number of species based on the taxonomic status summary by Howe and Richardson footnote 3) in a genus may not be known. In some cases the genera are monotypic (*Chitonotus*, *Dasycottus*, *Gilbertidia*, *Leptocottus*, *Orthonopias*, *Paricelinus*, *Rhamphocottus*, *Scorpaenichthys*) and thus larval characters of the genus may readily be defined. At least some developmental stages are known for all six species of *Hemilepidotus*, providing good generic level definition. In some cases larvae of a few, but not all species within a genus are known [*Artedius* (3 species out of 7); *Gymnocanthus* (3 of 6); *Hemitripterus* (2 of 2 or 3); *Myoxocephalus* (5 of 18); *Oligocottus* (2 of 4); *Radulinus* (2 of 5); *Triglops* (3 of 9)]. In those instances, constancy of larval characters among species provides good indications of generic level definition. Larvae of *Icelinus* spp. have only been described at the generic level as none of the eight species have yet been distinguished. For some genera, larvae are known for only one of a few species: *Blepsias* (1 of 2), *Cottus* (1 of 2 brackish water species), *Icelus* (1 of 13), *Malacocottus* (1 of 5), *Nautichthys* (1 of 3), *Psychrolutes* (1 of 2). In those, generic level definition may not be as precise; however, larvae of all species appear rather distinctive and thus may be good representatives of their genera. In the following summary those genera which provide the best examples of patterns are listed in parentheses.

Principal preopercular spines typically (18 of 25 genera) number 4 (*Scorpaenichthys*, *Icelinus*, *Leptocottus*, *Enophrys*) and may vary in degree of development. Modifications of this basic pattern may occur (*Myoxocephalus*, ?*Malacocottus*) in which four main spines are present with one or two auxiliary spines. Another pattern consists of multiple preopercular spines, usually small, numbering up to ca. 25 (*Artedius*, *Clinocottus*). Sometimes only one spine is present (*Rhamphocottus*) or none (*Psychrolutes*, *Gilbertidia*). Spines in other regions of the head (particularly parietal-nuchal, postocular, posttemporal-supracleithral, opercular) may also be important.

General body shape can range from rather stubby and deep (*Artedius*, *Enophrys*) to moderately slender and elongate (*Icelinus*, *Triglops*) to globose (?*Malacocottus*). The snout can be quite rounded (*Scorpaenichthys*, *Hemilepidotus*) or pointed (*Icelinus*, *Chitonotus*). Snout to anus length can be rather short, <40% SL (standard length) (*Dasycottus*), to moderately long, >60% SL (*Rhamphocottus*), although this can change with development. The gut may appear tightly compacted (*Dasycottus*) or be distinctively coiled (*Cottus*). The hindgut may trail somewhat below the body (*Artedius*, *Clinocottus*). Unusual gut diverticula may be present (*Artedius*, *Clinocottus*). Pectoral fins may be noticeably elongated (*Nautichthys*) or fanlike early in development (*Myoxocephalus*).

Melanistic pigment patterns range from relatively unpigmented to heavily pigmented. Pigment may be variously present or absent over the head, snout, cheek, jaws, cleithral base, throat. Pigment over the dorsolateral surface of the gut may vary in intensity, ventrolateral extent, and pattern (e.g., bars, *Leptocottus*; distinct round melanophores, *Enophrys*). In some species the entire gut region is pigmented (*Paricelinus*). The ventral midline of the gut may have a distinct line of melanophores (*Cottus*, some *Myoxocephalus*) or be unpigmented (*Scorpaenichthys*). The nape may be distinctively pigmented (*Artedius*, *Enophrys*). The lateral body surface above the gut may be unpigmented (*Chitonotus*), have dorsolateral pigment not extending to the gut (*Radulinus*) or be entirely pigmented (*Scorpaenichthys*). In the tail region posterior to the anus, pigment may be absent (some *Triglops*, *Dasycottus*), present along only the ventral midline (*Artedius*, *Chitonotus*), present along only the ventral and dorsal midlines [*Gymnocanthus*, small (<8 mm) *Hemilepidotus*], or present on the lateral body surface, sometimes in combination with a ventral midline series (*Scorpaenichthys*, *Radulinus*, *Blepsias*). Number, spacing, position, and shape of ventral midline melanophores are important as is the posterior extent of lateral pigment. Melanophores may variously appear along the caudal fin base (*Paricelinus*, *Chitonotus*). Pectoral fins are generally unpigmented, but some species have heavily pigmented fins (*Psychrolutes*, *Gilbertidia*) or a pigment band along the fin margin (*Nautichthys*).

LARVAL COTTID GROUPS

Within the 25 cottid genera considered, 6 groups of genera are apparent based on shared larval characters, i.e., similarity, and 6 genera do not fit into any group (Table 2). Characters within each

TABLE 2.—Groupings of 25 cottid genera reported to occur in the northeast Pacific Ocean between Baja California and the Aleutian Islands based on shared larval characters. Group characteristics were based on representative species for which larvae are known, as listed in Table 1. Also included in the groupings is an unidentified larval type, "Cottoid Type A" of Richardson and Washington (1980) which may represent a new genus.

Group	General characteristics	Genera
1	Multiple preopercular spines, rounded snout, stubby shape, slightly trailing gut, sometimes with gut protrusions or diverticula	*Artedius*, *Clinocottus*, *Oligocottus*, *Orthonopias*
2	Four preopercular spines, pointed snout, moderately slender, postanal pigment when present usually restricted to ventral midline	*Paricelinus*, *Triglops*, *Icelus*, *Chitonotus*, *Icelinus*
3	Four principal preopercular spines or none, rounded snout, often globose shape with loose skin, pigmented pectoral fins	*Dasycottus*, *Psychrolutes*, *Gilbertidia*, ?*Malacocottus*, Cottoid Type A (new genus?)
4	Four preopercular spines, rounded snout, relatively deep bodied, ca. 4-5 mm NL at hatching, postanal pigment dorsally, ventrally, and laterally	*Scorpaenichthys*, *Hemilepidotus*
5	Four preopercular spines not pronounced, rounded snout, relatively slender, postanal pigment dorsally, ventrally, laterally, probably >7 mm NL at hatching, pectoral fins unpigmented or with pigment band near margin	*Blepsias*, *Nautichthys*
6	Four preopercular spines, rounded snout, relatively slender, no additional head spines, postanal pigment restricted to ventral midline	*Leptocottus*, *Cottus*
Ungrouped genera	*Enophrys*, *Gymnocanthus*, *Myoxocephalus*, *Radulinus*, *Rhamphocottus*, *Hemitripterus*	

group and of each ungrouped genus are summarized to facilitate recognition and minimize taxonomic and identification problems involving cottid larvae. These groupings are based on complete developmental series to the extent available, but only representative figures illustrating one point on a developmental continuum are presented (Figures 1-9). The groupings are necessarily preliminary because not all species in all genera are known as larvae. The groups described below are not arranged in any particular order. Generic designations are used as discussed in the previous section.

Group 1

This is the tightest group among the 25 genera. Included are *Artedius*, *Clinocottus*, *Oligocottus*, and tentatively *Orthonopias* (Figures 1, 2). The unique multiple preopercular spine pattern distinguishes it from all other groups or genera. [Although a complete series of *Orthonopias* has not been described and the spine pattern is unknown, small larvae (Figure 2) are very similar to *Artedius* in form and pigment characteristics and are tentatively included in this group.] The stubby body shape, rounded snout, and somewhat trailing gut are remarkably consistent within the group. Presently, identification to genus based on larval characters is still difficult and in need of better definition. Characters used to distinguish species (besides fin ray counts) include: number, spacing, and shape of ventral midline melanophores; intensity of gut pigmentation; presence of unusual gut diverticula; total number of preopercular spines and position of largest spines; number of spines (e.g., none, two, cluster) in the parietal and posttemporal-supracleithral regions; presence or absence of pigment on the nape or head.

Although the multiple preopercular spine pattern persists through the larval period, adults have four preopercular spines with the lower three reduced and the upper variously modified. Remnants of the larval serrations have been observed only in adult *A. notospilotus* (Howe[4]). It is unclear which four spines of the larvae persist in adults.

Group 2

This is also a rather cohesive group (Figure 3) consisting of slender forms with pointed snouts and four prominent preopercular spines [*Paricelinus*, *Triglops*, *Icelus* (tentatively), *Chitonotus*, *Icelinus*]. This general body shape is remarkably similar among genera and is not found in any other genera considered. All have a relatively short snout to anus distance. Postanal ventral midline pigment is usually present (absent in one species of *Triglops*) with some additional melanophores along the caudal fin base. Dorsal midline pigment is usually absent except for a few spots in some *Icelinus* and possibly a row in some late stage *Triglops*. Generic differences include degree of gut pigmentation (e.g., darkest in *Paricelinus* and some *Triglops*), number and position of ventral midline melanophores, and degree of head spination (e.g., postocular spines in *Paricelinus* and *Triglops*).

[4]K. D. Howe, Ph.D. candidate, Department of Fisheries and Wildlife, Oregon State University, Corvallis, OR 97331, pers. commun. September 1978.

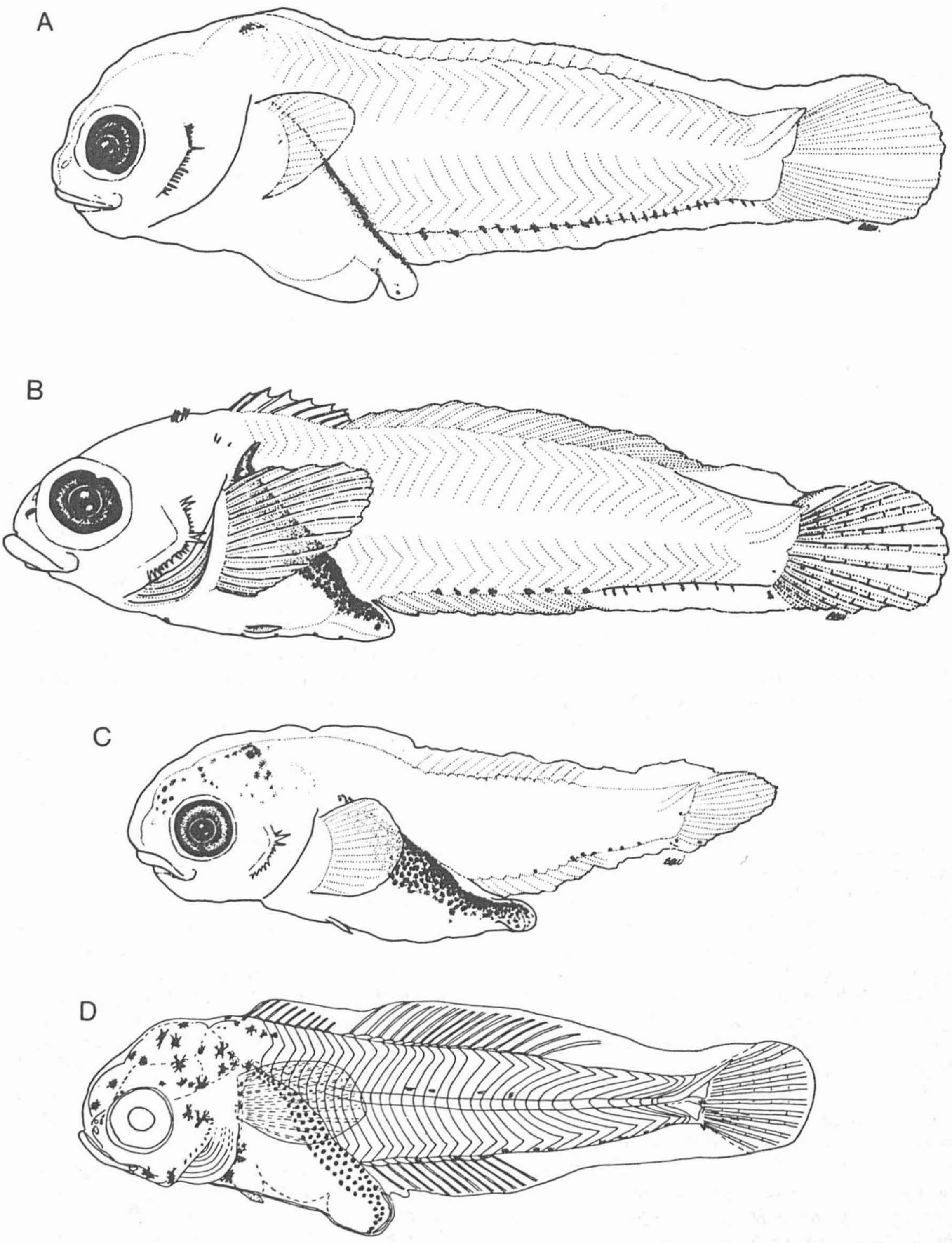

FIGURE 1.—Larvae of A) *Artedius harringtoni* (7.3 mm SL), B) *Artedius* Type 2 (9.9 mm SL), C) *Clinocottus acuticeps* (7.6 mm SL), D) *Oligocottus maculosus* (9.2 mm TL) (A-C, Richardson and Washington 1980; D, Stein 1973).

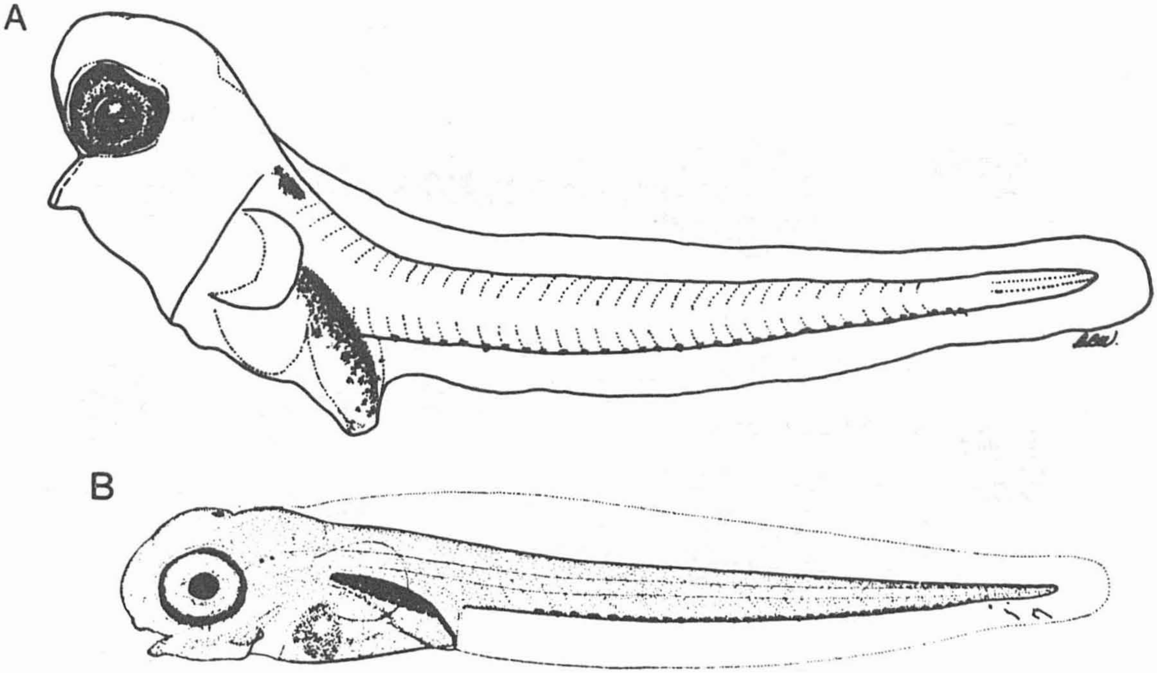

FIGURE 2.—Larvae of A) *Artedius harringtoni* (3.0 mm NL) and B) *Orthonopias triacis* (≈4 mm) (A, Richardson and Washington 1980; B, Bolin 1941).

The tentative placement of *Icelus* with this group is of interest as it has been considered to constitute a distinct family, the Icelidae (Jordan 1923; Greenwood et al. 1966) based on the presence of scales in adults. Although larvae of *Icelus* are known to the author only from descriptions in the literature (Table 1), they strongly resemble other members of this group in form and preopercular spine pattern. Inclusion of *Paricelinus* is also of interest as it has been considered to be a rather distinct and primitive form (Bolin 1947). It possesses five pelvic soft rays, the ancestral condition, whereas the number of soft rays is reduced to three or two in other members of the group.

Group 3

Group 3 (Figure 4) consists of the "psychrolutid" cottids [*Dasycottus*, *Psychrolutes*, *Gilbertidia*, ?*Malacocottus*,[5] "Cottoid Type A" (new genus?)] often considered a separate family (Nelson 1976). ["Cottoid Type A" may possibly be *Psychrolutes phrictus* but positive identification awaits additional specimens—see Discussion by Richardson and Washington (1980). If it is *P. phrictus*, larval evidence indicates that the species is incorrectly placed and that a new northeast Pacific genus of cottid is in need of description.] This group is not as cohesive as the two previous groups. The most distinctive character of Group 3 is the pattern of pigmentation of the pectoral fin, a pattern not found in any of the other genera considered. In all, at least the basal portion of the fin develops pigment with the entire fin pigmented in *Psychrolutes*, *Gilbertidia*, and small (<9 mm SL) ?*Malacocottus*. Pigment on small (<8 mm SL) *Dasycottus* is restricted to the inside surface of the pectoral fin base but later it develops distally on the outer surface. (The pigment band near the margin of the elongated pectoral fin of *Nautichthys* is a very different pattern.) Only *Dasycottus* and ?*Malacocottus* develop four preopercular spines, the latter genus with an accessory spine at the base of the second spine. All but the more slender *Dasycottus* have relatively rounded snouts and deep bodies. Both ?*Malacocottus* and "Cottoid Type A"

[5]Identification of larvae is tentative pending resolution of taxonomic problems of adults at the generic level [see Howe and Richardson footnote 3 and also Richardson, S. L., and C. E. Bond. 1978. Two unusual cottoid fishes from the northeast Pacific. Unpubl. manuscr., 6 p. + 25 figs. (Available from senior author.) (Paper presented at the American Society of Ichthyologists and Herpetologists, 1978.)]

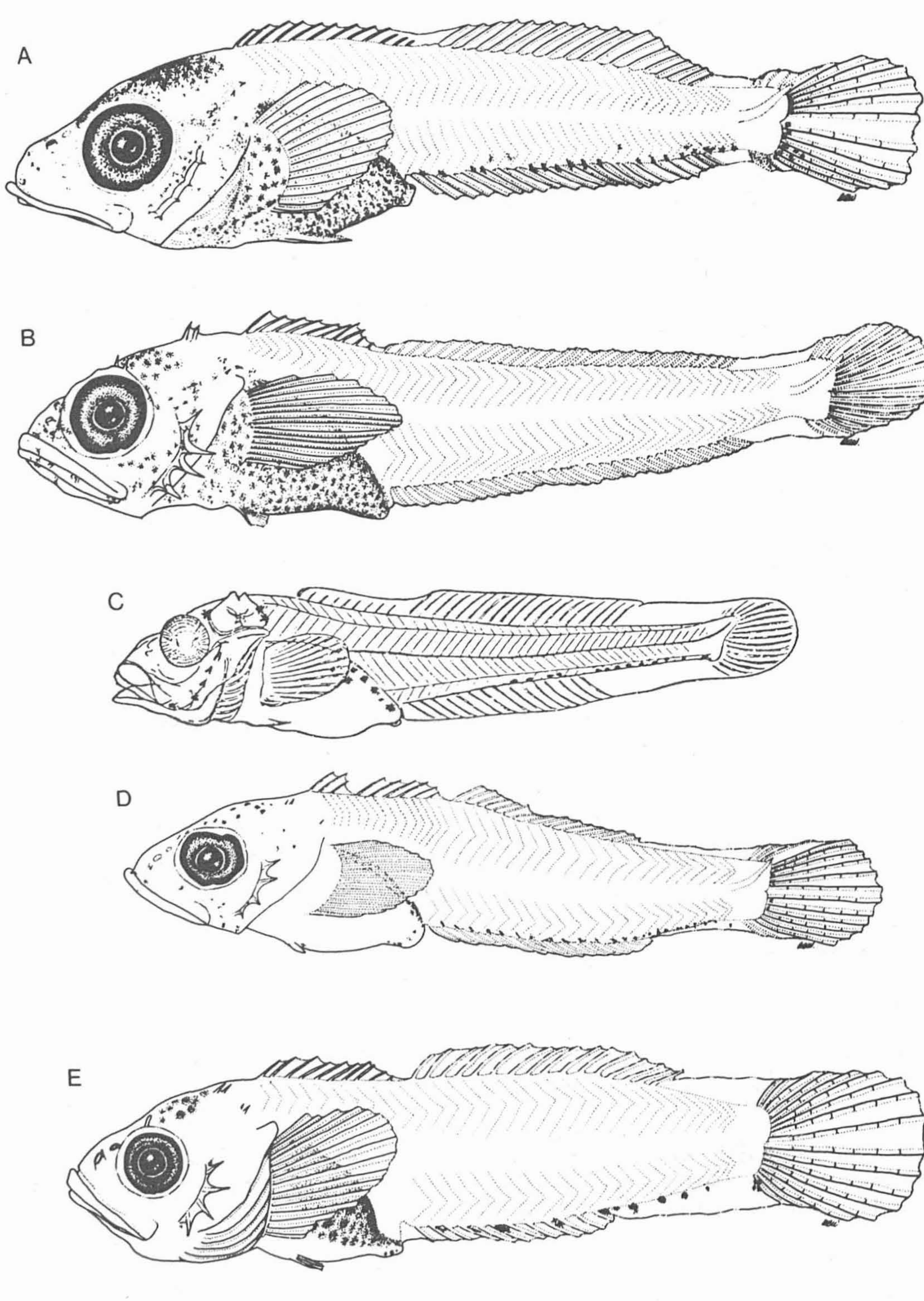

FIGURE 3.—Larvae of A) *Paricelinus hopliticus* (13.8 mm SL), B) *Triglops* sp. (15.4 mm SL), C) *Icelus bicornis* (25 mm), D) *Chitonotus pugetensis* (11.5 mm SL), E) *Icelinus* sp. (13.8 mm SL) (A, B, D, E, Richardson and Washington 1980; C, Ehrenbaum 1905-9).

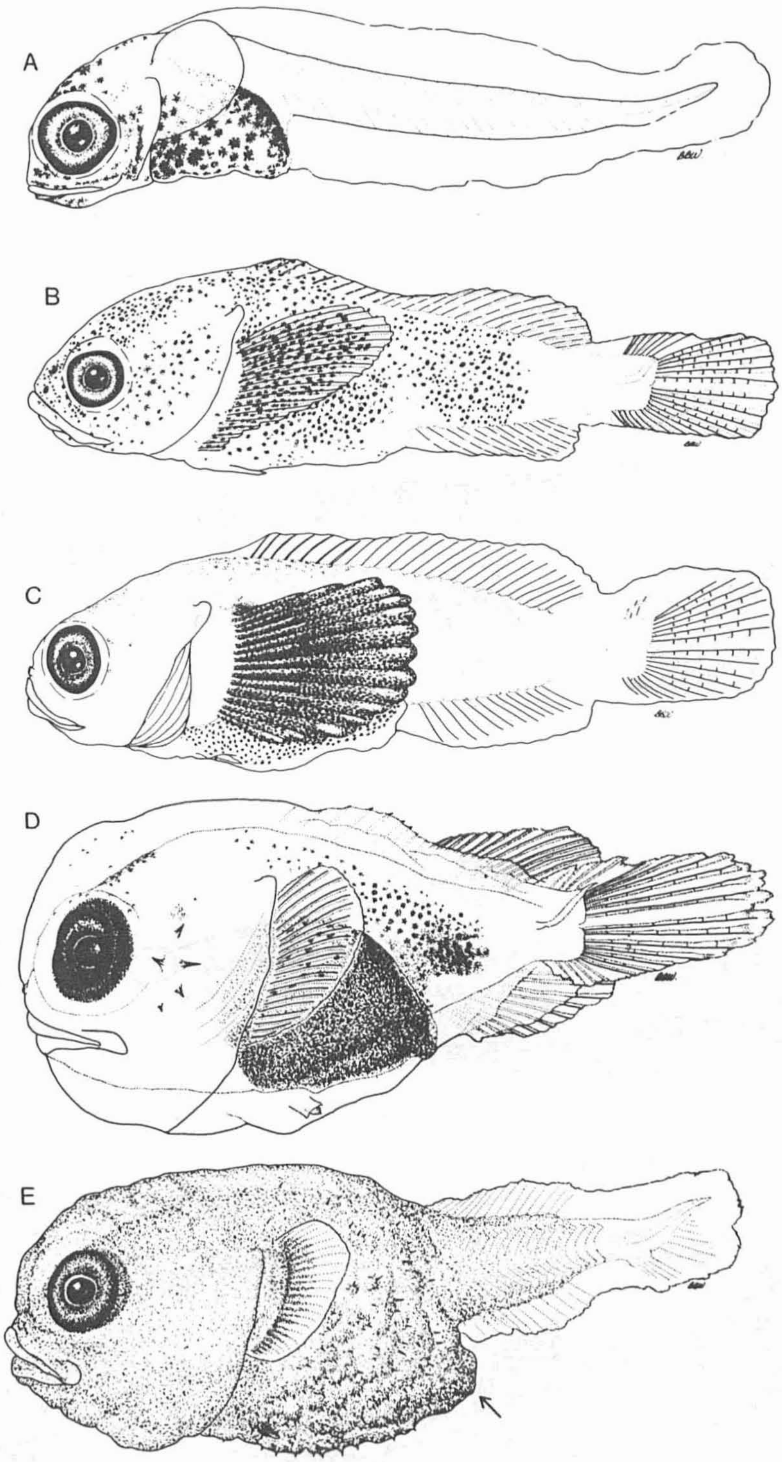

FIGURE 4.—Larvae of A) *Dasycottus setiger* (8 mm NL), B) *Psychrolutes paradoxus* (transforming, 13 mm SL), C) *Gilbertidia sigalutes* (13 mm SL), D) ?*Malacocottus zonurus* (10.4 mm SL), E) Cottoid Type A (9.8 mm SL) (A-D, original illustrations; E, Richardson and Washington 1980).

develop a pronounced globose appearance with an outer bubble of skin. Small larvae of all forms have head and gut pigment and "Cottoid Type A" also has lateral pigment posterior to the anus. Some lateral pigment develops later in all but *Dasycottus*. "Cottoid Type A" has unique "thumbtack" prickles covering the belly region. The pelvic fins of ?*Malacocottus* and "Cottoid Type A" often appear to be withdrawn into pockets of skin.

Group 4

Group 4 (Figure 5) includes larvae with four preopercular spines, conspicuously rounded snouts, and relatively deep bodies with rather heavy pigmentation, except at the smallest sizes (*Scorpaenichthys*, *Hemilepidotus*). Differences between genera include the longer gut and the preanal fin fold of *Scorpaenichthys* and the increased head spination of *Hemilepidotus* (parietal, nuchal, postocular, posttemporal-supracleithral). Pigmentation is generally heavier in *Scorpaenichthys* than in *Hemilepidotus* of comparable size. It is initially concentrated along the dorsal and ventral midlines, particularly in *Hemilepidotus*, filling in laterally with development. Larvae of both are neustonic.

The two genera in this group are certainly more

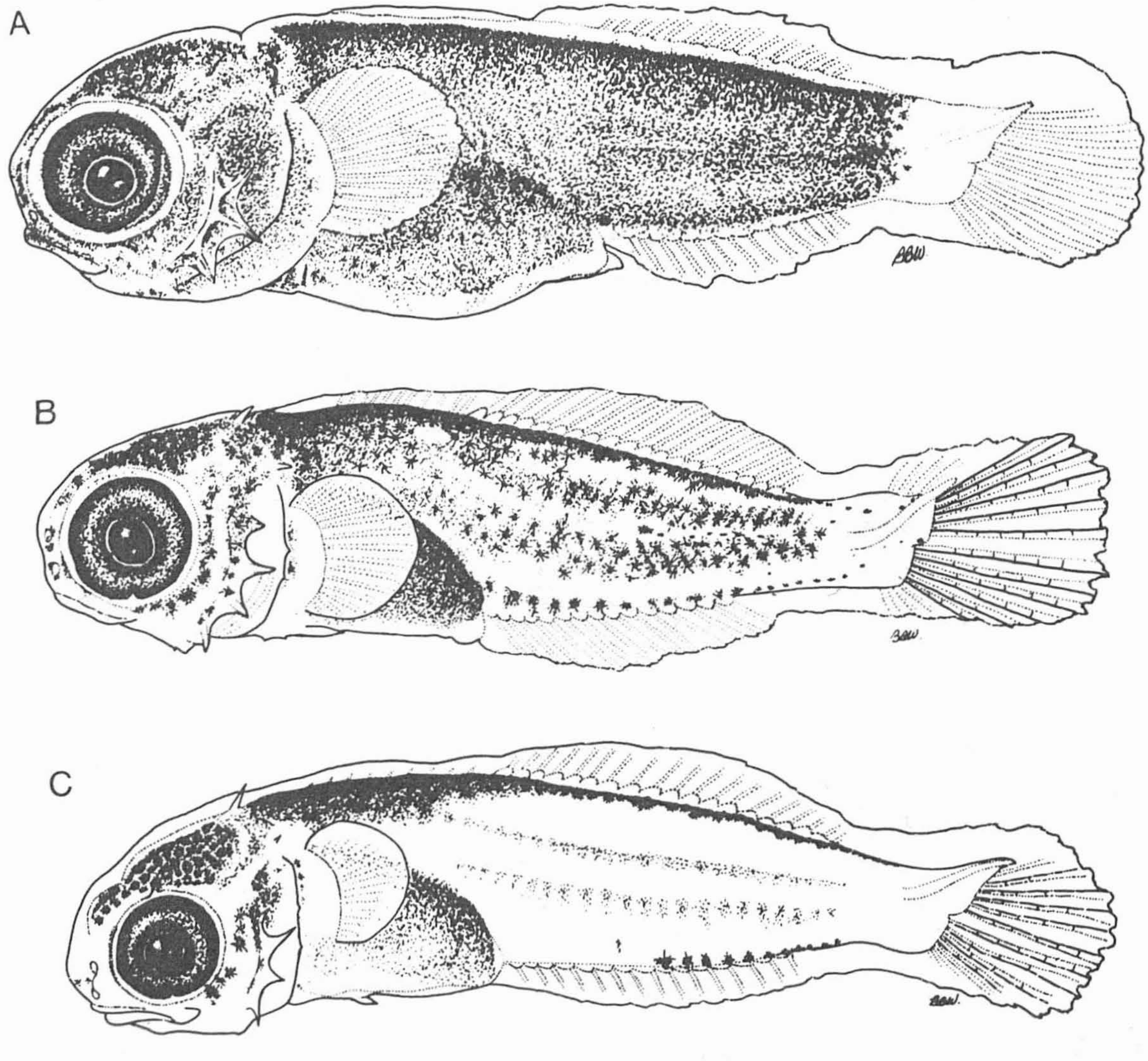

FIGURE 5.—Larvae of A) *Scorpaenichthys marmoratus* (8.7 mm SL), B) *Hemilepidotus spinosus* (11.0 mm SL), C) *H. hemilepidotus* (10.7 mm SL) (A-C, Richardson and Washington 1980).

similar to each other than to any other cottids considered, although *Scorpaenichthys* was given familial status in the past (Jordan 1923; Tarenets 1941).

Group 5

This group consists of two elongated, slender-bodied genera, *Blepsias* and *Nautichthys* (Figure 6). Both hatch at a relatively large size, >7 mm NL (notochord length). Both have rounded snouts, relatively heavy pigmentation, and four preopercular spines that never become pronounced and sharp. *Nautichthys* (at least *N. oculofasciatus*) develops greatly elongated pectoral fins soon after hatching, each of which develops a pigment band near its distal margin.

The genera *Blepsias* and *Nautichthys* have been placed in a separate family, Blepsiidae, in the past (Jordan 1923).

Group 6

Group 6 (Figure 7) contains *Leptocottus* and *Cottus* (as based on the brackish water species *C. asper*). They share several characters, including the relatively slender body, rounded snout, four preopercular spines, absence of other head spines, ventral midline pigment along gut, and postanal pigment restricted to ventral midline. Both hatch and transform at similar sizes, ca. 3-4 mm NL and ca. 10-12 mm SL, respectively. *Leptocottus* has a unique gut pigment pattern of bars, and *Cottus* has a distinctively coiled gut.

Ungrouped Genera

Enophrys (Figure 8) has four pronounced preopercular spines, rounded snout, deep stubby shape, pigmented nape, and postanal pigment only along the ventral midline. It has a postocular spine and opercular spines, and a preanal fin fold. Melanophores over the gut are distinctively round in shape and densely concentrated. This suite of larval characters is not shared by any other genus. *Enophrys* bears some resemblance to Group 6 (*Leptocottus-Cottus*) but differs too much to be part of it. The deep body, bulging gut, and pigmented nape somewhat resemble Group 1 (*Artedius* et al.) but spine patterns differ drastically. Larvae of *E. bubalis* and *E. lilljeborgi* from the North Atlantic (Table 1) are extremely similar to *E. bison* from the northeast Pacific.

Gymnocanthus (Figure 8) apparently never develops pronounced preopercular spines, according to the literature (Table 1). Larvae of *G. tricuspis*

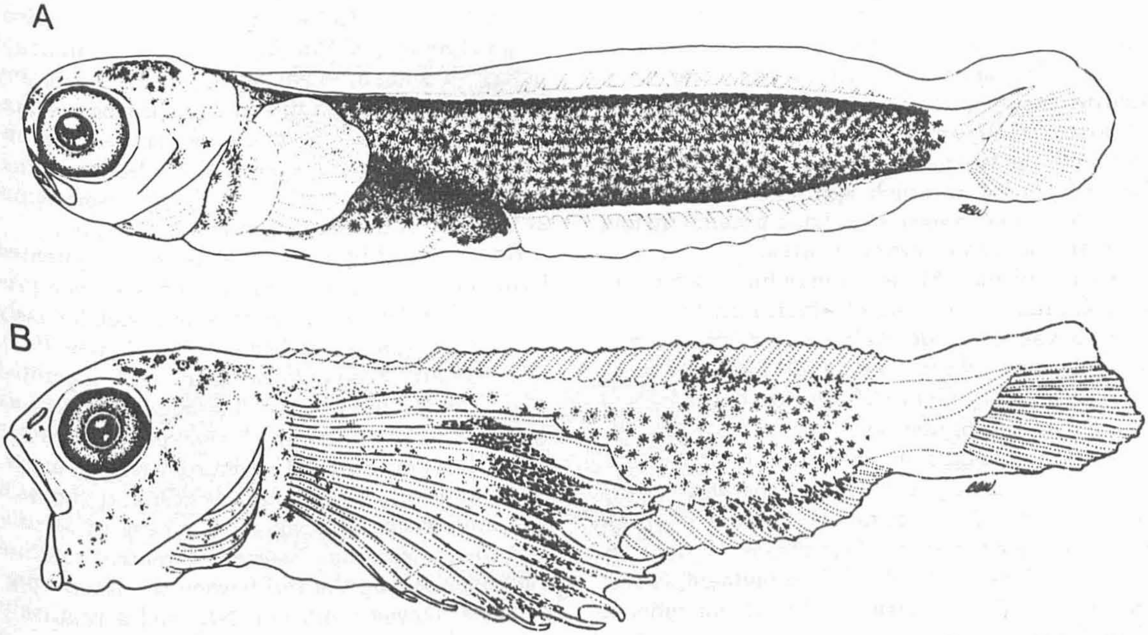

FIGURE 6.—Larvae of A) *Blepsias cirrhosus* (11 mm NL) and B) *Nautichthys oculofasciatus* (11.7 mm NL) (A, original illustration; B, Richardson and Washington 1980).

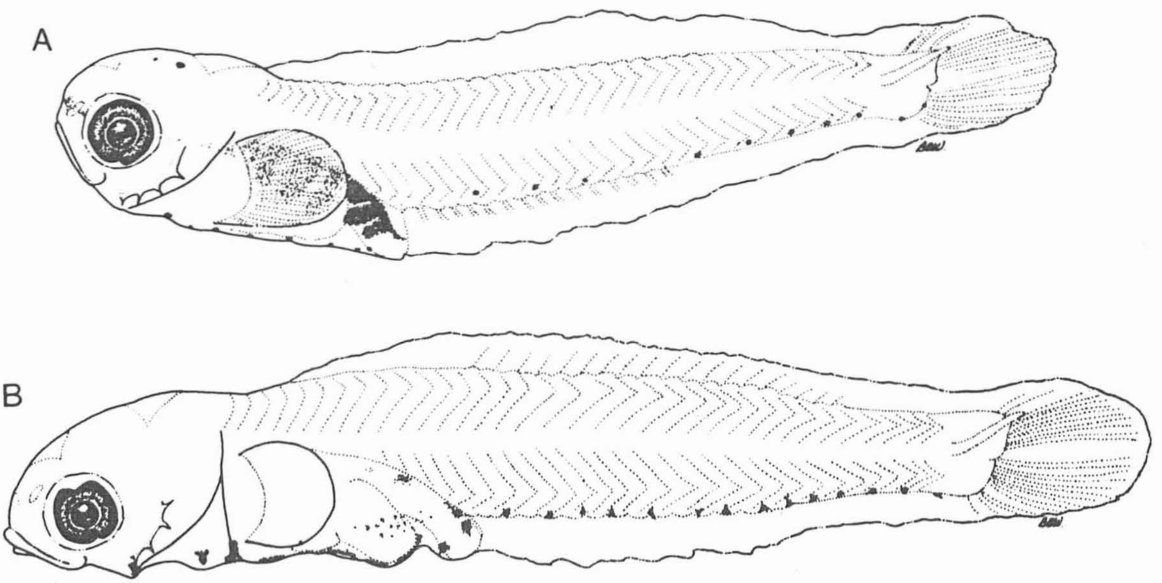

FIGURE 7.—Larvae of A) *Leptocottus armatus* (8.1 mm NL) and B) *Cottus asper* (8.2 mm SL) (A, B, Richardson and Washington 1980).

develop three very small preopercular spines, visible only on stained specimens, and the spines of 14-15 mm *G. ventralis* are barely perceptible. *Gymnocanthus* is relatively slender with a semipointed snout; it develops dorsal (at least *G. tricuspis*), ventral, and lateral midline pigment. Although it shares some characters with *Myoxocephalus*, grouping the two does not seem warranted. The spacing of the ventral series of midline melanophores somewhat resembles the situation in *Myoxocephalus*. General shape of species of the two genera is also similar although *Myoxocephalus* is much spinier. Some figures indicate that *Gymnocanthus* has a preanal fin fold as do at least some *Myoxocephalus*.

Myoxocephalus (Figure 8) may have four to six preopercular spines, two of which may be auxiliary. Larvae are moderately slender with a semipointed snout. Two distinct larval forms (subgenera?) occur in the genus. Those with dense lateral pigment in the region posterior to the anus (*M. polyacanthocephalus*, *M. scorpius*) and those with only ventral midline pigment postanally (*M. aeneus*, *M. octodecemspinosus*). Another relatively unpigmented species, *M. quadricornis* (marine form), develops a lateral midline pigment series. The spacing of the ventral midline melanophores is similar in all species as is gut pigment. The fan-shaped pectoral fin is obvious early in development (at least in some species) and a preanal fin fold is present (in some or maybe all species). The pattern of preopercular spination is unusual. All species apparently have four principal spines but some may have one or two posteriorly directed auxiliary spines anterior to and near the base of the second principal spine and/or an auxiliary spine ventral and adjacent to the fourth principal spine (Laroche[6]). Development of this unusual pattern has not been adequately described for any species of *Myoxocephalus* and needs closer examination. Auxiliary preopercular spines are unknown in other genera except ?*Malacocottus*, which has an anteriorly directed accessory spine at the base of the second preopercular spine.

Radulinus (Figure 9) is a heavily pigmented form with four preopercular spines (never pronounced), relatively pointed snout, slender body (*R. boleoides* is deeper bodied than *R. asprellus*), and long gut. It shares the characters of pointed snout and slender body with Group 2 (*Paricelinus* et al.) but differs too much (longer gut, heavier pigmentation, reduced prominence of preopercular spines) to be part of that group. It shares a few similarities with the dark species of *Myoxocephalus*, including a series of ventral midline melanophores on the tail beyond the lateral pigment (in larvae <8-9 mm NL) and a relatively

[6]J. L. Laroche, Research Assistant, Gulf Coast Research Laboratory, East Beach Drive, Ocean Springs, MS 39564, pers. commun. September 1978.

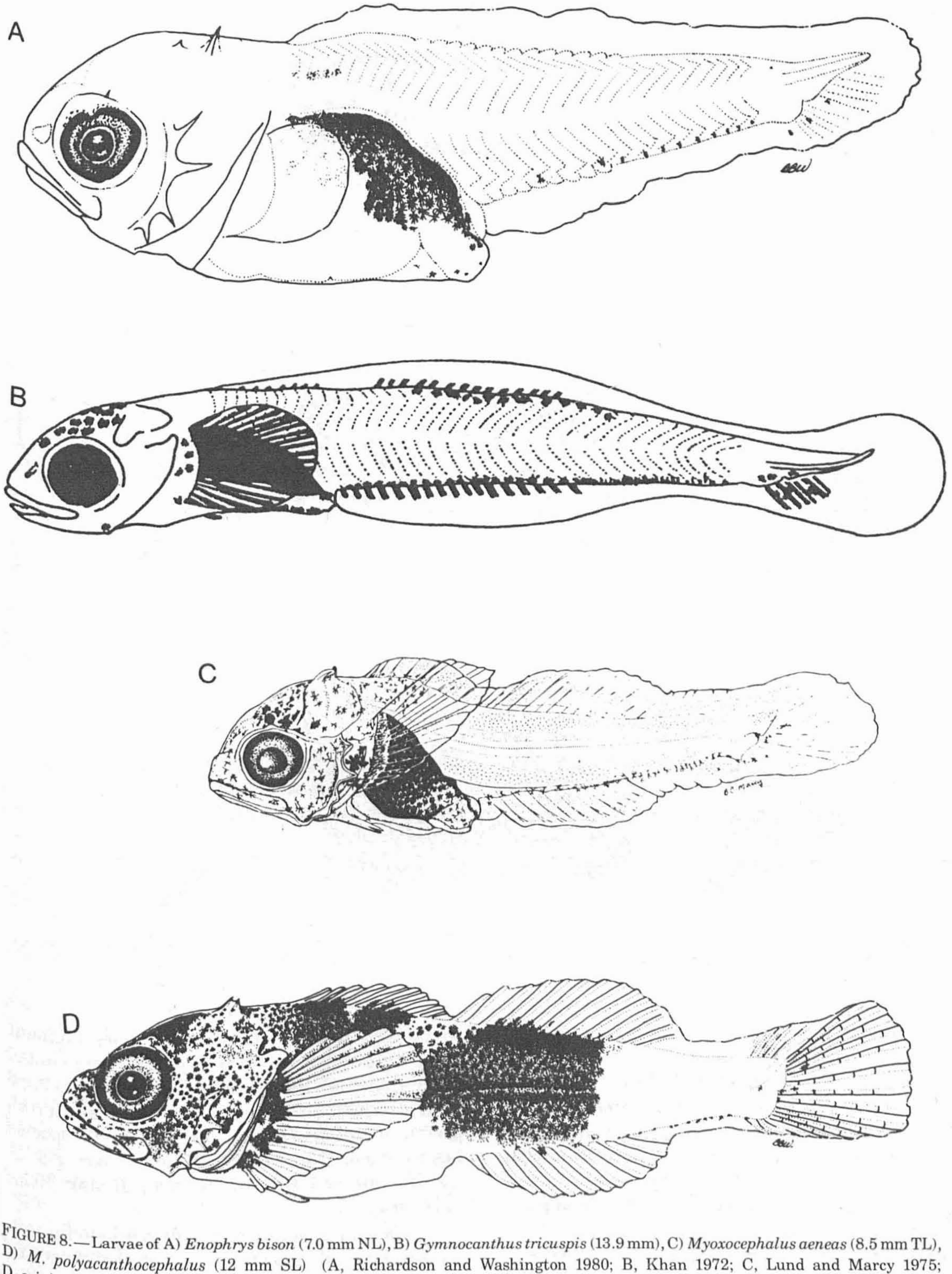

FIGURE 8.—Larvae of A) *Enophrys bison* (7.0 mm NL), B) *Gymnocanthus tricuspis* (13.9 mm), C) *Myoxocephalus aeneas* (8.5 mm TL), D) *M. polyacanthocephalus* (12 mm SL) (A, Richardson and Washington 1980; B, Khan 1972; C, Lund and Marcy 1975; D, original illustration).

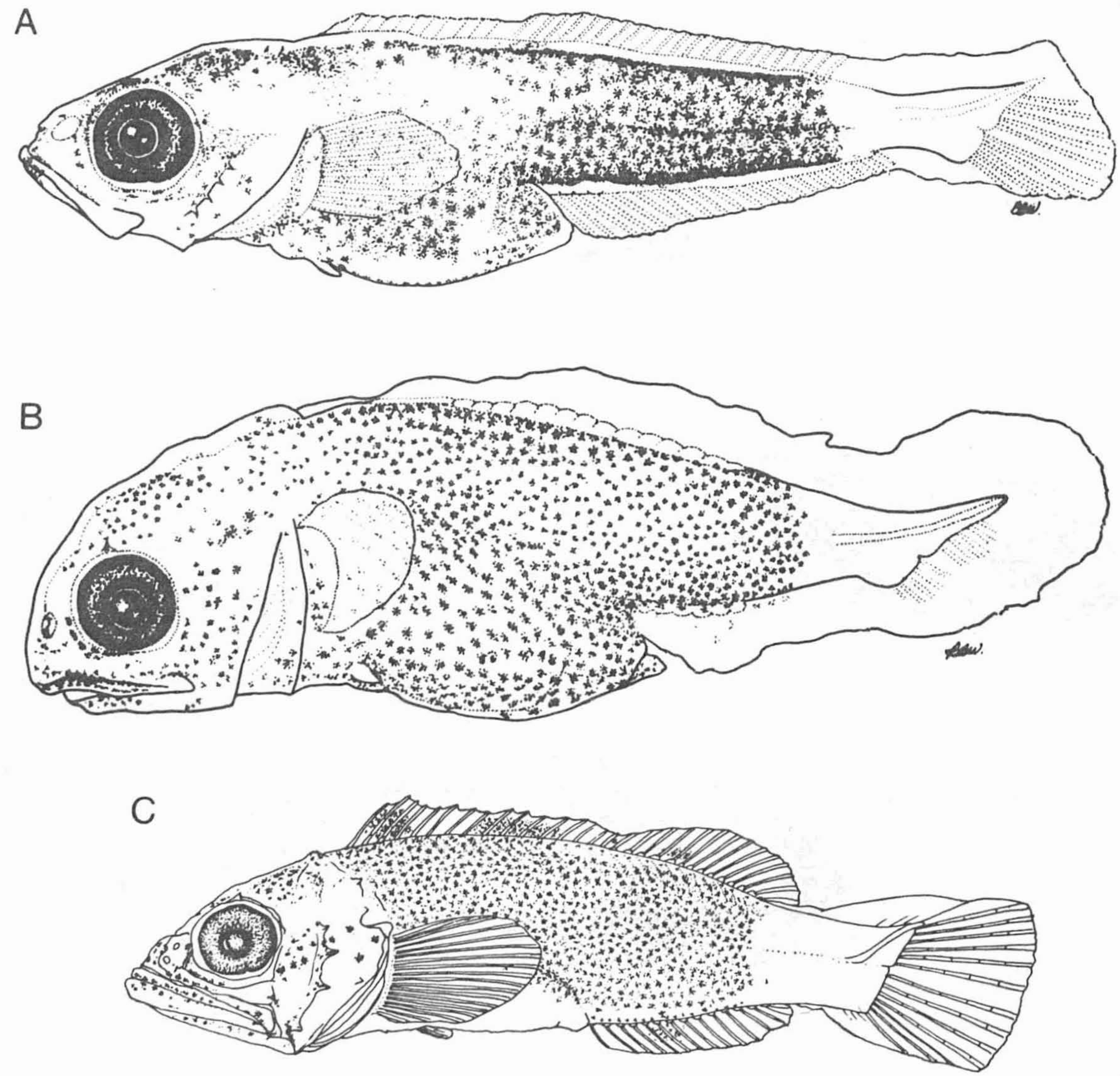

FIGURE 9.—Larvae of A) *Radulinus asprellus* (10.9 mm NL), B) *Rhamphocottus richardsoni* (8.4 mm NL), C) *Hemitripterus villosus* (17.4 mm SL) (A, B, Richardson and Washington 1980; C, Okiyama and Sando 1976).

unpigmented area on the body above the abdominal cavity. Small larvae also resemble *Scorpaenichthys* except that they have a distinct lateral midline series of melanophores and soon develop a pointed snout and more slender body.

Rhamphocottus (Figure 9) is one of the most aberrant cottid forms. It develops only one preopercular spine, an unusual snout, a deep body, heavy pigmentation, and a preanal fin fold. At small sizes, ca. 6-7 mm NL, it bears some resemblance to *Scorpaenichthys* in pigmentation and shape, but it has a longer gut, more pigment ventrally along the head and gut, and a pigmented preanal fin fold. By 8-9 mm SL, the distinct shape of *Rhamphocottus* is obvious and spinelike prickles develop over the body. The single species has been considered to represent a separate family (Jordan and Evermann 1898; Jordan 1923; Taranets 1941).

Hemitripterus (Figure 9) is also a heavily pigmented and distinct form. Based on the literature (Table 1), it has four preopercular spines, a moderately pointed snout, relatively deep body, and long gut. Larvae are quite large, ca. 12-14 mm NL, at hatching. The larvae of *H. americanus* from the Atlantic and *H. villosus* from Japan (Table 1) are very similar. The heavy body pigment is a character shared with a number of apparently unrelated cottid genera. The genus was considered to constitute a separate family, Hemitripteridae, by Jordan (1923) and Taranets (1941).

DISCUSSION

The present state of cottid systematics is confused and the group and its allies are in need of intensive study (Nelson 1976; Howe and Richardson footnote 3). Family limits are not well defined (compare, e.g., Jordan 1923; Berg 1940; Taranets 1941; Greenwood et al. 1966; Bailey et al. 1970; Nelson 1976). Some genera still need revision and potential new species remain to be described (e.g., Nelson 1977; Richardson and Washington 1980; Howe and Richardson footnote 3). Studies of intergeneric relationships have been few (e.g., Regan 1913; Taranets 1941; Bolin 1947; Watanabe 1960) and these had many disagreements (Table 3). Jordan and Evermann's (1898:1879-1800) comment of North American Cottidae still has merit, "The family is an extremely varied one which cannot be readily thrown into subordinate groups. Almost every species has an individuality of its own...."

Because of the confused state of cottid systematics it seems reasonable to consider whether this preliminary summary of 25 genera of cottid larvae may provide insight into intergeneric relationships within the group. Whether these phenetically derived larval groupings are indicative of relationships among cottid genera depends on whether the groups actually possess a set of shared, derived characters. Determination of derived states of larval characters is difficult when dealing with such a diverse group as the cottids and their allies because the larvae of many species are still unknown and complete developmental series have not been described for many other species. Such determinations are further hindered by the confused state of adult cottid systematics. Although an in depth analysis of derived character states is beyond the scope of this study, consideration of several factors allows discussion of the potential significance of, and possible relationships within, at least some of the larval cottid groups described here. Larval characters such as spine patterns, relative body form, and pigmentation have been used to demonstrate or clarify systematic relationships in other groups of fishes, e.g., scorpelarchids (Johnson 1974), gonostomatids (Ahlstrom 1974), myctophids (Moser and Ahlstrom 1974), myctophiforms (Okiyama 1974), marine teleosts in general (Ahlstrom and Moser 1976), bothids (Futch 1977), scombroids (Okiyama and Ueyanagi 1978), serranids (Kendall 1979). In these studies, similarity of larval form has been in remarkable agreement with relationships implied from adult characters. Although larval characters have not been used previously as indicators of relationship (i.e., based on synapomorphies) among cottids, it seems highly probable that at least some of these characters would be as useful in cottids as in other groups of fishes. In addition, if the cottids were derived from an ancestral stock related to the Scorpaenidae, the most generalized group in the Order Scorpaeniformes (Gill 1889; Taranets 1941; Bolin 1947) and if Bolin's (1947) ancestral cottid form is valid and *Scorpaenichthys* closely resembles the primitive condition, then primitive or derived states of at least some larval characters of cottids can be postulated. Primitive states of larval characters may include four strong preopercular spines, relatively deep but compact body, compact gut, lack of gut diverticula, possession of a preanal fin fold, rounded snout, relatively short pectoral fin. Derived character states may include reduced size and/or numbers of preopercular spines or modification of the basic pattern of four, slender or globose body, trailing gut, presence of gut diverticula, no preanal fin fold, semipointed or pointed snout, elongated pectoral fin. Pigment patterns are more difficult to evaluate as presumably they may possibly reflect responses to habitat or may be more easily modified genetically than other morphological characters. This idea has been generally discredited in other groups where larval characters have been used to imply relationships (e.g., Ahlstrom 1974; Moser and Ahlstrom 1974; Kendall 1979) as pigment patterns have substantiated findings based on other characters. Recent experiments on larvae of the zebrafish, *Brachydanio rerio*, (Milos and Dingle 1978) have demonstrated constancy in numerical regulation of melanophores which indicates larval pigment patterns may not be as plastic as once thought. Among the cottids, *Scorpaenichthys* is heavily pigmented but *Enophrys*, also considered to be a relatively primitive form (Sandercock and Wilimovsky 1968), is not. Heavy pigmentation seems to be related to a neustonic habitat in some (e.g., *Scorpaenichthys*, *Hemilepidotus*) but not others (e.g., *Radulinus*). Relative constancy of pigment pattern (such as presence or absence of lateral pigment posterior to the anus) within a group used in conjunction with other characters, however, may provide additional evidence for within-group relationships.

If this line of reasoning and these assumptions are valid, then certain trends seem apparent which may be indicative of relationships. Group 1 (*Artedius* et al.) appears to be a natural group sharing a number of derived characters not present in any other group or genus (i.e., multiple preopercular spines, somewhat trailing gut, unusual gut diverticula, or at least bulging guts). A preanal fin fold is apparently absent and pigment pattern is relatively constant. The grouping agrees with findings of Taranets (1941), in part, and Bolin (1947), who considered the genera to be closely related (Table 3). It seems to be a rather specialized group as Bolin (1947) implied, and, based on the distinctiveness of larval characters, may warrant consideration at possibly the subfamilial level.

Group 2 (*Paricelinus* et al.) shares the derived slender body form with pointed snout, and also possesses relative constancy of pigmentation, i.e., no lateral pigment. Relationships among at least some of the genera in this group have been implied previously (Table 3). The distinctiveness of larval form within this group suggests a separate lineage; this group may warrant possible subfamilial status.

In Group 3, all but *Dasycottus* share a highly modified larval form tending in degrees toward globose. The constancy of the pigmented pectoral fin is unique among all groups or genera considered. With the possible exception of *Dasycottus*, the genera appear to bear at least some relationship to each other.

Group 4 is the most generalized in that a number of primitive character states are exhibited and relationships cannot be assessed on given present

TABLE 3.—Intergeneric relationships of cottids as interpreted by A = Regan (1913), B = Taranets (1941), C = Bolin (1947), and D = Watanabe (1960). Included are only those 25 northeast Pacific genera for which larvae are known and discussed in this paper. Parentheses indicate a more distant relationship.

Genus	*Artedius*	*Blepsias*[1]	*Chitonotus*	*Clinocottus*	*Cottus*	*Dasycottus*	*Enophrys*	*Gilbertidia*[4]	*Gymnocanthus*[5]	*Hemilepidotus*[6]	*Hemitripterus*	*Icelinus*	*Icelus*	*Leptocottus*	*Malacocottus*	*Myoxocephalus*	*Nautichthys*	*Oligocottus*	*Orthonopias*	*Paricelinus*	*Psychrolutes*	*Radulinus*	*Rhamphocottus*[7]	*Scorpaenichthys*[8]	*Triglops*[9]
Artedius	···																								
Blepsias[1]		···																							
Chitonotus	B,[2](C)		···																						
Clinocottus	B,[3]C			···																					
Cottus					···																				
Dasycottus						···																			
Enophrys					A		···																		
Gilbertidia[4]						B		···																	
Gymnocanthus[5]									···																
Hemilepidotus	(C)		(C)							···															
Hemitripterus[6]		(A),D									···														
Icelinus	B,[2](C)		B,C							(C)		···													
Icelus	B[2]		B							D		A,B	···												
Leptocottus					B		C							···											
Malacocottus						B,D		B							···										
Myoxocephalus							B									···									
Nautichthys		A,C,D									(A),D						···								
Oligocottus	B,[3]C			B,C	A		A											···							
Orthonopias	B,[3]C			B,C														B,C	···						
Paricelinus																				···					
Psychrolutes						B		B							B						···				
Radulinus	(C)		C							(C)		C										···			
Rhamphocottus[7]												A	A										···		
Scorpaenichthys[8]										A										(C)				···	
Triglops[9]												A	A										A		···

[1]Considered in family Blepsiidae by Taranets (1941).
[2]*Artedius* as *Ruscarius*, *Ruscariops* of Taranets (1941).
[3]*Artedius* including *Arylas*, *Allartedius*, *Astrolytes*, *Parastrolytes* of Taranets (1941).
[4]Considered in subfamily Gilbertinae by Watanabe (1960).
[5]Considered in subfamily Gymnocanthinae by Watanabe (1960).
[6]Considered in family Hemitripteridae by Taranets (1941).
[7]Considered in family Rhamphocottidae by Taranets (1941).
[8]Considered in order Nototheniiformes by Taranets (1941).
[9]Considered in subfamily Triglopsinae by Watanabe (1960).

knowledge. Group 5 shares derived character states of a very elongate, slender body form and reduced prominence of preopercular spines; it also exhibits relative constancy in pigment pattern suggesting relationships between the genera. The relatively large hatching size (>7 mm NL) of larvae in Group 6 represents another specialization indicative of relationship; such a large size is not known in any of the other genera except *Hemitripterus* whose larvae are ca. 12-14 mm NL at hatching. Group 6 genera share a somewhat elongate form and constancy of pigmentation, i.e., lack of lateral pigment, although these characters alone do not provide strong evidence of relationship. That the six ungrouped genera did not share a set of derived characters suggests that they bear no close relationship with one another.

In summary, this preliminary examination of larval characters within 25 genera of cottids has provided some new insights into cottid systematics. Larval evidence seems to support current concepts of generic limits in most instances (e.g., *Enophrys*, *Hemitripterus*, *Hemilepidotus*) and has indicated a potentially new northeast Pacific genus represented by "Cottoid Type A." Larval characters offer support for the distinctiveness of some genera (e.g., *Rhamphocottus*) and strong relationships among others (e.g., the *Artedius* group). Some of the larval groupings discussed here tend to support previously implied relationships within the cottids (compare Tables 2 and 3) but some important differences seem apparent [e.g., the distinctiveness of Group 1 demonstrated herein; the separation of *Artedius* and *Icelus*, once considered closely related (Jordan 1923); the relationship of *Paricelinus*, generally considered a primitive and rather distinct form (Bolin 1947; Sandercock and Wilimovsky 1968), with other members of Group 2; the apparent relationship of *Icelus* to other genera in Group 2 and its questionable placement in a separate family (Jordan 1923; Greenwood et al. 1966); the distinctiveness of *Radulinus*, previously considered related to *Chitonotus* and *Icelinus* (Bolin 1947)]. Because of the wide diversity of form among cottid larvae, they offer great potential for helping to clarify relationships and evolutionary trends within this difficult group of fishes. However, larvae of many species remain to be described (rearing may be the best approach), generic limits of larval characters must be defined, and developmental sequences including osteology need to be examined before that potential can be fully realized.

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