Argentinoidei: Development and Relationships

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THE argentinoid fishes as here discussed have been considered a suborder by Cohen (1964b) and many other authors and a super-family of an expanded suborder that also includes the alepocephaloids by Greenwood and Rosen (1971). The latter group is not treated at length in this book, because little information on alepocephaloid ELH stages has appeared since Beebe's (1933a) survey which showed they hatch from large eggs and have direct development. The argentinoids *sensu strictu* appear to be monophyletic on the basis of four derived characters. One character concerns the development of rays in the finfold of the larva and is described later in this paper. A second character is the development of pustules on the inner surface of the chorion (not known for opisthoproctids). A third character relates to the swimbladder, which, when present, is served by a unique kind of rete mirabile, first described by Fange (1958) and further investigated by Marshall (1960) who named these structures micro-retia mirabilia. A fourth unique character, and one which never has been adequately studied and documented, is the tendency in the group for the vomer and palatines to assume the functions of the premaxillary and maxillary.

TABLE 38. LITERATURE REFERENCES FOR ONTOGENETIC STAGES OF ARGENTINOIDS.

Species	Egg	Larva	Transformation stage
Argentinidae			
Argentina elongata	Robertson, 1975a	—	—
A. silus	Schmidt, 1906c	Holt, 1898; Schmidt, 1906c	—
A. sphyraena	Sanzo, 1931d	Schmidt, 1906c; Sanzo, 1931d	Schmidt, 1906
Glossanodon leioglossus	Sanzo, 1931d	Schmidt, 1918; Sanzo, 1931d	Sanzo, 1931d
G. polli	—	—	Poll, 1953
G. semifasciatus	Nishimura, 1966	Nishimura, 1966	Nishimura, 1966
Microstoma microstoma	Sanzo, 1931d	Lo Bianco, 1903; Schmidt, 1918; Sanzo, 1931d	Schmidt, 1918
Nansenia groenlandica	—	Schmidt, 1918	Schmidt, 1918
N. oblita	Sanzo, 1931d	Schmidt, 1918; Sanzo, 1931d	Schmidt, 1918
Xenopthalmichthys danae	—	—	Bertelsen, 1958
Bathylagidae			
Bathylagus antarcticus	Yefremenko, 1982	Yefremenko, 1979a, 1983	—
B. euryops	—	Brauer, 1906; Tåning, 1931	Tåning, 1931
B. longirostris	—	Ehrenbaum, 1905–09; Murray and Hjort, 1912; Roule and Angel, 1930; Beebe, 1933b	Beebe, 1933b
B. nigrigenys	Pertseva-Ostroumova and Rass, 1973	Pertseva-Ostroumova and Rass, 1973	—
B. ochotensis	—	Ahlstrom, 1972b	Ahlstrom, 1972b
B. schmidti	Ahlstrom, 1969	Dunn, 1983a	Dunn, 1983a
B. stilbius	Ahlstrom, 1969	Ahlstrom, 1965, 1972b	—
B. wesethi	Ahlstrom, 1969	Ahlstrom, 1965, 1972b	—
Opisthoproctidae			
Bathylychnops exilis	—	—	Cohen, 1960
Dolichopteryx spp.	—	Roule and Angel, 1930	—
Dolichopteryx longipes	—	Beebe, 1933a	—
Macropinna microstoma	—	Chapman, 1939	—
Opisthoproctus grimaldii	—	Schmidt, 1918	—
Rhynchohyalus natalensis	—	Bertelsen et al., 1965	—
Winteria telescopa	—	Belyanina, 1982b	—

Although now there seems to be general agreement as to the genera to be included in the group, their internal arrangement is an unsettled matter. Opinions range from those of C. L. Hubbs (1953), who relegated all to a single family, to those of Chapman (1948 and papers cited therein), who advocated eight different families. Subsequently Cohen (1964b) classified the group in three families using inadequately evaluated characters.

Family Argentinidae (most genera are probably worldwide):
Subfamily Argentininae (benthopelagic, outer shelf to slope):
  Argentina (12 species) and
  Glossanodon (seven or more species).
Subfamily Microstomatinae (mesopelagic)[1]:
  Microstoma (one or two species),
  Nansenia (13 species) and
  Xenophthalmichthys (one or two species).
Family Bathylagidae (meso-to bathypelagic):
  Bathylagus (including *Leuroglossus* and *Therobromus*; about a dozen to 15 species; several species in the Arctic and Antarctic).
Family Opisthoproctidae (mesopelagic):
  Group I:
  Macropinna (one species; restricted to N. Pacific and eastern S. Pacific),
  Opisthoproctus (two species),
  Rhynchohyalus (one species; Atlantic and Indian Oceans) and *Winteria* (one species).
  Group II:
  Bathylychnops (one or more species), and
  Dolichopteryx (perhaps half a dozen species).

An alternate arrangement presented by Greenwood and Rosen (1971) and essentially based on inadequately evaluated characters in the branchial arches and caudal fin skeleton proposed two families within a superfamily Argentinoidea: Family Argentinidae and Family Bathylagidae with Subfamily Bathylaginae (including Microstomatidae) and Subfamily Opisthoproctinae.

Unanswered questions concerning the systematics of the group are numerous and exist at all levels. Following is a summary. (1) What are the external relationships of the argentinoids? (2) How many distinct lineages exist within the group, how should they best be arranged with respect to each other, and how many families should be recognized? (3) Do *Argentina* and *Glossanodon* constitute a monophyletic group? If not, where does each belong? (4) How many genera should be recognized among the bathylagids? (5) Within the opisthoproct group do the elongate species in the *Bathylychnops-Dolichopteryx* group and the short-bodied species in the *Opisthoproctus* group constitute monophyletic lineages and if so should they be named? (6) Since species complements of genera are inadequately known, espe

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[1] Herein considered a distinct family.

TABLE 39. CHARACTERS OF THE EGGS OF ARGENTINOIDEI.

Species	Diameter	Number of oil globules	Distribution of oil globules	Diameter of oil globules	Source
Argentina sialis	1.31–1.66	1	vegetal pole	0.27–0.46	Original
Argentina silus	3.0–3.5	1	vegetal pole	0.95–1.16	Schmidt, 1906c
Argentina sphyraena					
(Mediterranean)	1.60–1.68	1	vegetal pole	0.44	Sanzo, 1931d
(North Sea)	1.70–1.85	1	vegetal pole	0.37–0.47	Schmidt, 1906c
Argentina elongata	1.67–1.80	1	vegetal pole	0.35–0.45	Robertson, 1975a
Glossanodon leioglossus	1.44–1.52	1	vegetal pole	0.36	Sanzo, 1931d
Glossanodon semifasciatus	1.5–1.6	1	vegetal pole	0.36	Nishimura, 1966
Microstoma microstoma					
(Atlantic)	1.60–1.72	1	vegetal pole	0.48–0.52	Sanzo, 1931d
(Pacific)	2.05–2.38	1	vegetal pole	0.49–0.82	Original
Nansenia candida	1.39–1.56	1	vegetal pole	0.41–0.49	Original
Nansenia crassa	1.05–1.30	1	vegetal pole	0.30–0.35	Original
Nansenia oblita	1.39–1.56	1	vegetal pole	0.40–0.53	Sanzo, 1931d
Bathylagus antarcticus	1.8–2.2	3–8	*	0.2–0.3	Yefremenko, 1982
Bathylagus schmidti	1.65–1.90	up to 9	*		Ahlstrom, 1969
Bathylagus stilbius	1.01–1.21	15–25	*		Ahlstrom, 1969
Bathylagus urotranus	1.03–1.21	15–25	*		Pertseva-Ostroumova and Rass, 1973, and original
Bathylagus ochotensis	0.92–1.1	many to two clumps	**		Original
Bathylagus wesethi	0.90–1.10	12–20	**		Ahlstrom, 1969
Bathylagus nigrigenys	0.83–1.09	12–20	**		Pertseva-Ostroumova and Rass, 1973, and original

* First grouped at vegetal pole, then move to beneath embryo, then coalesce to one at each equatorial pole.

** Numerous globules at vegetal pole then coalesce to one clump at each equatorial pole.

cially the mesopelagic ones, do presently available early life history specimens help define the species composition of argentinoid genera?

DEVELOPMENT

Eggs are known for 13 species of argentinoids and larvae for 22 species (Table 38). We present in this paper eggs of 5 additional argentinoid species and larvae of 8 additional species. These are: eggs and larvae of *Argentina sialis, Microstoma* sp., *Nansenia candida* and *N. crassa*; larvae only for *Bathylagus argyrogaster, B. bericoides, B. pacificus* and *Bathylychnops exilis*; eggs only for *Bathylagus ochotensis.*

Eggs

The eggs of argentinoids are pelagic, round, have a moderate to narrow perivitelline space, segmented yolk and a chorion with distinctive pustules on the inner surface (Table 39, Fig. 82). Egg diameters and oil globule characters are given in Table 39.

Argentinoid larvae hatch as relatively undifferentiated yolk-sac larvae, regardless of egg size. That is, yolk-sac larvae of *A. silus* at 7.5 mm, newly hatched from eggs 3.0–3.5 mm diameter, are at about the same stage of development as 3 mm bathylagid yolk-sac larvae which hatch from 1 mm eggs. In most marine fishes larger eggs produce more highly differentiated hatchlings.

Larvae

Body form.—Argentinid and bathylagid larvae are slender, those of microstomatids are deeper-bodied, and opisthoproctids have a wide variety of body shapes ranging from the slender larvae of *Bathylychnops* to the deep-bodied *Opisthoproctus* (Table 40, Figs. 83–87).

The gut is elongate and straight in argentinids and bathylagids, with the exception of *B. milleri* where the gut is straight but only about half the body length. In argentinids the gut is lined with transverse rugae for almost the entire length. In most bathylagids the gut has two distinct sections: an anterior section with longitudinal internal ridges, separated by a valve from a shorter posterior section with transverse rugae. The anterior section in *B. bericoides* and *B. longirostris* is markedly smaller in diameter compared with other species. Larvae of *B. wesethi, B. nigrigenys* and *B. argyrogaster* have transverse rugae along the entire length of the gut and the anterior section is relatively larger in diameter and thin-walled. Also the posterior section is subdivided by a second valve. *B. ochotensis* larvae develop a similar structure.

The gut in microstomatid larvae is long, but anteriorly has an elongate S-shaped fold that lies flat on the left side (Fig. 84). The lumen of the anterior folded section is characterized by longitudinal ridges whereas the posterior straight section has transverse rugae. The short pyloric section has longitudinal ridges. Schmidt (1918) shows the gut extended beyond the finfold margin in *Nansenia oblita* and trailing in early stage *Microstoma microstoma* larvae but we have not seen this in any specimens of these genera.

In opisthoproctids the gut is elongate in *Bathylychnops* and *Dolichopteryx* and relatively shorter in the deeper-bodied genera, *Macropinna, Rhynchohyalus* and *Opisthoproctus.* In all genera there is a sac-like stomach, which exits through a constricted pyloric section to the intestine. In *Bathylychnops* and *Dolichopteryx* the sac is elongate and pointed at its tip whereas in the other genera it is more rounded in form. The sac lies on the left side, except in *Bathylychnops* where it lies on the right. In the latter genus the pyloric constriction leads into a short but prominent bulbous section. *Dolichopteryx* is similar but lacks

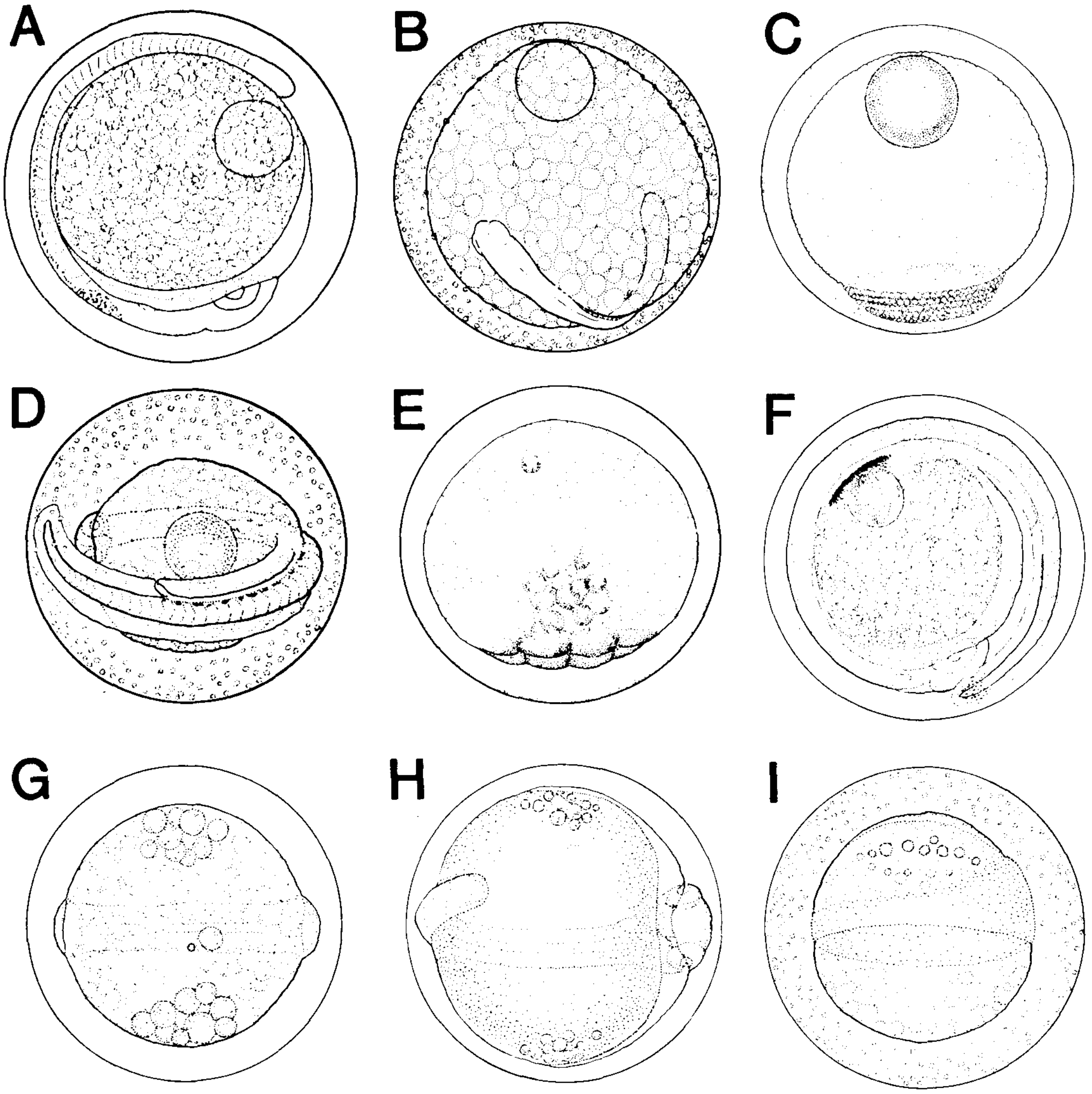

Fig. 82. Eggs of argentinoids. (A) *Argentina sialus*, 1.5 mm, CalCOFI 5103, Sta. 117.35; (B) *Microstoma* sp., 2.2 mm, CalCOFI 7511, Sta. 87.90; (C) *Nansenia candida*, 1.4 mm, CalCOFI Sta. 60.90; (D) *N. crassa*, 1.5 mm, CalCOFI; (E) *Bathylagus stilbius*, 1.1 mm, from Ahlstrom (1969); (F) *B. schmidti*, 1.8 mm, from Ahlstrom (1969); (G) *B. ochotensis*, 1.1 mm, CalCOFI 5002 Sta. 60.90; (H) *B. wesethi*, 1.0 mm, Ahlstrom (1969); (I) *B. nigrigenys*, 0.96 mm, CalCOFI 5106 Sta. 157.20.

the post-pyloric bulb. In *Macropinna* and *Opisthoproctus* there is a straight section leading posteriorly from the pylorus, which ends in an S-shaped fold and an enlarged rectal bulb, the latter described by Bertelsen and Munk (1964). The anterior section including the sac and pylorus have longitudinal internal ridges while sections posterior to this have transverse rugae. In late larval stages the entire section posterior to the pylorus becomes part of the S-shaped coil.

The head is relatively small in argentinids and has a rounded blunted anterior profile (Fig. 83, Table 40). It is slightly larger in most microstomatids, with the exception of *Microstoma* sp. (Pacific form) which has a small head. In most microstomatids the head has a rounded, blunted anterior profile and is bent slightly downward from the longitudinal axis. In both families the eye is either round or slightly ellipsoidal. In bathylagids the head is moderate in size but highly various in shape (Figs. 85, 86; Table 40). The snout is generally longer than in Argentinidae and Microstomatidae.

Eye shape and structure vary greatly within the bathylagids. *Bathylagus milleri* has a large, nearly round eye in contrast to

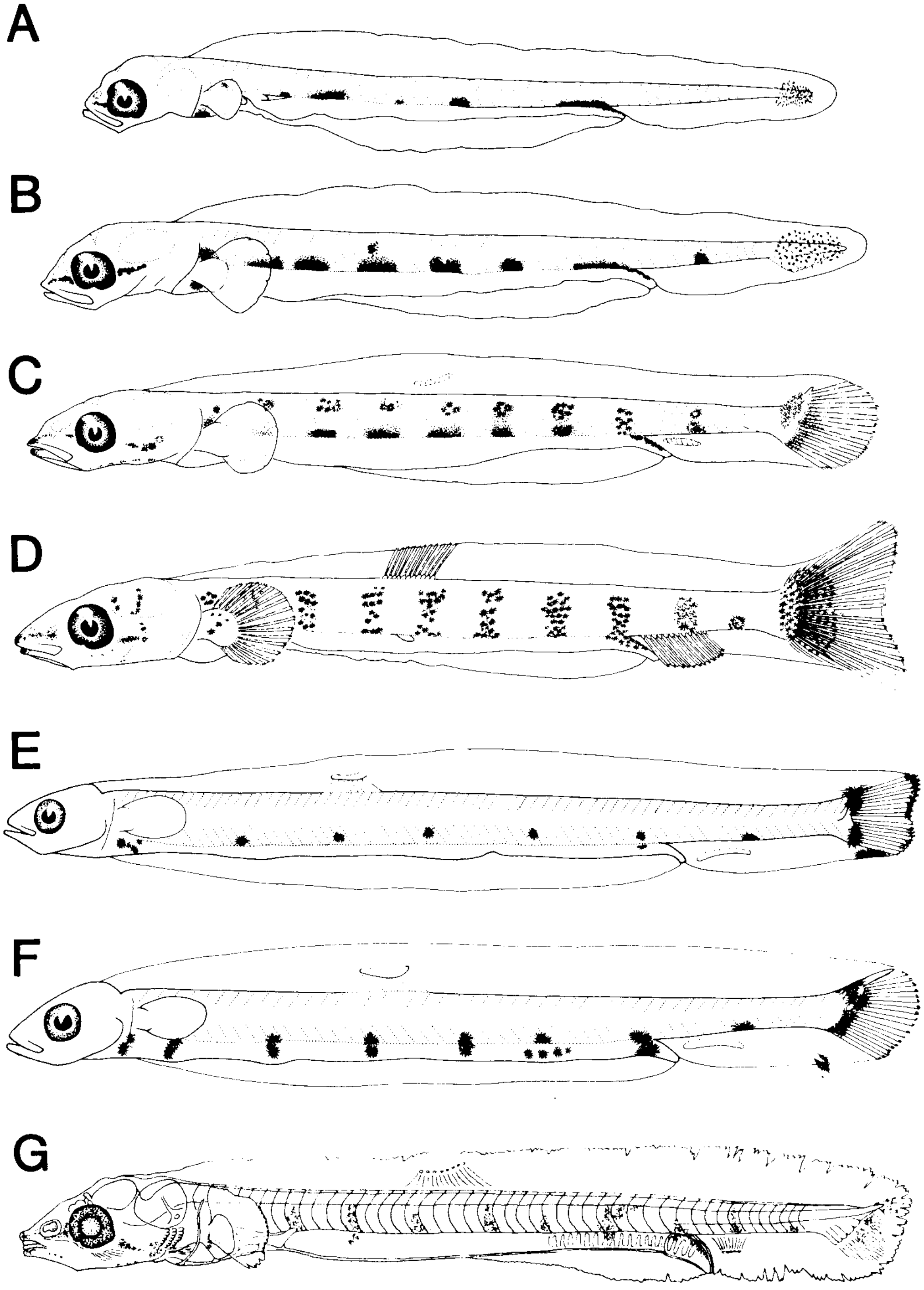

Fig. 83. Larvae of Argentinidae. (A) *Argentina sialis*, 7.0 mm, CalCOFI 5103 Sta. 117.35; (B) *A. sialis*, 9.0 mm, CalCOFI 5104 Sta. 97.40; (C) *A. sialis*, 17.5 mm, CalCOFI 5103 Sta. 120.35; (D) *A. sialis*, 21.0 mm, CalCOFI 5105 Sta. 123.40; (E) *A. silus*, 32.5 mm, redrawn from Schmidt (1906c); (F) *A. sphyraena*, 19.2 mm, ibid; (G) *Glossanodon semifasciatus*, 12.5 mm, from Nishimura (1966).

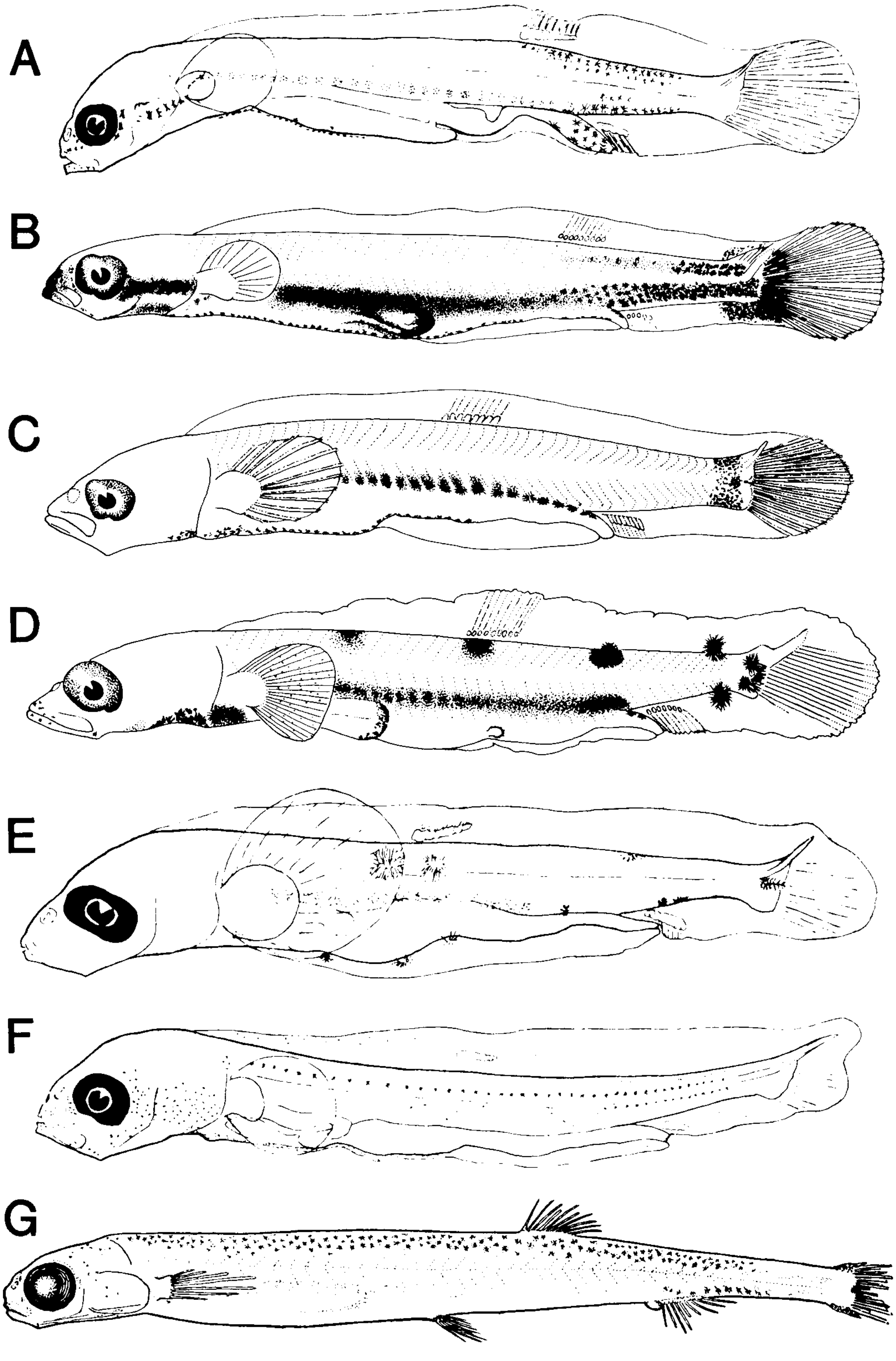
A
B
C
D
E
F
G

TABLE 40. COMPARATIVE MORPHOMETRY OF ARGENTINOID LARVAE. Mean values (%) of body proportions for three ontogenetic stages (preflexion-flexion-postflexion) are listed.

	Snout–anus distance	Head length	Head width	Eye length	Eye stalk length	Body depth	Snout–anal fin distance	Snout–dorsal fin distance	Snout–pelvic fin distance
Species	Body length	Body length	Head length	Head length	Head length	Body length	Body length	Body length	Body length
Argentina sialis	76-78-84	17-21-22	54-44-41	28-24-24	—	9-10-10	0-78-81	0-46-47	0-0-49
Microstoma microstoma	?-?-80	?-?-23	?-?-45	?-?-27	—	?-?-13	?-?-80	?-?-68	0-?-64
Microstoma sp. (Pacific)	76-79-80	17-19-19	53-49-44	31-29-27	—	8-10-10	0-78-81	0-70-72	0-64-67
Nansenia candida	74-77-82	21-25-26	60-50-44	36-28-28	—	12-14-16	0-75-82	0-54-58	0-56-61
Nansenia crassa	74-78-80	22-25-28	58-50-44	36-29-24	—	10-12-15	0-76-80	0-52-57	0-56-60
Nansenia groenlandica	?-78-80	?-27-25	?-50-42	?-21-23	—	?-15-15	?-77-80	?-52-52	?-54-57
Xenophthalmichthys danae	?-?-82	?-?-24	?-?-48	?-?-21	—	?-?-12	?-?-86	?-?-74	?-?-52
Bathylagus milleri	59-57-61	20-19-26	56-54-52	31-27-26	—	9-9-15	0-0-71	0-0-50	0-0-45
Bathylagus schmidti	72-76-78	16-19-22	50-52-46	39-26-25	.04-0-0	7-8-10	0-0-79	0-0-57	0-0-55
Bathylagus stilbius	74-77-80	20-22-24	54-53-47	32-25-20	.03-0-0	8-10-13	0-0-79	0-0-57	0-0-55
Bathylagus urotranus	78-82-81	20-24-28	56-53-46	27-18-21	.03-0-0	10-10-12	0-0-81	0-0-61	0-0-59
Bathylagus pacificus	76-85-81	22-24-25	39-42-44	29-22-18	28-29-20	8-10-13	0-81-80	0-49-48	0-51-51
Bathylagus euryops	78-80-82	18-20-20	46-50-50	31-26-25	10-7-3	10-11-12	0-78-80	0-45-48	0-0-47
Bathylagus bericoides	84-85-89	25-26-26	34-38-36	27-25-22	60-64-36	8-8-9	0-83-88	0-0-52	0-0-53
Bathylagus longirostris	85-88-92	26-27-25	34-34-34	24-20-19	54-48-27	8-10-10	0-88-90	0-0-53	0-0-57
Bathylagus ochotensis	81-85-90	20-23-23	44-44-44	32-21-21	17-15-15	8-10-11	0-83-87	0-53-54	0-56-56
Bathylagus wesethi	79-89-94	13-26-27	59-53-50	27-16-13	—	9-14-16	0-85-90	0-58-60	0-57-59
Bathylagus nigrigenys	80-86-93	20-29-28	78-60-53	30-18-14	—	12-16-18	0-86-90	0-57-60	0-0-60
Bathylychnops exilis	?-80-82	?-21-22	?-42-38	?-22-18	—	?-8-7	?-82-84	?-71-73	?-66-67
Dolichopteryx longipes	?-74-75	?-24-26	?-44-34	?-22-16	—	?-8-10	?-0-77	?-0-71	?-62-62
Macropinna microstoma	?-64-59	?-26-35	?-52-47	?-22-21	—	?-15-21	?-0-70	?-0-66	?-43-48
Opisthoproctus soleatus	?-?-80	?-?-37	?-?-46	?-?-18	—	?-?-18	?-?-83	?-?-63	?-?-40

other species which have relatively smaller, more elliptical eyes. Eyes are sessile in *B. milleri* and in the *B. wesethi* group but are stalked to some degree in all other species known. In *B. stilbius* and relatives (*B. urotranus*, and *B. schmidti*) the stalks are short and found only in early larvae. Stalks are longer and persist into later larval stages in other species, reaching a maximum of 65% of the head length in *B. bericoides*.

In opisthoproctids the head is moderate in size in the slender forms, *Bathylychnops* and *Dolichopteryx*, and longer and more massive, with a pronounced hump or bend at the nape, in the deep-bodied genera. All genera have an elongate snout and *Bathylychnops* has a unique triangular flap at its tip. *Bathylychnops* has round eyes that are rotated slightly dorsoanteriad. In the other genera, the eyes are tubular and directed dorsally, even in the smallest larvae available. Eye diverticulae with associated accessory retinae, characteristic of opisthoproctid adults, begin to form at the end of the larval period.

Fins.—A major feature of all argentinoid larvae is the development of a prominent median finfold in which the dorsal and anal fins develop, connected to the trunk by a series of hyaline strands (Figs. 83–87). The first fins to form are the pectorals. In argentinids and bathylagids they are relatively small and develop rays late in the larval period. Microstomatid and opisthoproctid pectoral fins are generally larger; however, there is a wide size range, from relatively small fins in *Microstoma* to large, fan-like fins in some species of *Nansenia* (e.g., *N. groenlandica*) to very elongate pectorals in *Dolichopteryx binocularis*. Ossification of rays begins earlier in these groups, usually before notochord flexion.

After the pectorals, the caudal fin is usually the next to form. In argentinids notochord flexion and development of principal caudal rays occurs at a size about midway in larval growth whereas in opisthoproctids this occurs earlier in the larval period. In bathylagids the process is somewhat delayed and in some species (e.g., *B. euryops*, *B. milleri*) notochord flexion may not be completed until near the end of the larval period.

The dorsal and anal fins begin to form at about the stage of notochord flexion in all argentinoids except opisthoproctids, where notochord flexion slightly precedes the appearance of dorsal and anal fins. The anal fin begins forming far posteriad in argentinoids, just posterior to the anus or the point of deflection of the free terminal gut section. In *B. milleri* and in the deep-bodied opisthoproctids with coiled guts there is a space between the anus and the anal fin origin.

The position of the dorsal fin is varied among argentinoids and forms in the larvae in approximately the same position that it will occupy in the adult. The fin has its most anteriad location in *Argentina* where its origin is well forward of the midpoint of the body (Fig. 83). The extreme case is found in *A. silus* where snout to dorsal origin is about 38% of the body length in larvae and about 43% in adults. In most bathylagids the dorsal origin is slightly anterior to mid-body. The exceptions are *B. stilbius* and relatives, where the dorsal origin is slightly posterior to mid-body, and *B. wesethi* and relatives where it is located still further posteriad.

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Fig. 84. Larvae of Microstomatidae. (A) *Microstoma microstoma*, 11.0 mm, from Schmidt (1918); (B) *Microstoma* sp., 12.0 mm, CalCOFI 5104 Sta. 90.52; (C) *Nansenia candida*, 8.4 mm, CalCOFI 5007 Sta. 100.70; (D) *N. crassa*, 8.5 mm, CalCOFI 5103 Sta. 137.50; (E) *N. groenlandica*, 10.0 mm, from Schmidt (1918); (F) *N. oblita*, 9.0 mm, ibid; (G) *Xenopthalmichthys danae*, 16.5 mm, from Bertelsen (1958).

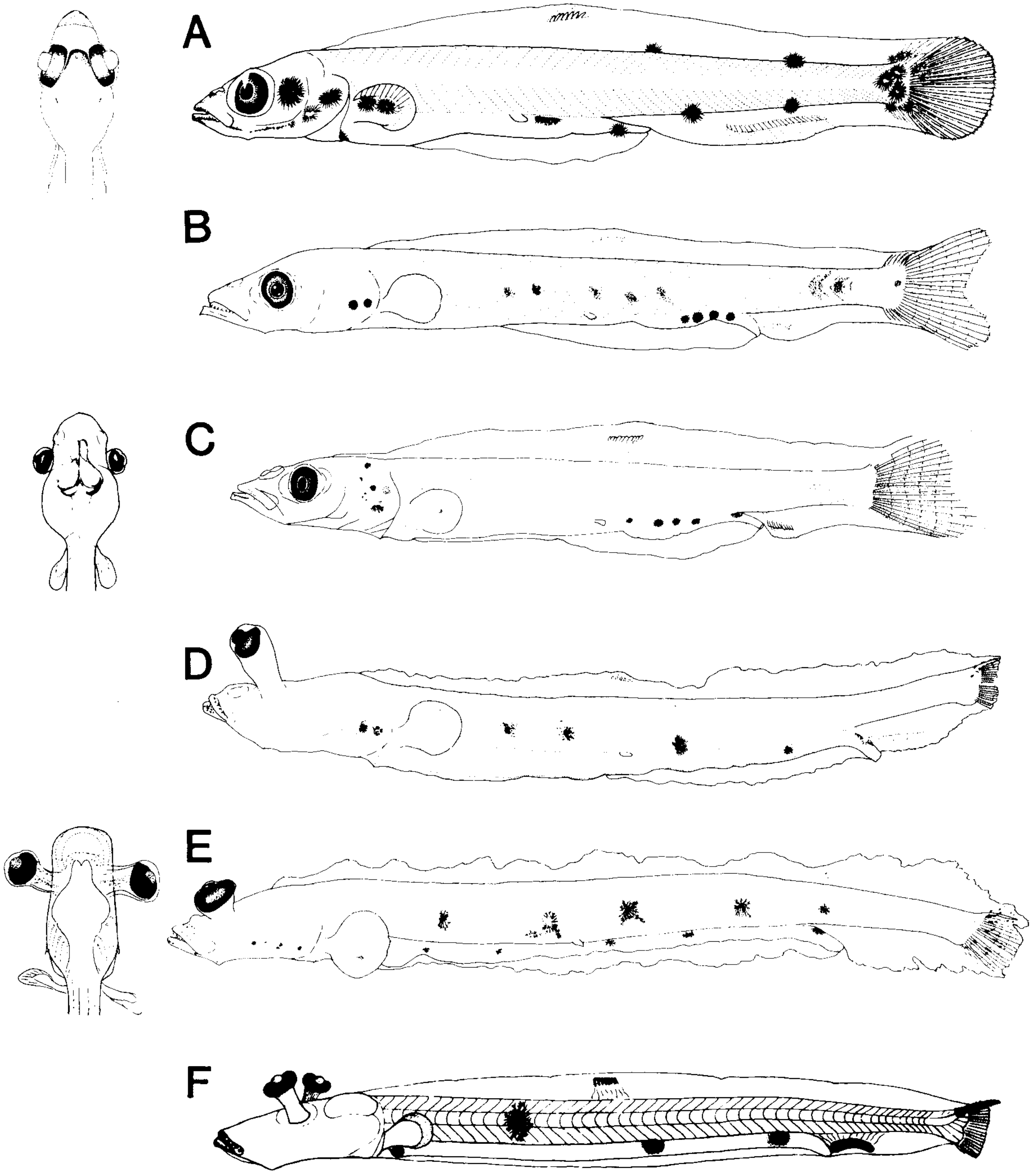

Fig. 85. Larvae of *Bathylagus.* (A) *B. milleri,* 27.5 mm, CalCOFI 5106 Sta. 70.60, dorsal view of 9.5 mm specimen at left; (B) *B. schmidti,* 31.5 mm, CalCOFI Northern Holiday Exped. Sta. 31; (C) *B. stilbius,* 23.2 mm, CalCOFI 4905 Sta. 111.38, dorsal view of 8.5 mm specimen at left; (D) *B. pacificus,* 21.4 mm, CalCOFI 7905 Sta. 63.60; (E) *B. euryops* 24.0 mm, dorsal view of 14.0 mm specimen at left, from Tåning (1931); (F) *B. antarcticus,* 26.5 mm, from Yefremenko (1983).

TABLE 41. MERISTICS OF ARGENTINOID FISHES.

Species	Vertebrae	Branchiostegal rays	Dorsal fin rays	Anal fin rays	Pectoral fin rays	Pelvic fin rays	Procurrent caudal fin rays
Argentina							
aliceae	43–46	5	11–13	13–15	16–18	10–12	
australiae	50–53	5	10–12	12–13	13–14	11–13	
brucei	45–47	5	10–12	11–13	18–20	13–14	
elongata	52–55	5	10–12	11–14	13–16	11–12	
euchus	48–49	5	12	13–15	16–18	10–11	
georgei	48–51	5	10–12	10–13	16–19	12–14	
kagoshimae	51–52	5	10–12	11–13	15–17	11–12	
sialis	47–51	5	10–13	12–15	11–18	10–12	12+11
silus	65–70	6	11–13	11–17	15–18	12–13	
sphyraena	46–55	6	10–12	11–15	12–15	10–12	
stewarti	53–54	5	10–12	12–13	18–21	13–15	
striata	48–52	5	10–12	11–14	18–21	11–15	10+9
Glossanodon							
leiglossus	49–51	5	12–14	10–13	19–22	11–12	
lineatus		4	11–13	15	18–21	11–13	
mildredae	50–52	5	13	13	23	12–13	
polli		5	12–14	11–14	19–22	12–13	
pygmaeus	43–44	5	10–12	11–13	12–14	10–12	
semifasciatus	49	5	11–13	11–13	18–21	10–12	
struhsakeri	51–53		12–14	12–13	23–25	13–15	
Microstoma							
microstoma	45–47	3–4	11–12	8–9	8	9–11	11+11
sp. (Pacific)	49–50	4	9–11	7–8	11	9	10–11+10
Xenophthalmichthys							
danae		3	10–12	9–10	7	8–9	10+9
Nansenia							
atlantica	41–42	4	9–10	8–9	12–13	10–11	
ardesiaca	46–48	4	9–10	9–10	11–14	10–12	
candida	44–47	3	9–10	8–9	9–11	9–11	11+14
crassa	43–46	4	9–10	8–9	11–13	10–11	
groenlandica	42–45	3	9–10	8–10	11–13	10–12	
oblita	42–45	4	10–11	9–10	10–11	10–11	
Bathylagus							
antarcticus		2	9–11	21–25		9–10	
argyrogaster		2	12	14–15		8	
bericoides	48–53	2	10–11	18–22	10–12	9–10	
euryops	44–46	2	9–11	16–19	7–12	7–9	
greyae		2	11–13	13	12–13	10–11	
longirostris	48–51	2	10–12	19–21	9–12	9–10	
milleri	51–55	2	6–9	20–28	11–16	6–8	16–18+15–17
nigrigenys	41	2	11–12	14–17	10	8–10	
ochotensis	47–49	2	9–12	12–15	9–11	9–10	13–14+15–16
pacificus	45–49	2	8–9	15–22	7–11	7–10	13+13–14
schmidti	47–52	2	10–11	11–14	8–9	8–9	16–17+16
stilbius	38–42	2	9–11	11–14	8–11	8–10	12–16+13–15
urotranus	39–42	2	9–10	10–11	9–11	7–8	12–14+12–13
wesethi	43–46	2	12–13	14–16	10–11	9–11	14–15+14–15
Dolichopteryx							
anascopa		2	10	12	14	12	
binocularis		2	15	11	14	9	
brachyrhynchus		2	13	12	13	8	
longipes	41–44	2	10–11	8–9	13	8–9	
Bathylychnops							
exilis	81–84	2	14–16	13–14	12–13	7	
Rhynchohyalus							
natalensis		4	10–12	10	19–20	11–12	
Macropinna							
microstoma	36	3	11–12	14	17–19	10	
Winteria							
telescopa			8	8	12–14	9	

TABLE 41. CONTINUED.

Species	Vertebrae	Branchiostegal rays	Dorsal fin rays	Anal fin rays	Pectoral fin rays	Pelvic fin rays	Procurrent caudal fin rays
Opisthoproctus							
grimaldii		2	12–14	8	11	10	
soleatus	31	2	10–12	13–14	9–11		

The dorsal fin forms in a variety of positions among microstomatids. In most species of *Nansenia*, the dorsal fin originates slightly posterior to mid-body, although in some species (e.g., *N. groenlandica*), its origin is slightly anterior to mid-body. The dorsal origin is further posteriad in *Microstoma*. In *M. microstoma* predorsal length is about 67–68% of the body length and assumes a more anterior position in adults (ca. 63%). In larvae of the Pacific species predorsal length is about 75% of the body length, and is slightly more posteriad in adults. In adult *Xenophthalmichthys* the dorsal origin is at mid-body; however, in the 16.5 mm specimen from the Atlantic (Bertelsen, 1958) predorsal length is 62% of the body length. In our single larva (12.2 mm) from the Pacific predorsal length is 75% of body length, indicating a marked anteriad migration during ontogeny or strong allometric growth posterior to the dorsal fin. Alternatively, the Pacific form may prove to be distinct when adult specimens are captured.

The dorsal fin in opisthoproctids is located posteriad on the body. This is most marked in the slender forms, *Bathylychnops* and *Dolichopteryx*, and reaches an extreme in *D. binocularis* where predorsal length is greater than ¾ of the body length. In the deep-bodied genera the dorsal origin is posterior to mid-body, but less so than in the slender-bodied forms.

The pelvic fins are the last fins to form in most argentinoids, usually late in the larval period. The exception is opisthoproctids where the pelvic fins form early in the larval period. In argentinids, bathylagids and microstomatids the pelvic fins form at about mid-body, below the dorsal fin. In the slender opisthoproctid genera the pelvics form well back on the body, but anterior to the dorsal fin. Among the deep-bodied genera, *Opisthoproctus* forms the pelvics far back on the body, beneath the dorsal fin. In *Rhynchohyalus* and *Macropinna* the pelvics develop just posterior to mid-body and anterior to the dorsal fin. In the larvae the fins are elevated to the sides of the body. This position persists in juvenile and adult *Macropinna* where the fins are located just behind and below the pectoral fin bases. The pelvic fins become elongate in *Dolichopteryx* and the deep-bodied genera. The pelvic fin base is pedunculate in opisthoproctid larvae, a condition that persists into the adults of some genera, notably *Dolichopteryx*. Argentinoids, except *Microstoma, Xenophthalmichthys* and some species of *Dolichopteryx*, develop adipose fins late in the larval period.

A summary of meristics of argentinoids is given in Table 41. The sequence of ossification of fins and other skeletal elements of *Bathylagus schmidti* is described by Dunn (1983a).

Pigmentation.—In argentinids, pigmentation consists of a series of 6–8 ventral trunk blotches that extend from the pectoral fin base to the end of the gut (Fig. 83). The series is continued posteriorly as 1 or 2 median ventral blotches and ends as a large blotch at the caudal region. The number of blotches is constant for each species, as is the sequence of formation. In *Argentina sialis* and *Glossanodon* the ventral blotches expand dorsally as lateral bars, but this does not occur in *A. silus* and *A. sphyraena*. These latter species differ additionally in lacking the internal head pigment which develops in *A. sialis* and *Glossanodon* larvae.

A feature common to most microstomatid larvae is a heavy line of embedded pigment above the gut (Fig. 84). In *Microstoma* this pigment continues forward to the gill arches and within the head anteriorly to the snout. In *Nansenia*, head pigmentation is superficial, or concentrated ventrally on the head. In *Microstoma*, an embedded dorsal line of pigment is located posterior to the dorsal fin. Dorsal pigmentation in *Nansenia* may take the form of a series of embedded blotches (e.g., *N. crassa*) or an embedded line of melanophores running the length of the body (e.g., *N. oblita*). Most microstomatids have conspicuous melanistic pigment associated with the caudal fin region. A notable feature of *Microstoma* and some *Nansenia* (e.g., *N. crassa*) is the presence of heavy melanistic pigment at the curve of the gut loop. Our single damaged specimen of *Xenophthalmichthys* (12.2 mm) has pigmentation similar to *Microstoma* but lacks the posterior dorsal body pigment and has a series of slanted melanophores along the hypaxial myosepta.

Pigment patterns in bathylagids may be grouped into two categories—those species with large isolated melanophores (Fig. 85) and those with linear series of smaller melanophores (Fig. 86). *Bathylagus milleri* has a unique pattern of opposing dorsal and ventral midline melanophores, large melanophores on the head and pectoral fin base and a large lateral blotch on the notochord tip.

Bathylagus stilbius and *B. urotranus* develop a series of 5–6 melanophores on each side of the posterior section of the gut. A single large melanophore, is found on the lower trunk midway between the pectoral fin and the anus and the head has melanophores, chiefly on the upper and lower jaws and opercle (Fig. 85). *B. schmidti* differs in having a series of lower trunk blotches and 1 or 2 postanal lateral blotches.

Bathylagus euryops has a series of 3–6 melanophores on the lateral surface of the gut and 3–5 large melanophores on the lateral surface of the trunk (Fig. 85). Other pigmentation consists

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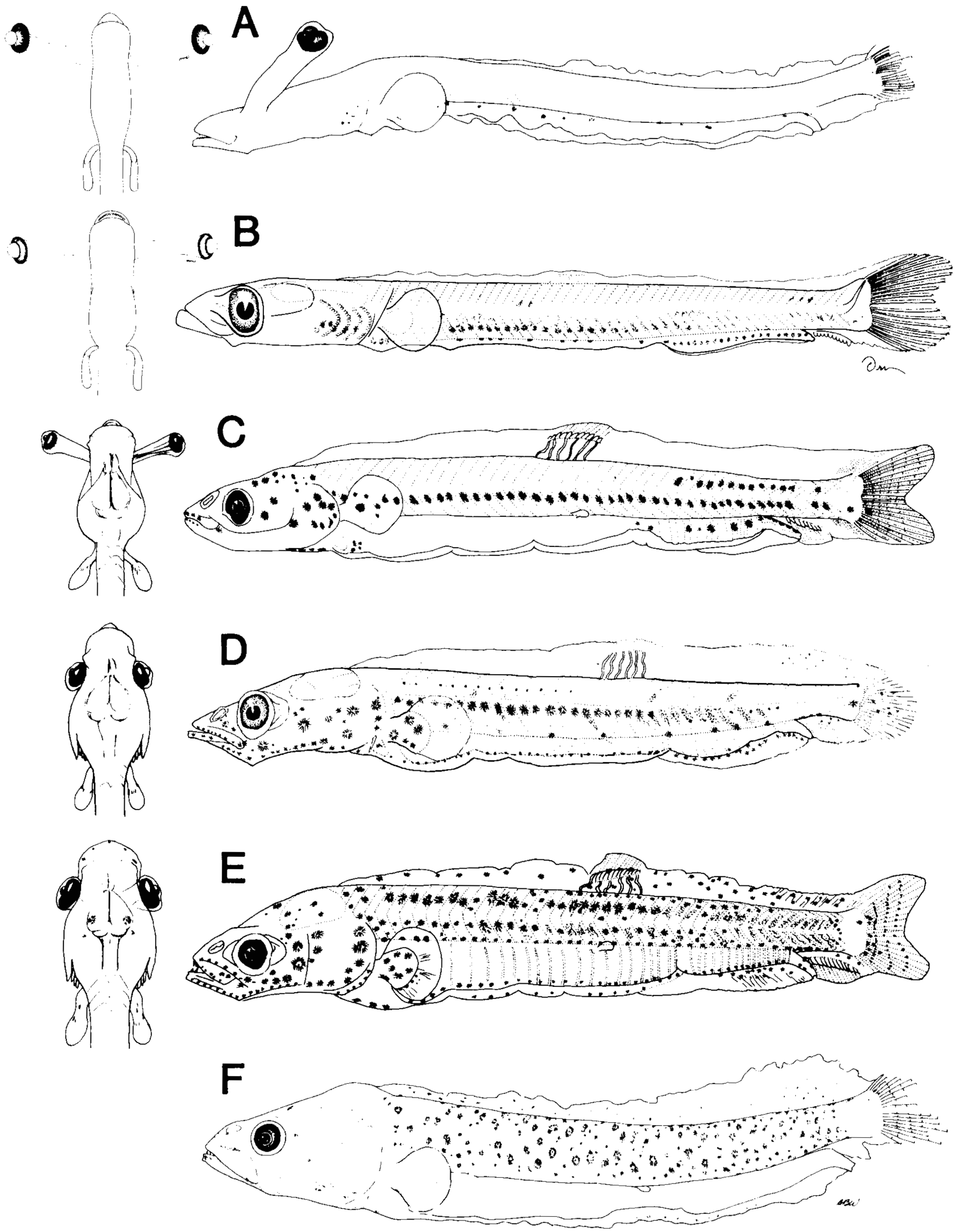
Fig. 86. Larvae of *Bathylagus*. (A) *B. bericoides*, 17.7 mm, Dana Sta. 4007, dorsal view of 11.8 mm specimen at left; (B) *B. longirostris*, 20.1 mm, SIO/STOW XIII Exped., dorsal view of 12.4 mm specimen at left; (C) *B. ochotensis*, 21.5 mm, CalCOFI 5106 Sta. 77.65, dorsal view of 8.5 mm specimen at left; (D) *B. wesethi*, 11.3 mm, from Ahlstrom (1972b), dorsal view of 8.5 mm specimen at left; (E) *B. nigrigenys*, 21.8 mm, SIO Shellback Exped. Sta. 92, dorsal view of 8.7 mm specimen at left; (F) *B. argyrogaster*, 17.1 mm, Dana Sta. 4003.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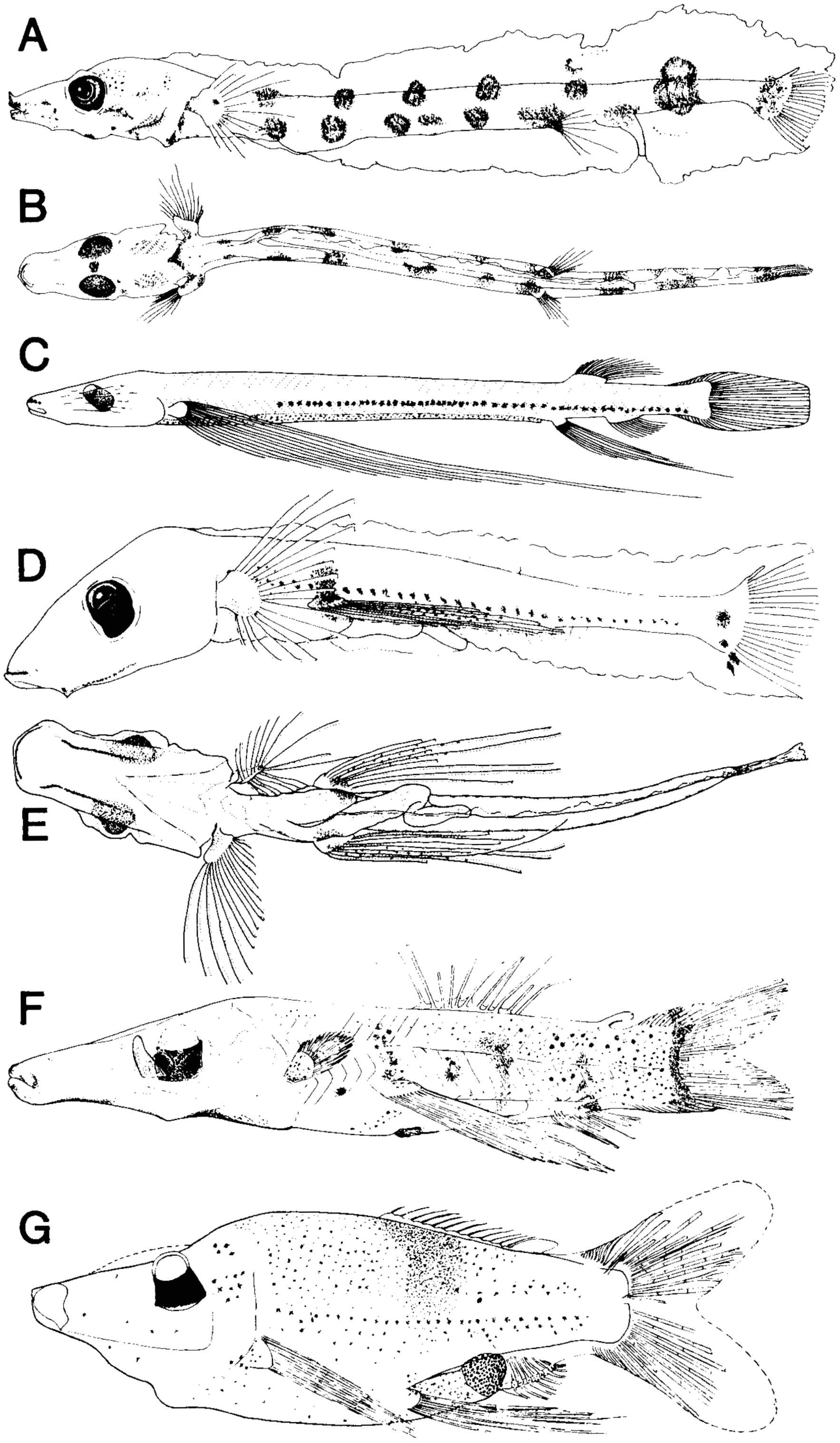
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TABLE 42. CHARACTERS USED IN ANALYSIS OF FOUR ARGENTINOID GROUPS.

Character number	Dervied character state	Outgroup	Reference
1	Accessory cartilage at posterior tip ceratobr. 5	Osmerids	Greenwood and Rosen, 1971
2	$PU_1 + U_1$ fused	Teleosts in general	Goody, 1969
3	Light organs present	Teleosts in general	Bertelsen and Munk, 1964
4	Frontals fused	Teleosts in general	Cohen, 1964b
5	Epibr. 4 with one post. art. surface	Osmerids	Greenwood and Rosen, 1971
6	Larval gut with stomach	Osmerids	This paper, Hearne (this volume)
7	Pelvic fins form early and large	Osmerids	This paper, Hearne (this volume)
8	Swimbladder absent	Teleosts in general	Cohen, 1964b
9	Urodermal absent	Teleosts in general	Greenwood and Rosen, 1971
10	LL scales extend onto caudal fin	Teleosts in general	
11	Larval gut folded	Osmerids	Hearne (this volume)
12	Extrascapular attached to pterotic	Teleosts in general	Chapman, 1942
13	Uncinate process lacking on epibr. 4	Osmerids	Greenwood and Rosen, 1971
14	Pectoral fin forms early and large	Osmerids	This paper, Hearne (this volume)

of a line of small melanophores above and below the notochord tip, a patch of melanophores on the opercle and groups of small melanophores on the upper and lower jaws. *Bathylagus antarcticus* has 3 lateral gut spots, a large lateral trunk melanophore at the 10th–12th myomere, and head and notochord pigment similar to that of *B. euryops.* Early larvae of *B. pacificus* have a large lateral blotch at mid-body and another one posteriad on the body. Initially these melanophores are located at the junction of the gut and body but in later larvae are located on the trunk. Later a 3rd blotch forms midway between these two. A 4th lateral trunk blotch forms in some late larval specimens between the pectoral fin and the large mid-body blotch and melanophores form lateral to the liver and at the free terminal section of the gut. Head and notochord pigment is similar to *B. euryops* and *B. antarcticus.*

Bathylagus bericoides is unusual in having only a series of as many as 18 lateral gut melanophores (Fig. 86). Late postflexion larvae develop pigment on the lower jaw, isthmus, opercle, pectoral fin base and lateral caudal peduncle. *Bathylagus longirostris* develops a heavier pattern of pigmentation, beginning with a series of small melanophores on the posterior section of the gut in early larvae. Also in preflexion larvae a series of rectangular-shaped melanophores develops on the hypaxial myomeres. Later in the larval period the lateral gut series is extended forward along the entire gut, although with wider spacing than on the posterior gut section. Also, the epaxial myomeres develop rectangular-shaped melanophores, beginning posteriorly and accruing anteriorly. The head develops pigmentation from the opercle to the jaws (Fig. 86). *Bathylagus ochotensis* develops a similar pigment pattern except that the melanophores on the posterior gut section are comparatively larger and fewer, the anterior region of the gut lacks melanophores and the epaxial myomere series is limited to the posterior region.

Larvae of *B. wesethi, B. nigrigenys* and *B. argyrogaster* have a similar pigment pattern that differs markedly from that of other *Bathylagus* (Fig. 86). Initially there is a series of paired melanophores dorsolateral to the gut, extending from the pectoral fin base to the terminal section. These remain throughout the larval period but become embedded and obscured in late larvae. *Bathylagus nigrigenys* begins with about 8 pairs, which increase to 10, whereas *B. wesethi* begins with 6 pairs and has 7–8 during most of the larval period. Both species develop pigment at the notochord tip; *B. wesethi* has a dorsal and ventral spot, while *B. nigrigenys* has only a ventral spot. At notochord flexion a series of melanophores appears along the hypaxial region of the body and, soon after, a series develops along the epaxial myomeres. More lateral series are added and in late larvae the entire body is covered. Melanophores also form in the median finfold of advanced larvae. Initially head pigmentation consists of melanophores on the opercle and jaws but in later larvae the entire head is covered.

Opisthoproctid larvae have distinctive and, in some genera, heavy pigment patterns (Fig. 87). *Bathylychnops* has a dorsal series of 6 large paired blotches that permeate the musculature, bridge across the longitudinal septum and expand onto the finfold. A series of 8 large ventrolateral blotches alternate with those of the dorsal series, with the exception that the postanal blotch lies opposite the dorsal blotch and expands to form a band. A large blotch covers the base of the caudal fin. The head is heavily pigmented with superficial melanophores on the branchiostegals, urohyal and lateral brain and deeply embedded melanophores in the snout, jaws, cheek and ventral brain region. The lower limbs of the gill arches and their filaments are heavily pigmented as are both the pectoral and pelvic fin bases.

The species of *Dolichopteryx* have lateral series of melanophores above the gut and some species develop serial melanophores on the hypaxial myomeres (Fig. 87). Head pigment consists of melanophores on the jaws, gill arches and, in most species, the internal snout region. *Macropinna* develops a series of slanted melanophores, one on each hypaxial myomere, and a heavy embedded blotch at the pelvic fin base, that expands both dorsad and ventrad as a band. The caudal fin base has a large blotch

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Fig. 87. Larvae of Opisthoproctidae. (A) *Bathylychnops exilis,* 15.6 mm, CalCOFI 7203 Sta. 67.80; (B) Ventral view of above; (C) *Dolichopteryx binocularis,* 58.0 mm, redrawn from Roule and Angel (1930); (D) *Macropinna microstoma,* 11.7 mm, CalCOFI 7412 Sta. 120.50; (E) Ventral view of above; (F) *Rhynchohyalus natalensis,* 23.0 mm, from Bertelsen et al. (1965); (G) *Opisthoproctus grimaldii,* 14.0 mm from Schmidt (1918).

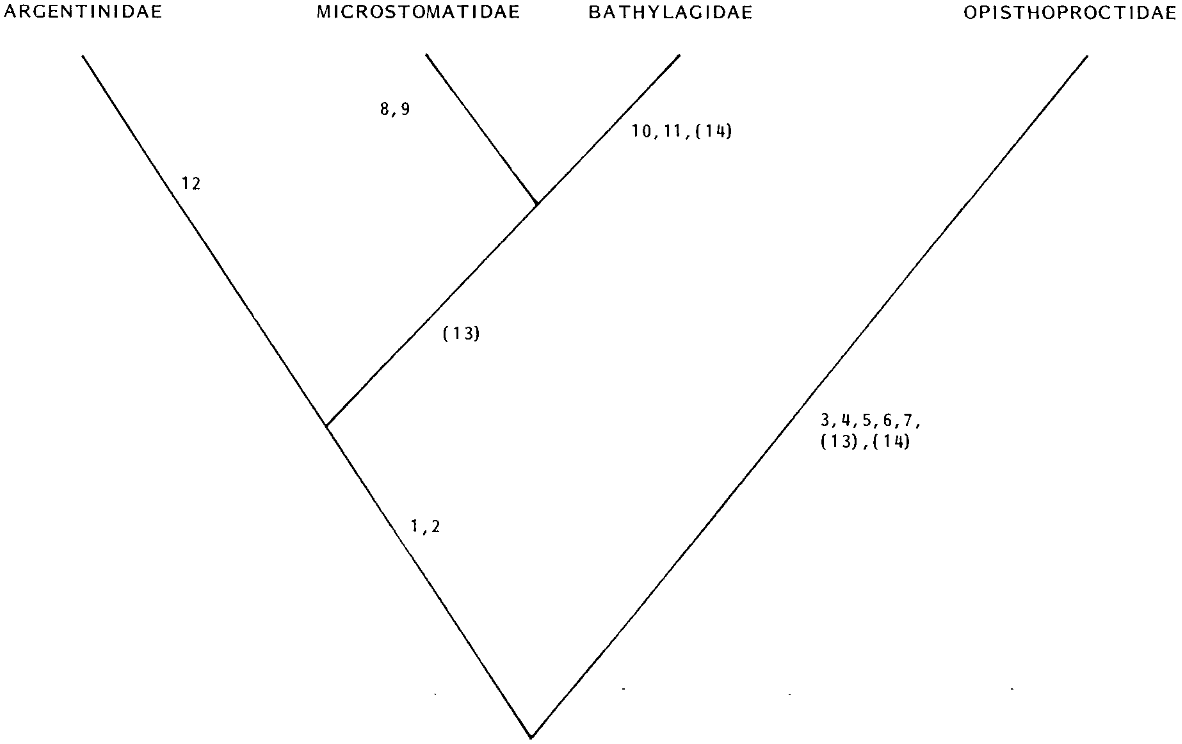

Fig. 88. Cladogram showing the distribution of character states in four nominal families of argentinoid fishes. Numbers refer to characters in Tables 42 and 43. Parentheses indicate character reversals.

and in the gut region there is pigment above the terminal section and ventral to the liver. Head pigment is confined to the lower jaw. The pigment pattern of *Rhynchohyalus* as described by Bertelsen et al. (1965) consists of a series of four dusky bars beginning at the pelvic fin and ending at the caudal fin base. Embedded beneath these is a layer of diffuse melanophores which becomes denser toward the caudal. The pectoral fin bases are pigmented and in the ventral region there are melanophores on the isthmus and gut. The anal light organ is covered with a melanistic sheath. The late larval specimen of *Opisthoproctus grimaldii* illustrated by Schmidt (1918) shows a diffuse covering of melanophores over the body and a dusky bar extending down from the dorsal fin. A 10 mm larva of *O. soleatus* in our collection has a pigment pattern similar to *Macropinna,* with a series of slanted melanophores on the hypaxial myomeres, embedded blotches at the pelvic and caudal fin bases, pigment at the liver and ventrally at the angles of the lower jaw.

Transformation stage

In argentinids transformation from larva to demersal juvenile is a prolonged process and pelagic juveniles with the retained larval pigment blotches or bars have been reported many times (see Cohen, 1958; Nishimura, 1966). Morphological changes (e.g., deepening of the body, prolongation of the snout, eye enlargement) and the masking of the larval pigment occur gradually. The beginning of this stage may be defined by the folding of the anterior gut region to form a stomach. This occurs at 25–30 mm in *Argentina sialis,* but has not been documented for other species. Pelagic juveniles of *Glossanodon* and *A. sialis* develop a silvery stripe at the lateral line region. This has not been reported for pelagic juveniles of *A. silus* and *A. sphyraena* and may afford an additional character for separating *Argentina* into two groups. The end of the pelagic juvenile stage, marked by the development of scales and silvery integument, is attained

TABLE 43. DISTRIBUTION OF CHARACTER STATES IN FOUR NOMINAL FAMILIES OF ARGENTINOID FISHES. Direction of transformation A → B.

Character number	Argentinidae	Micrstomatidae	Bathylagidae	Opistho-proctidae
1	B	B	B	A
2	B	B	B	A
3	A	A	A	B
4	A	A	A	B
5	A	A	A	B
6	A	A	A	B
7	A	A	A	B
8	A	A	B	A
9	A	A	B	A
10	A	B	A	A
11	A	B	A	A
12	B	A	A	A
13	A	B	B	B
14	A	B	A	B

at various lengths by different species. Schmidt (1906c) reports complete transformation at about 50 mm in *A. sphyraena* and at a much larger size in *A. silus*. Size at completion of transformation in *Glossanodon* species is also in the 50–100 mm size range (Nishimura, 1966).

Microstomatids develop a lustrous guanine layer on the integument in late larvae and some species develop distinct juvenile pigmentation. In *Microstoma* juveniles the region of the body from the dorsal fin origin posteriad is more darkly pigmented than the rest of the body, and grades to a solid black pigment at the caudal fin base. Juveniles of some *Nansenia* species develop heavy melanistic pigment at the base of the caudal fin and often at the base of the adipose fin (Schmidt, 1918; Kawaguchi and Butler, in press).

Bathylagids have a direct transformation and undergo a marked morphological change from the slender larval form to the juvenile form, characterized by a large head and eyes and deeper body. The gut becomes coiled and covered by a black peritoneal sheath. The head becomes heavily pigmented but the body is slower to develop the black pigment characteristic of all *Bathylagus* species (other than the *B. stilbius* group) and, in species such as *B. euryops* and *B. milleri*, the large larval melanophores are visible in specimens up to 30 mm and 50 mm respectively.

In the deep-bodied opisthoproctid genera transformation to the juvenile stage is marked by deepening of the body and attainment of melanistic integument and large scales. Cohen (1960) described the large (up to 124 mm) transitional specimens of *Bathylychnops* which are semi-transparent and retain the large larval pigment blotches. Sexually mature specimens of *Dolichopteryx* are semi-transparent, have a membranous body envelope, poorly developed musculature, an exposed gut covered only by peritoneum, weakly attached fins and melanistic pigment of the type usually associated with larvae (Cohen, 1960).

RELATIONSHIPS

Our survey of argentinoid ontogenetic characters provides insight into some of the systematic questions posed at the beginning of the paper. A close relationship between argentinoids and alepocephaloids is not supported since the latter hatch from large eggs (estimated at 3–4 mm based on size of yolk-sac larvae), have direct development, and share no specialized ontogenetic characters with argentinoids. Four major argentinoid lineages can be defined by specializations of the eggs and larvae and thus four families recognized: Argentinidae, Microstomatidae, Bathylagidae, and Opisthoproctidae. *Argentina* and *Glossanodon* have generalized larvae except that all known species have distinct lateral series of melanistic blotches or bands, not found elsewhere among argentinoids. The pattern of banding does not separate the two genera.

All known bathylagid eggs have multiple oil globules. A number of bathylagid groups are apparent from larval characters: 1) *milleri*, 2) *stilbius-schmidti-urotranus*, 3) *euryops-pacificus-antarcticus*, 4) *bericoides-longirostris*, 5) *wesethi-argyrogaster-nigrigenys*. Of these groups, *stilbius-schmidti-urotranus* has the most generalized morphology and pigmentation, lending no support for its separation as a distinct genus.

Opisthoproctid larvae share a number of neotenic features, including a saccular stomach. Except for body shape, *Dolichopteryx* shares more derived larval characters with the deep-bodied genera than with *Bathylychnops*, and the latter has a number of characters unique to opisthoproctids. Division of the family based on body shape is not supported by ontogenetic evidence.

Ontogeny offers little information on species composition of genera, because only a fraction of argentinoid eggs and larvae are known. However, egg and larval characters clearly separate Atlantic and Pacific *Microstoma* as distinct species. *Bathylagus bericoides* larvae from the Atlantic and Pacific are indistinguishable. The same is true for *B. longirostris* from all oceans. *Bathylagus nigrigenys* and *B. argyrogaster* larvae are indistinguishable, lending support for a single circumtropical species. *Bathylagus stilbius* eggs and larvae are indistinguishable from those of *B. urotranus*.

We have attempted to analyze the distribution among four nominal groups of argentinoids, of 14 characters, four of which are taken from developmental stages and 10 from the adult (Table 42). We have used teleosts in general and osmerids as our outgroup following Fink and Weitzman (1982). Distribution of character states are presented in Table 43.

A possible arrangement of groups based on the fewest number of character reversals is presented in Figure 88. Opisthoproctidae appears to be a well-founded family. More precise interpretation of the inter-relationships and nomenclatural ranking for argentinids, microstomatids, and bathylagids requires additional data.

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