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Families Gonostomatidae, Sternoptychidae, and Associated Stomiiform Groups: Development and Relationships

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A summary of known information about the larvae and relationships of the stomiiforms with elongate gill rakers in adults was published by Ahlstrom (1974). The present paper is an addendum to that contribution and includes additional information, both published and unpublished, gleaned from early life history stages and from adults. We also append some tentative new hypotheses of relationships within this "group" of stomiiforms.

TABLE 47. SUMMARY OF DIAGNOSTIC CHARACTERS FOR EGGS OF CERTAIN STOMIIFORM FISHES.

Species	Egg diameter	Oil globule	Diameter	Yolk	Special features	Illustrated	Source
Argyropelecus hemigymnus	0.92–1.04	1	0.26–0.28	segmented	large oil globule	Yes	Sanzo, 1928
Ichthyococcus ovatus	0.80	1	0.24	segmented	large oil globule	Yes	Sanzo, 1930b
Maurolicus	1.63	1	0.25	segmented	hexagonal pattern	Yes	Mito, 1961a
muelleri	1.32–1.58	1	0.26–0.28	segmented	on shell	Yes	Sanzo, 1931d
Vinciguerria lucetia	0.58–0.74	none		irregularly segmented	thin inner shell membrane	Yes	Ahlstrom and Counts, 1958
poweriae	0.75–0.85	1	0.17–0.19	segmented	no thin inner shell membrane	Yes	Ahlstrom and Counts, 1958
nimbaria	0.64–0.72	none		irregularly segmented	thin inner shell membrane	No	Ahlstrom and Counts, 1958
attenuata	0.84–0.92	1	0.18–0.195	segmented	no thin inner shell membrane	No	Sanzo, 1931d
Gonostoma denudatum	0.80–0.81	1	0.20–0.21	—	—	No	Sanzo, 1931d

Ahlstrom (1974:672) favored recognition of one family for those stomiiforms with elongate gill rakers in adults. According to the rules of priority this would be the Sternoptychidae. Weitzman (1974:338) recognized three families, Gonostomatidae, Photichthyidae, and Sternoptychidae, for the same stomiiforms, the last family including the "maurolicin" genera formerly assigned to the Gonostomatidae and the deep-bodied sternoptychids traditionally assigned to the family. In a phylogenetic or cladistic analysis this elongate gill raker bearing "group," if recognized as a single family, is paraphyletic if one considers certain of its subgroups as equivalent or higher taxonomic categories. For example, recognition of Ahlstrom's Sternoptychidae, which would include the Stomiidae, a monophyletic group with its members having a median barbel attached to the ventral surface of the head in association with the hyoid bone and lacking elongate gill rakers in adults, is incompatible with a phylogenetic classification based on nested monophyletic groups, since the Stomiidae is the sister group of another group within Ahlstrom's Sternoptychidae. Furthermore, the character used here to "define" the paraphyletic Sternoptychidae, the presence of elongate gill rakers in adults, is excellent for use in a key for identification purposes, but cannot be used as a synapomorphy relating these fishes because it is primitive for stomiiforms. Ahlstrom's Sternoptychidae is undefinable in a phylogenetic analysis based on the information at hand. A resolution of the use of familial and subordinal names in stomiiform fishes must await completion of ongoing phylogenetic studies of these fishes. Because these studies are incomplete, it is difficult to make recommendations for names of certain stomiiform subgroups. Among the stomiiforms with elongate gill rakers in adults, the "family" problem is more complex than that recognized by Ahlstrom (1974) or Weitzman (1974). We here recognize two family names but these apply to only some of the 24 genera listed below. We recognize the Sternoptychidae of Weitzman (1974) and the Gonostomatidae in a new and restricted sense. See discussion below.

The stomiiforms discussed here include the following 24 genera, listed alphabetically, which have been variously recognized as belonging to the families Gonostomatidae, Sternoptychidae, Maurolicidae, and Photichthyidae: *Araiophos* Grey (two species), *Argyripnus* Gilbert and Cramer (four, possibly a few more), *Argyropelecus* Cocco (about seven), *Bonapartia* Goode and Bean (one), *Cyclothone* Goode and Bean (twelve), *Danaphos* Bruun (one, possibly two), *Diplophos* Günther (two), *Gonostoma* Rafinesque (six), *Ichthyococcus* Bonaparte (three), *Manducus* Goode and Bean (two),[1] *Margrethia* Jespersen and Tåning (one, possibly two), *Maurolicus* Cocco (one, possibly two), *Photichthys* Hutton (one), *Pollichthys* Grey (one), *Polyipnus* Günther (about sixteen), *Polymetme* McCulloch (one, possibly four), *Sonoda* Grey (two), *Sternoptyx* Hermann (two or three), *Thorophos* Bruun (two, including *Neophos* Myers), *Triplophos* Brauer (one), *Valenciennellus* Jordan and Evermann (one, possibly two), *Vinciguerria* Jordan and Evermann (five), *Woodsia* Grey (one), and *Yarella* Goode and Bean (one).

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[1] Grey (1964:88) recognized *Manducus* Goode and Bean, 1896 as a junior synonym of *Diplophos* Günther, 1873 because, as she stated ". . . the differences appear to be of a specific rather than a generic nature . . ." This was in the context of the kinds of differences Grey noted separating other species of "gonostomatids." She did recognize both as subgenera of *Diplophos*. We recognize both as genera. The species were most recently reviewed by Mukhacheva (1978) who recognized four species, *D. maderensis* (Johnson), *D. rebainsi* Krefft and Parin, *D. greyae* R. K. Johnson, and *D. taenia* Günther. We have examined all four species and find that *D. taenia* and *D. rebainsi* have the cartilages of the two medial proximal pectoral radials, radials III and IV in the terminology of Fink and Weitzman (1982:66), fused while retaining two bony elements separate as reported for *D. taenia* by Fink and Weitzman (1982:65–67). Furthermore, one of the distal radials is out of line, not in a single series in these two species. These characters are specialized for these species. In *Manducus maderensis* and *M. greyae* there are four completely distinct proximal radials and the distal radials are all in a simple straight series. Because the pectoral radial morphology in *Diplophos taenia* and *D. rebainsi* may be an intermediate stage of a transition series between radials such as are found in *Manducus maderensis* and *M. greyae* and those in the "photichthyid" genera, we recognize *Manducus* as a genus and apparent sister group of the "photichthyid" genera as well as the Stomiidae, nearly all of which have the radials III and IV completely fused to one bone. A few stomiids have an apparent neomorph condition in which the third proximal radial is divided into two radials, giving a total of four proximal radials. See also text discussion.

TABLE 48. SUMMARY OF MERISTIC CHARACTERS FOR ADULTS OF CERTAIN STOMIIFORM FISHES.

Genera	No. species	Fin rays				Branchiostegal rays	No. of vertebrae	No. of gill rakers
		Dorsal	Anal	Pectoral	Pelvic			
Araiophos	2	13–20	20–29	16–18	5	9–11	43–45	2–3 + 12–19 = 14–22
Argyripnus	4+	11–12	11–15 + 8–12 = 22–29	15–19	6–7	8–10	41–46	4–7 + 12–19 = 16–26
Argyropelecus	7	(8) 9 (10)	6–8 + 5–6 = 11–13	10–11	?	?	34–40	15–24
Bonapartia	1	17–20	29–31	14–16	7–8	13–16	37	5–6 + 11–12 = 16–18
Cyclothone	12+	12–15	16–21	9–13	6–7	10–14	29–33	4–10 + 9–18 = 14–27
Danaphos	1	6	24–25	13–14	6	9–10	38	2 + 11–13 = 13–15
Diplophos	2	10–13	47–69	8–9	7	10–14	44–94	3 + 7–9 = 10–12
Gonostoma	6	10–18	21–31	9–13	6–8	10–13	37–40	5–11 + 10–17 = 15–27
Ichthyococcus	3	10–15	13–17	7–8	6–7	11–12	38–47	7–11 + 15–26 = 22–37
Manducus	2	11–13	36–59	9–11	8	11–14	63–76	3–5 + 8–10 = 12–14
Margrethia	1	15–16	21–26	13–15	8	13	34	5 + 10–11 = 15–16
Maurolicus	1	9–12	8–10 + 11–15 = 19–27	17–20	6–7	9–10	33–35	4–8 + 17–22 = 22–30
Photichthys	1	12–13	23–26	9	6–7	20–21	51	4–5 + 11 = 15–16
Pollichthys	1	10–12	22–30	8	6–7	11–12	40	4–5 + 11–12 = 15–17
Polyipnus	17	10–17	13–19	12–16	?	?	31–36	10–28
Polymetme	3	11–13	24–33	9–11	7 (8?)	12–14	44–45	5–8 + 9–12 = 15–19
Sonoda	2	8–9	8–10 + 14–16 = 22–25	13–15	6	8–10	40?	3–5 + 15–18 = 18–21
Sternoptyx	3	8–11	14–16	10–11	?	?	28–31	7–9
Triplophos	1	10–12	53–63	9–11	6–7	11–14	ca 60	9 + 14–16 = 23–25
Thorophos	2	8	38	13	7	7–8	40–45	5 + 13–14 = 18–19
Valenciennellus	2 or 3	7–12	22–25	12–13	6–9	9–10	32–33?	2–3 + 12 = 14–15
Vinciguerria	4	13–16	12–17	9–10	7	10–12	38–42	3 + 11–23–11 = 15–33
Woodsia	1	11–12	14	9–10	7–8	17	42–45	3–5 + 13 = 16–18
Yarella	2	14–16 (17)	(28) 29–31	8–10	6–7	13–16	45–54	6–7 + 12–16 = 18–22

TABLE 49. POSITION OF THE DORSAL AND ANAL FIN AND CONDITION OF THE ADIPOSE FIN IN CERTAIN STOMIIFORM FISHES.

Genus	Dorsal fin position		Adipose fin
	Adult	Larvae	
Araiophos	Anal origin in advance of dorsal fin. Dorsal origin opposite 5th or 6th anal ray	Anal opposite dorsal at 8 mm, adult position at 11 m	Present or absent
Argyripnus	Anal origin opposite dorsal origin	Anal origin opposite dorsal origin	Present
Argyropelecus	Anal origin opposite last dorsal fin ray	Anal origin behind dorsal fin	Present or absent
Bonapartia	Anal origin well in advance of dorsal by 9 rays	Same as adult	Absent
Cyclothone	Anal origin opposite dorsal fin or slightly behind	Same as adult	Absent
Danaphos	Anal origin behind dorsal fin	Same as adult	Absent
Diplophos	Anal origin beneath 5th ray or behind dorsal fin	Anal origin beneath end of or behind dorsal fin	Absent
Gonostoma	Anal origin opposite or 3–4 rays in advance of dorsal origin	Same as adult	Present or absent
Ichthyococcus	Anal origin behind dorsal fin by a space = ½ dorsal base	Anal origin behind dorsal fin	Present
Manducus	Anal origin beneath 3rd from last or last dorsal fin ray	Unknown	Absent
Margrethia	Anal origin beneath 5th dorsal fin ray	Same as adult	Present
Maurolicus	Anal origin beneath last dorsal fin ray	Anal origin beneath middle of dorsal fin, advances to adult condition as juveniles	Present
Photichthys	Anal origin behind dorsal fin	Unknown	Present
Pollichthys	Anal origin beneath 3rd dorsal fin ray	Anal origin advances forward beneath dorsal fin	Present
Polyipnus	Anal origin usually beneath middle of dorsal fin	Same as adult	Present or absent
Polymetme	Anal origin beneath end of dorsal fin	Unknown	Present
Sonoda	Anal origin in advance of dorsal. Dorsal origin above 5th anal ray	Unknown	Absent
Sternoptyx	Anal origin opposite dorsal origin	Anal origin behind dorsal fin	Present
Triplophos	Anal origin beneath end of dorsal fin	Unknown	Absent
Thorophos	Anal origin in advance of dorsal origin by 3 or 4 rays	Unknown	Present or absent
Valenciennellus	Anal origin 1 or 2 rays in advance of dorsal origin	Same as adult	Present
Vinciguerria	Anal origin beneath middle of dorsal fin	Same as adult	Present
Woodsia	Anal origin behind middle of dorsal fin by distance about = dorsal base	Same as adult	Present
Yarella	Anal origin beneath middle of dorsal fin	Same as adult	Absent

TABLE 50. DEFINITION OF ALPHABETICAL SYMBOLS USED FOR DESIGNATING PHOTOPHORES IN DEEP BODIED STERNOPTYCHIDS AND OTHER STOMIIFORM FISHES.

Other stomiiforms		Deep bodied sternoptychids	
Code	Definition	Code	Definition
SO	Symphyseal photophores (organs) located at tip of lower jaw.	SO	Subopercle photophore which is equivalent to posteriomost photophore in opercular series of gonostomatids.
Orb	Photophores associated with the eye located anterior and posterior of orbit.	PO	Photophore located anterior to orbit.
Op	Photophores on opercle series generally three, coded as follows 1/(1 + 1).	PTO	Photophore located posterior to orbit and may be equivalent to upper photophore of opercular series of gonostomatids.
Br(BRP)	Photophores located on the branchiostegal membranes.	PRO	Preopercular photophore, used for an PO photophore dorsal to ventral limb or preopercle.
Is(I)	Photophores located on the isthmus.	Br	Same as gonostomatid definition.
IP	Photophores of the ventral series found from the isthmus to the base of the pectoral fin.	Is	Same as gonostomatid definition.
PV	Photophores of the ventral series found from the pectoral fin base to the pelvic (ventral) fin base.	AB	Photophores of ventral series located abdominally between pectoral fin base and pelvic fin base and equivalent to PV in gonostomatids, plus a few posterior photophores of the IP series.
VAV	Photophores of the ventral series found from the pelvic (ventral) fin base to the anal fin base.	PAN	Photophores found anterior to anal fin and may be equivalent to VAV or VA in gonostomatids.
AC	Photophores of the ventral series found from the anal fin base to caudal fin base of the ventral series.	AN	Photophores found above anal fin.
IC	Summary of photophores of the ventral series from the isthmus to caudal fin base (IP+PV+VAV+AC).	SC	Photophores found on lower (sub) caudal peduncle. Together with AN group may be equivalent to AC in gonostomatids.
IV	Summary of photophores of the ventral series from isthmus to pelvic (ventral) fin base (IP+PV).	SAB	Photophores located above (supra) to the abdominal series and may be equivalent to VA in gonostomatids.
OV	Photophores of the lateral series from the opercle to pelvic (ventral) fin base.	SP	Photophores located above (supra) the pectoral fin and may be equivalent to OV in gonostomatids.
VA(VALA)	Photophores of the lateral series from the pelvic (ventral) fin base to the anal fin base.	L	Photophore located laterally above PAN (found only in *Polyipnus*).
OAA	Summary of photophores of OV plus VA series.	SAN	Photophores located above (supra) to anal photophores and equivalent to part of AC series.
OA(OAB)	Summary of lateral photophores from the opercle to anal fin base (OV+VA).		
OAC(OC)	Entire lateral series on body sides just dorsal to ventral series and extending from opercular border, or just medial to it, over anal fin to caudal fin base.		
ODM	Photophores (organs) found dorsal to the lateral midline (found only in *Gonostoma gracile*).		

Some genera are extremely rare (i.e., *Thorophos* and *Sonoda*) while others represent the most abundant vertebrate animals on earth (*Cyclothone* and *Vinciguerria*).

Developmental information has been published for 16 of these genera (12 prior to Ahlstrom, 1974; 3 by Ahlstrom, 1974; and one by Ozawa, 1976).

DEVELOPMENT

Eggs.—Eggs were described for *Argyropelecus hemigymnus* by Sanzo (1928); for *Ichthyococcus ovatus* by Sanzo (1930b); for *Maurolicus muelleri* by Sanzo (1931d), Mito (1961a), and Okiyama (1971); for *Vinciguerria lucetia*, *V. poweriae*, and *V. nimbaria* by Ahlstrom and Counts (1958); for *V. attenuata* by Sanzo (1931d); and for *Gonostoma denudatum* by Sanzo (1931d). Other accounts provide minimal details of ovarian eggs of other species. The details of egg characters are summarized in Table 47.

Larvae.—Much has been accomplished for the identification of the larvae of these stomiiform genera and now descriptions are available for all except *Manducus*, *Triplophos*, *Polymetme*, *Photichthys*, *Thorophos*, and *Sonoda*. The larvae tentatively identified as *Polymetme* by Ahlstrom (1974), on further examination by one of us (Richards), were determined to be *Pollichthys*. One stomiiform larval form has been described but not assigned to a genus [designated "Maurolicine Alpha" by Ahlstrom (1974: 670)]. It presumably is the larva of some sternoptychid (as defined by Weitzman, 1974). Descriptive details and illustrations of several species were given by Ahlstrom (1974). Here we provide new or additional data including characters useful in identifying these larvae and illustrations of all the species described to date, including some illustrated for the first time.

The identification of stomiiform larvae with elongate gill rakers as adults requires a knowledge of developmental data from larvae, juveniles, and data from adults of the following characters: counts of fin rays, teeth, and other meristic characters as photophores; patterns of photophore development; and distributions (patterns) of dark chromatophores (dark pigment cells). With those sets of data, nearly all species should be identifiable at least to genus, and in cases of complete data, to species. A

TABLE 51. PHOTOPHORE DISTRIBUTION IN CERTAIN STOMIIFORM GENERA. Refer to text and Table 50 for definition of codes.

	No. of rows	SO	ORB	OP	BR	IS	IV	VAV	AC	Photophores in group of glands
Araiophos	1	No	1	1	5–7	Yes	(2) + (3) + 3–4 + (2) = 10–11	3–5	6–8	Yes
Argyripnus	2	No	1	3	6	Yes	(6) + (10)	(18–28)	(4–5) + (12–18) = 35–51	Yes
Argyropelecus	2	No	2	2	6	Yes	18	4	10	Yes
Bonapartia	1	Yes	1	3	11–13	No	14–16	5–6	18–20	No
Cyclothone	2	No	1	2	8–11	No	12–14	4–5	12–16	No
Danaphos	2	No	1	2–3	6	Yes	18	5	22–26	Yes
Diplophus	3+	Yes	1	3	7–12 + 0–3	Yes	33–49	13–17	33–49	No
Gonostoma	2	Yes	1	2–3	9	No	11–16	3–10	15–23	No
Ichthyococcus	2	No	2	3	11–12	Yes	25–28	9–14	12–14	No
Manducus	2+	Yes	1	3	8–13	Yes	30–33	12–14	28–39	No
Margrethia	1	No	1	3	9–12	No	13–15	4	17	No
Maurolicus	2	Yes	1	3	(6)	Yes	(6) + (12–13) = 18–19	(6)	1 + (14–18) + (7–9) = 22–27	Yes
Photichthys	2	Yes	2	3	17–18	Yes	10 + 14–15 = 24–25	15–17	16–18	Yes
Pollichthys	2	Yes	2	3	8	Yes	21–23	7–9	18–21	No
Polyipnus	2	No	2	2	6	Yes	16	5	10–18	Yes
Polymetme	2	Yes	1	3	9–10	Yes	19–21	7–8	21–25	No
Sonoda	2	No	1	3	6–7	Yes	6 + 10 = 16	7–8	(16–21) + (19–24) or (5–6) + (5–6) + (5–6) = 36–43	Yes
Sternoptyx	2	No	2	2	3	Yes	15	3	7	Yes
Triplophos	2 + 3 or 4	Yes	1	3	8–13	Yes	24–30	5–7	35–41	No
Thorophos	2	Yes & no	1	3	6	Yes	17	5	13–15	Yes
Valenciennellus	2	No	1	3	6	Yes	(3) + (4) + (16–17) = 23–24	(4)–(5)	3–6 or 9–17	Yes
Vinciguerria	2	Yes or no	2	3	7–9	Yes	21–24	7–11	12–15	No
Woodsia	2	Yes	2	3	14	Yes	25	11–12	12	No
Yarella	2+ sev	Yes	1	3	11–13	Yes	23–25	9–12	20–28	No

summary of several meristic characters for genera is given in Table 48. The position of the dorsal and anal fins is also a helpful aid, but caution must be used since their positions relative to other structures may change with growth. Also, the presence or absence of the adipose fin is helpful, but again, caution is in order because this fin is fragile and often damaged or lost due to contact with a net. These fin features are given in Table 49. Of special importance in identifying larvae and adults is the distribution and patterns of the photophores. This includes the number in each series, the patterns of their distribution in relation to each other, and especially the sequence of development which Ahlstrom (1974) stressed. Some confusion appears in the literature because more than one alphanumeric code has been developed to indicate, in some cases, the same sets of photophores in different stomiiform groups. A further complication is that the deep-bodied sternoptychids have a different code because of their altered body shape as adults and homologies were considered uncertain. Weitzman (1974:461), because he united the "maurolicin" and deep-bodied stomiiforms as one family considered the different terminologies "artificial" and as obscuring homologies. He therefore discussed and presented a synonymy of stomiiform photophores. We have defined the alphabetical codes in Table 50 and included what we believe are equivalent photophores in stomiiforms. In this code, parenthetical numbers indicate photophores found in common glands whereas non-parenthetical numbers indicate that the photophores are single. The distribution of photophores for each genus is given in Table 51. Table 52 provides sequences of photophore formation for *Bonapartia, Margrethia,* and *Gonostoma.* Table 53 provides similar information for *Araiophos, Maurolicus, Danaphos, Valenciennellus,* and *Argyripnus*; while Table 54 provides similar data for *Polyipnus, Argyropelecus,* and *Sternoptyx.* Diagnostic pigmentation and morphometric characters are summarized in Table 55. Illustrations (Figs. 98 to 104) are provided for the genera for which larvae are known and for many of the known species. In addition, the following authors provide specific information which will aid in larval identifications: Jespersen and Tåning (1919, 1926), Sanzo (1931d), Ahlstrom and Counts (1958), Ahlstrom and Moser (1969), Ozawa (1976), Grey (1964), Badcock and Merrett (1972), Kawaguchi and Marumo (1967), Okiyama (1971), Badcock (1982), Rudometkina (1981), Gorbunova (1981), Mukhacheva (1964), and Ahlstrom (1974).

RELATIONSHIPS

There has been a dichotomy of opinions about the interrelationships of the genera and the use of family names based on the use of larval versus adult morphological characters. Ahlstrom (1974:670–672) presented his views on this group based on larval characters, principally the mode of photophore formation. The suggested relationships resulting from his analysis contrasted in part with those of Weitzman (1974:472), whose views were based on study of adult osteology and soft anatomy Both Ahlstrom and Weitzman in addition to their own data,

TABLE 52. Sequence of Photophore Formation in *Bonapartia*, *Margrethia*, and *Gonostoma*.

		ORB	OP	SO	BR	PV	VAV	AC	OA + ODM	Source
Bonapartia pedaliota	adult	1	3	1	11–13	14–15	5–(6)	16–18 + 2–3	0	Grey, 1964
	9.5	0	1	0	2	3	0	0	0	Grey, 1964
	11.5	0	1	0	3	5	2	0	0	Original
	12.0	0	1	0	4	5	2	0	0	Grey, 1964
	14.0	1	1	0	5	10	4	3 + 1	0	Grey, 1964
	15.0	1	1	0	5	9	3	1 + 1	0	Original
	16.0	1	1	0	6	11	5	5 + 2	0	Jespersen and Tåning, 1919
	23.0	1	3	0	11	14	5	14 + 2	0	Grey, 1964
Margrethia obtusirostra	adult	1	3	0	9–12	13–15	4	13–14 + 3–4	0	Grey, 1964
	5.8	0	1	0	0	2	0	0	0	Ahlstrom, 1974
	6.4	0	1	0	0	6	2	1 + 2	0	Ahlstrom, 1974
	8.0	0	1	0	2	10	4	1 + 2	0	Ahlstrom, 1974
	11.3	–	2	0	6	14	4	5 + 3	0	Ahlstrom, 1974
	15.0	1	3	0	9	14	4	11 + 4	0	Ahlstrom, 1974
Gonostoma elongatum	adult	1	3	1	9	15	(4)–5	21–23	13–15	Grey, 1964
	6.0	0	1	0	0	0	0	0	0	Ahlstrom, 1974
	7.5	0	1	0	0	5	0	0	0	Ahlstrom, 1974
	7.9	0	1	0	0	4	0	0	0	Original
	10.2	0	1	0	2/1	10	2	0	0	Ahlstrom, 1974
	13.0	0	1	0	2	11	3	0	0	Ahlstrom, 1974
	14.0	1	1	0	2	11	2/3	1+	0	Grey, 1964
	16.7	1	1	0	3	11	4	1+	0	Jespersen and Tåning, 1919
	22.5	1	3	1	9	15	5	22	13	Grey, 1964
Gonostoma denudatum	adult	1	3	1	9	15–16	5	17–20	13–15	Grey, 1964
	18.25	0	1	0	0	1	0	0	0	Sanzo, 1912b
	19.0	0	1	0	0	2	0	+2	0	Sanzo, 1912b
	20.75	0	1	0	1	3	1	+3	0	Sanzo, 1912b
	24.75	0	1	0	3	6	3	3 + 3	0	Sanzo, 1912b
	29.65	0	2	0	5	14	5	11 + 3	0	Sanzo, 1912b
	34.0	1	3	0	9	16	5	15 + 5	13	Sanzo, 1912b
	39.0	1	3	1	9	16	5	15 + 5	13	Sanzo, 1912b
Gonostoma gracile	adult	1	2	1	9	13–15	4–5	17–19	11–12 + 6–7	Kawaguchi and Marumo, 1967
	15.5–5–17.0	0	1	0	0	0	0	0	0	Kawaguchi and Marumo, 1967
	20.0	1	2	1	2	13	5	17	0	Kawaguchi and Marumo, 1967
	22.0	1	2	1	9	14	4	18	12 + 4	Kawaguchi and Marumo, 1967
Gonostoma ebelingi	adult	1	2	1	9	15	10	19	21	Grey, 1964
	13.8	0	1	0	0	7	0	0	0	Ahlstrom, 1974
	15.0	0	1	0	0	9	0	0	0	Ahlstrom, 1974
Gonostoma bathyphilum	adult	1	2	0	9	11–12	4–5	20–21	14	Grey, 1964
	11.0	0	1	0	0	5	0	0	0	Ahlstrom, 1974
	14.8	1	1	0	4	10	2	0	0	Ahlstrom, 1974
Gonostoma atlanticum	adult	1	2	1	9	15–16	5	19	13	Grey, 1964
	12.0	0	1	0	0	0	0	0	0	Ahlstrom, 1974
	13.0	0	1	0	0	1	0	0	0	Ahlstrom, 1974
	14.5	0	1	0	0	2	0	0	0	Ahlstrom, 1974
	17.8	1	1	0	4	13	3	1	0	Original
	18.8	1	2	0	9	16	5	19	0	Ahlstrom, 1974
	23.8	1	3	0	9	16	5	19	13	Original

used the results of photophore anatomy research by Bassot (1966, 1971) to support their conclusions. These results seemingly completely supported Weitzman's referral of genera to family groups and agreed with Ahlstrom except for placement of three genera—*Cyclothone*, *Diplophos* (including *Manducus*), and *Triplophos*.

One of us (Weitzman), continues to study relationships of the stomiiforms with elongate gill rakers in adults and we offer the following analysis as a current comment on the status of our knowledge of these fishes. The two concepts of relationships by Ahlstrom and Weitzman may be compared as follows: Ahlstrom (1974:670–672) stressed relationships of taxa based on photophore patterns and development. Ahlstrom (1974:672) considered the stomiiforms with elongate gill rakers in adults as a group comprised of three groups of genera, with any subdivision being into two subfamilies based on photophores occurring individually or in clustered groups. These groups of genera include: (1) Those with individual separate photophores, most of the photophores developing simultaneously and initiated as a "white" photophore stage. This group includes *Manducus*, *Diplophos*, *Cyclothone*, *Yarella*, *Pollichthys*, *Vinciguerria*, *Woodsia*, *Ichthyococcus*, and presumably *Triplophos* and *Polymetme*,

TABLE 53. SEQUENCE OF PHOTOPHORE FORMATION IN *ARAIOPHOS*, *MAUROLICUS*, *DANAPHOS*, *VALENCIENNELLUS*, AND *ARGYRIPNUS*.

		ORB	OP	SO	BR	IP	PV	VAV	AC	OA	Source
Araiophos eastropas	adult	1	1	0	(6)	(2)	(3) + 3–4 + (2)	(3)	(2) + 2 + (2)	No	Ahlstrom and Moser, 1969
	11.2	0	0	0	(3)	0	(2)	0	0	—	Ahlstrom and Moser, 1969
Maurolicus muelleri	adult	1	3	1	(6)	(6)	(12)	(6)	3/(4) + (8)	(2) + 7	Ahlstrom, 1974
	5.5	0	0	0	(1/2)	0	0	0	0	0	Ahlstrom, 1974
	6.2	0	0	0	(2)	0	(2)	0	0	0	Ahlstrom, 1974
	6.5	0	0	0	(2)	0	(4)	0	0	0	Ahlstrom, 1974
	6.7	0	1	0	(3)	0	(5)	0	0	0	Ahlstrom, 1974
	6.9	1	1	0	(4)	0	(8)	0	0	0	Ahlstrom, 1974
	7.5	1	1	0	(4)	1	(9)	0	0 + (2) + 0	0	Ahlstrom, 1974
	8.6	1	2	0	(5)	(3)	(12)	(2)	0 + (3) + (3)	0	Ahlstrom, 1974
	9.0	1	2	0	(5)	(3)	(11)	(2)	0 + (3) + (3)	1	Ahlstrom, 1974
	9.7	1	3	0	(5)	(5)	(11)	(3)	0 + (4) + (6)	(2) + 1	Ahlstrom, 1974
	10.8	1	3	0	(6)	(5)	(12)	(4)	0 + (5) + (6)	(2) + 2	Ahlstrom, 1974
	13.5	1	3	0	(6)	(6)	(12)	(6)	0 + (9) + (7)	(2) + 6	Ahlstrom, 1974
Danaphos oculatus	adult	1	3	0	(6)	(3) + (4)	(11)	(5)	(3) + 16 + (4) + 1	6	Ahlstrom, 1974 Ahlstrom, 1974
	16.5	0	0	0	(2)	0	0	0	0	0	Ahlstrom, 1974
	16.5	0	0	0	(3)	0	(3)	0	0	0	Ahlstrom, 1974
	19.2	0	0	0	(4)	0	(10)	0	0	0	Ahlstrom, 1974
	21.0	1	1	0	(5)	(2) + (4)	(10/11)	0	(2) + 0 + 0 + 0	0	Ahlstrom, 1974
	21.3	1	1	0	(4/5)	(3) + (4)	(10)	0	(3) + 0 + (2) + 0	0	Ahlstrom, 1974
	21.8	1	2	0	(5)	(3) + (4)	(11)	(2)	(3) + 8 + (4) + 0	2	Ahlstrom, 1974
	24.2	1	2	0	(6)	(3) + (4)	(11)	(2)	(3) + 9 + (4) + 0	2	Ahlstrom, 1974
Valencinnellus tripunculatus	adult	1	3	0	(6)	(3) + (4)	(16–17)	(4–5)	(3) + (3) + (3) + (2) + (4)	(2) + 3	Ahlstrom, 1974
	7.8	0	0	0	0	0	0	0	0	0	Original
	8.6	0	0	0	(3)	0	(3)	0	0	0	Ahlstrom, 1974
	9.5	0	0	0	(4)	0	(6)	0	0	0	Ahlstrom, 1974
	11.0	0	0	0	(4)	0	(10)	0	0	0	Original
	12.0	0	0	0	(4)	0	(13)	(2)	0	0	Ahlstrom, 1974
	12.4	1	0	0	(5)	0	(15)	(2)	0	0	Original
	13.0	1	0	0	(5)	(2)	(15)	(2)	0	0	Original
	13.2	0	0	0	(4)	0	(14)	(3)	0	0	Ahlstrom, 1974
	14.0	1	0	0	(5)	(4)	(15)	(5)	0	0	Original
	17.0	1	2	0	(4–5)	(3) + (4)	(15)	(5)	(3) + (3) + 0 + (3) + (4)	(2)	Grey, 1964
Argyripnus atlanticus	adult	1	3	0	(6)	(6)	(10)	(26)	(5) + (17)	(3) + 4	Badcock and Merrett, 1972
	18.7	1	2	0	(6)	(3)	(10)	(3)	(4) + (4)	0	Badcock and Merrett, 1972
	16.8	1	2	0	(6)	(3)	(10)	(2)	(4) + (3)	0	Badcock and Merrett, 1972

although their development is not known. (2) Those with individual, separate photophores that have a gradual, protracted metamorphosis. This group includes *Bonapartia*, *Margrethia*, and *Gonostoma*. (3) Those with some individual photophores but some or most of the photophores with common bases [actually a common lumen, during development at least] and having a gradual, protracted metamorphosis. This group includes *Araiophos*, *Maurolicus*, *Danaphos*, *Valenciennellus*, *Argyripnus*, *Polyipnus*, *Argyropelecus*, *Sternoptyx*, and presumably *Thorophos* and *Sonoda* although their development is unknown. Groups (1) and (2) comprised the subfamily Gonostomatinae and Group (3) comprised the Sternoptychinae in Ahlstrom's concept. Group (3) is equivalent to Weitzman's Sternoptychidae. The genus *Gonostoma* was considered "pivotal" by Ahlstrom; that is, its relationships could be with either the gonostomatines or the sternoptychines of his concept. In Ahlstrom's conclusions, the photophore pattern of Group (1) is most like that of the stomiid groups discussed by Fink in this volume.

Weitzman's classification (1974) concentrated in most detail on a hypothesis of phylogenetic relationships within the family Sternoptychidae as he defined it. Weitzman (1974) pointed out that more detailed studies should be conducted on other stomiiform genera in the future, but he did discuss their possible relationships. Based on the number of proximal pectoral-fin radials, he established two infraorders for stomiiform fishes. Members of the Infraorder Gonostomata were considered to have four proximal pectoral-fin radials (except *Cyclothone* with one). This infraorder was divided into two families based principally on Bassot's photophore findings; Family Gonostomatidae with Beta type photophores comprised of *Diplophos* including *Manducus*), *Triplophos*, *Bonapartia*, *Margrethia*, *Gonostoma*, and *Cyclothone* and the Family Sternoptychidae with Alpha type photophores comprised of *Thorophos*, *Araiophos*, *Maurolicus*, *Danaphos*, *Valenciennellus*, *Argyripnus*, *Sonoda*, *Polyipnus*, *Argyropelecus*, and *Sternoptyx*. The problem with Weitzman's Gonostomata is that it was based on a primitive character for the stomiiforms, four pectoral-fin radials, and this character cannot be used as a synapomorphy to define a subgroup of stomiiforms. The non-sternoptychid and non-gonostomatid genera, along with the stomiiform families possessing barbels originating from the hyoid bone and lacking elongate gill rakers in the adults (the Stomiidae of Fink, this volume),

TABLE 54. SEQUENCE OF PHOTOPHORE FORMATION IN *POLYIPNUS, ARGYROPELECUS* AND *STERNOPTYX*.

	Size	PO	PTO	BR	IS	OP PRO + SO	SP	AB	SAB	PAN	AN	SAN	LSC	Source
Polyipnus polli	adult	1	1	6	6	1 + 1	3	10	3	5	8	3	14	Baird, 1971
	4.3	0	0	2	0	0 + 1	0	1	0	0	0	0	0	Original
	4.8	1	0	4	2	1 + 1	0	3	0	0	0	0	0	Original
	5.5	1	1	6	4	1 + 1	2	8	0	0	0	0	0	Original
	6.0	1	1	6	6	1 + 1	2	10	0	1	0	0	0	Original
	7.5	1	1	6	6	1 + 1	2	10	0	3	0	0	0	Original
	9.0	1	1	6	6	1 + 1	2	10	0	3	2	0	2	Original
	9.6	1	1	6	6	1 + 1	2	10	1	3	2	0	2	Original
	13.5	1	1	6	6	1 + 1	3	10	3	5	4	0	14	Original
	15.3	1	1	6	6	1 + 1	3	10	3	5	4	1	14	Original
	17.0	1	1	6	6	1 + 1	3	10	3	5	4	2	14	Original
	18.4	1	1	6	6	1 + 1	3	10	3	5	6	3	14	Original
	23.5	1	1	6	6	1 + 1	3	10	3	5	7	3	14	Original
Argyropelecus hemigymnus	adult	1	1	6	6	1 + 1	2	12	6	4	6	0	4	Baird, 1971
	10.92	0	0	4	6	0 + 1	0	7	0	0	1	0	2	Sanzo, 1931d
	9.92	0	0	6	6	0 + 1	0	9	0	0	2	0	3	Sanzo, 1931d
	7.84	1	0	6	6	1 + 1	2	12	0	0	3	0	4	Sanzo, 1931d
	11.20	1	1	6	6	1 + 1	2	12	2	3	4	0	4	Sanzo, 1931d
Arygropelecus sp.	adult	1	1	6	6	1 + 1	2	12	6	4	6	0	4	Baird, 1971
	4.5	0	0	0	0	0 + 0	0	0	0	0	0	0	0	Original
	9.5	0	0	6	6	0 + 1	0	6	0	0	1	0	0	Original
	9.5	0	0	6	6	0 + 1	0	8	0	0	3	0	0	Original
	7.0	1	0	6	6	1 + 1	2	12	0	0	3	0	3	Original
	7.0	1	0	6	6	1 + 1	2	10	0	0	3	0	4	Original
	7.4	1	1	6	6	1 + 1	2	12	4	4	4	0	3	Original
	10.0	1	1	6	6	1 + 1	2	12	5	4	5	0	4	Original
Sternoptyx sp.	adult	1	1	3	5	1 + 1	3	10	0	3	3	1	4	Baird, 1971
	4.8	0	0	0	0	0 + 1	0	0	0	0	0	0	0	Original
	7.5	0	0	0	0	0 + 1	0	0	0	0	0	0	0	Original
	7.8	0	1	2	3	0 + 1	0	4	0	0	0	0	0	Original
	8.1	0	1	2	4	0 + 1	2	7	0	0	0	0	0	Original
	7.6	0	1	2	5	0 + 1	3	10	0	1	3	0	1	Original

TABLE 55. DIAGNOSTIC PIGMENT CHARACTERS AND UNUSUAL MORPHOMETRIC FEATURES OF SOME STOMIIFORM LARVAE.

Genus/species	Diagnostic character
Diplophos taenia	Pigment spots on dorsal and ventral midline. Extremely elongated larvae.
Bonapartia pedaliota	Similar to *Gonostoma* but lacks deep pigment spot behind eyes and has pigment on medial portion of caudal peduncle.
Margrethia obtusirostre	A distinct vertical streak of pigment on caudal peduncle in most specimens.
Gonostoma	All species usually have deep pigment spot behind eyes. Specific differences among the species are as follows: *G. elongatum, G. gracile* and *G. ebelingi* lack pigment on caudal peduncle; *G. bathyphilum* has pigment spots on dorsal edge of caudal peduncle; *G. atlanticum* has pigment over medial portion of caudal peduncle (closely resembles *Cyclothone* in ventral pigmentation and swimbladder position); *G. denudatum* has broad streak of pigment diagonally over caudal fin base from dorsal caudal peduncle to base of lower caudal fin rays.
Cyclothone	A distinct, dark streak or intense melanophore over and parallel to the parhypural on the caudal fin base, pigmentation over gut and along ventral margin of tail and a conspicuous swimbladder.
Yarella blackfordi	Myosepta pigmented over caudal peduncle giving chevron appearance.
Pollichthys mauli	No pigment except for the eyes. Very similar to *Vinciguerria* in other aspects.
Vinciguerria	All species have medial or ventral margin caudal pigment spot. *V. nimbaria* and *V. lucetia* have the caudal pigment spot restricted to the ventral margin of the caudal fin base and pigment above the anal fin. *V. attenuata* and *V. poweriae* has the caudal pigment spot in a medial position and no pigment above the anal fin. *V. attentuata* has pigment over the airbladder which is lacking in *V. poweriae*. *V. poweriae* has a structure above the anal papilla which may appear as pigment. *V. mabahiss* is similar to *V. nimbaria* and is restricted to the Red Sea (Johnson and Feltes, 1984).
Woodsia nonsuchae	Melanophores profusely distributed on all myomeres below the lateral midline. Broad pigment band along roof of mouth continuous with trunk pigment. Also has a trailing gut and elongated rays on pectoral fin, both of which may be missing.
Ichthyococcus ovatus	Pigment profusely distributed on all myomeres below the lateral midline. Elongate pectoral fin rays and a trailing gut, both of which may be missing.

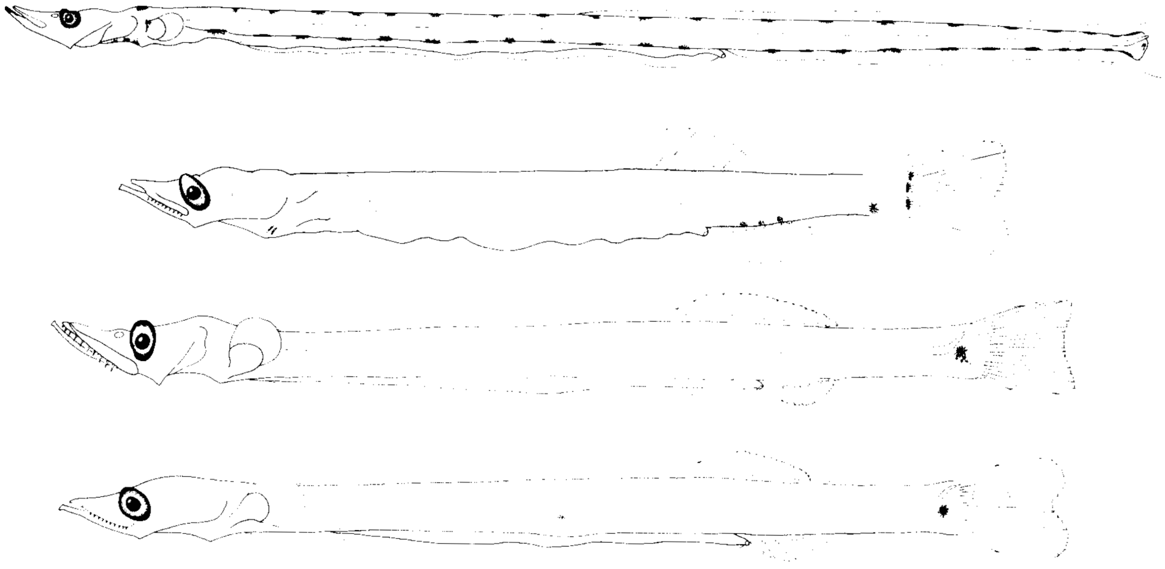


Fig. 98. Lateral views from top to bottom: *Diplophos taenia* 22.0 mm SL, R/V OREGON II Cr. 126, Sta. 36754, 27°30'N, 092°30'W, May 10, 1982, drawn by J. C. Javech; *Vinciguerria lucetia* 9.0 mm SL modified after Ahlstrom and Counts (1958); *Vinciguerria poweriae* 11.5 mm SL, R/V OREGON II Cr. 126, Sta. 36746, 27°59.9'N, 088°00'W, May 8, 1982, drawn by J. C. Javech; and *Vinciguerria attenuata* 9.7 mm SL modified after Jespersen and Tåning (1926).

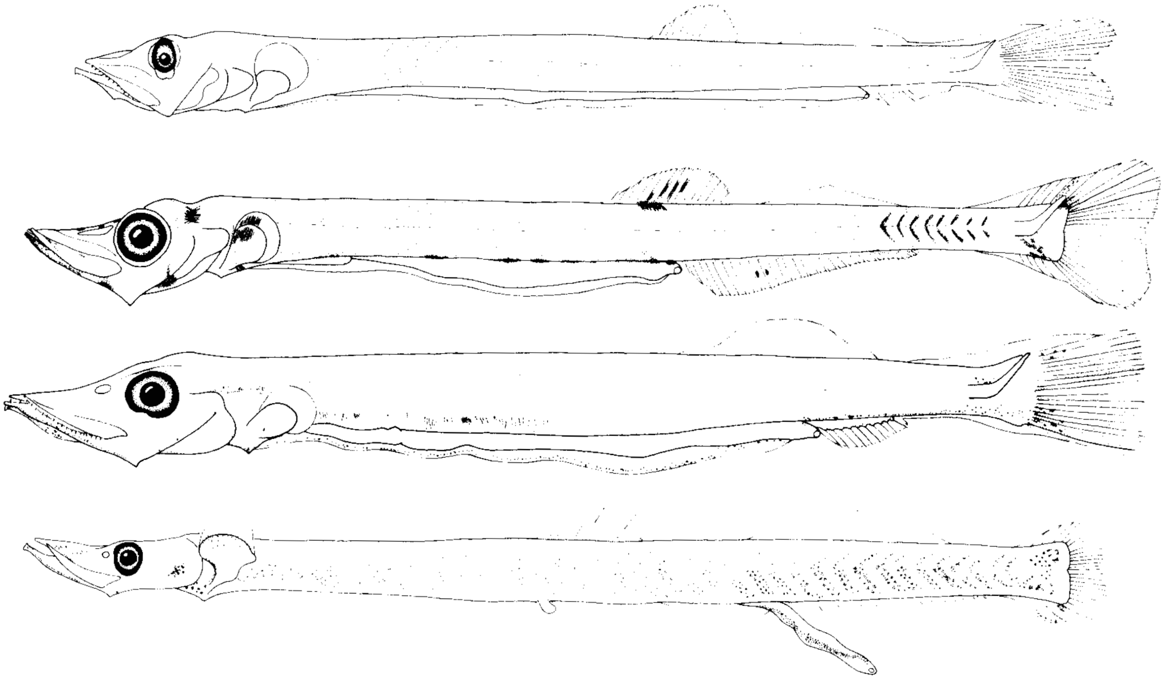


Fig. 99. Lateral views from top to bottom: *Pollichthys mauli* 14.5 mm SL, R/V OREGON II Cr. 126, Sta. 36688, 26°00.5'N, 0.88°00.4'W, April 20, 1982, drawn by J. C. Javech; *Yarella blackfordi* 23.5 mm SL, R/V OREGON II Cr. 126, Sta 36752, 27°30'N, 094°30.3'W, May 9, 1982, drawn by-J. C. Javech; *Woodsia nonsuchae* 11.5 mm SL, Eastropac, Sta. 75.225, drawn by J. C. Javech; and *Ichthyococcus ovatus* 18.1 mm SL, R/V OREGON II Cr. 126, Sta. 36746, 27°59.9'N, 0.88°00'W, May 8, 1982, drawn by J. C. Javech.

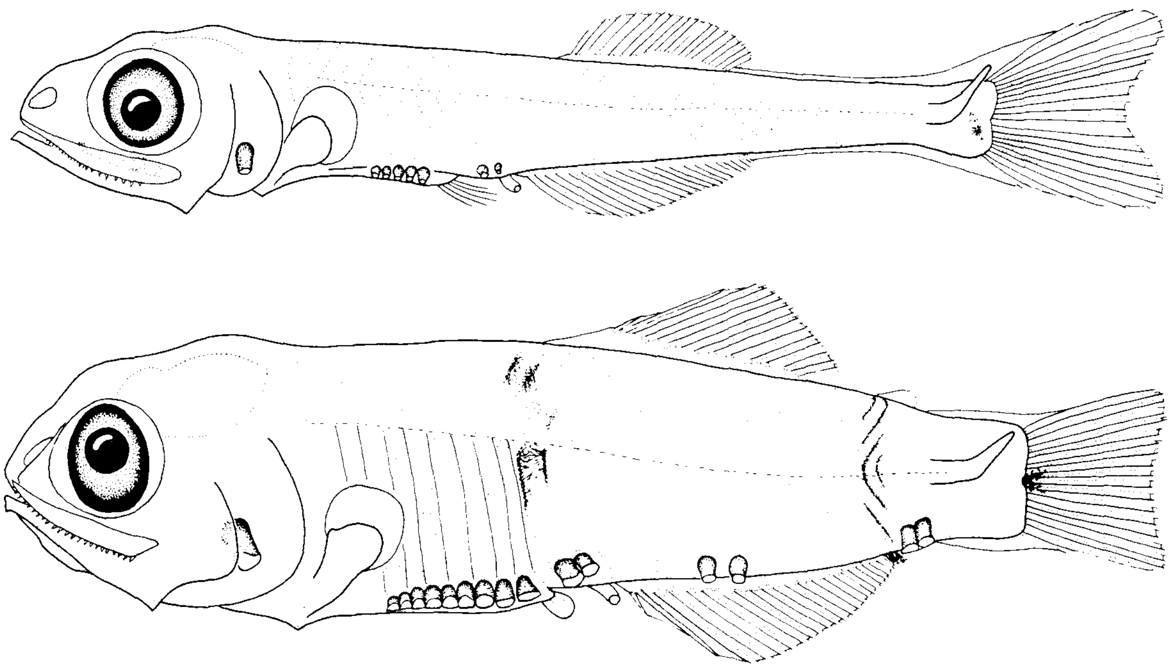


Fig. 100. Lateral views from top to bottom: *Bonapartia pedaliota* 11.5 mm SL, R/V OREGON II Cr. 126, Sta. 36688, 26°00.5′N, 088°00.4′W, April 20, 1982, drawn by J. C. Javech; *Margrethia obtusirostra* 6.7 mm SL, R/V OREGON II Cr. 126, Sta. 36773, 26°00.1′N, 094°00.2′W, May 23, 1982, drawn by J. C. Javech.

were placed in the Infraorder Photichthya. Nearly all have three, or rarely fewer, proximal pectoral-fin radials, a specialized character which can be used as a synapomorphy uniting this group. As noted above, there are a few exceptions which bear four proximal radials but these appear to be either reversals or are neomorphic. Within the Infraorder Photichthya the stomiiform genera with elongate gill rakers in adults were placed in the Family Photichthyidae comprised of the genera *Polymetme, Yarella, Pollichthys, Photichthys, Vinciguerria, Woodsia,* and *Ichthyococcus.* This placement was done on the basis of the presence of Type Gamma photophores in at least most of the genera, a specialization for the group (as well as for at least some of the stomiid genera) and therefore a synapomorphy. The presence of elongate gill rakers in this group is not a synapomorphy because it is primitive for the group.

Essentially, Ahlstrom and Weitzman disagreed on the relationships of three genera. Alhstrom's Group (1) was mostly equivalent to Weitzman's Photichthyidae but included three genera, *Cyclothone, Diplophos* (including *Manducus*), and *Triplophos,* placed in the Gonostomatidae by Weitzman. Otherwise, Weitzman's Gonostomatidae was equivalent to Ahlstrom's Group (2). Based on evidence available to Ahlstrom and Weitzman, on some supplementary evidence provided by Fink and Weitzman (1982), and on some of our own data, we here present a somewhat different arrangement based on a more rigorous phylogenetic analysis than done by Weitzman (1974). It turns out that Weitzman's analysis of the Sternoptychidae and its genera is consistently phylogenetic but that of outgroup stomiiforms is not. Ahlstrom (1974) did not attempt to analyze his groups phylogenetically. The evidence available now seems to resolve the conflict between Ahlstrom (1974) and Weitzman (1974). However, we would note that the analysis below is to be regarded as a guide to future studies rather than any sort of well-corroborated phylogeny. Parts, at least, of the arrangement need much additional study. Furthermore, the relationships of the genera in contention by Ahlstrom and Weitzman are still not fully clear. Some of these genera, *Manducus, Diplophos,* and perhaps *Triplophos,* are relatively primitive within stomiiforms with few characters specialized beyond the stomiiform level. This makes placing them in stomiiform subgroups difficult. *Cyclothone* is more derived but retains certain primitive stomiiform features and its relationship, although in our view is undoubtedly with the gonostomatids, at this time is somewhat uncertain because our data are not fully analyzed.

The conflict between Ahlstrom (1974) and Weitzman (1974) arose in part because they both utilized one or the other of certain characters, Type Beta photophores and "white" photophore development, as though they were shared specialized characters, synapomorphies indicating relationships. Instead, we believe these features are plesiomorphous for stomiiform subgroups and cannot be used to support a hypothesis of relationships among stomiiform genera. Our current analysis is as follows.

Fink and Weitzman (1982:69–75) list and discuss eight synapomorphies for stomiiform fishes. One of these, stomiiform-type photophores, was described in some detail based in part on Bassott (1966, 1971). Bassot (1966:574–576), Weitzman (1974:338), and Fink and Weitzman (1982:70) recognized Type Beta photophores as primitive for stomiiforms. Bassot (1966, 1971) recognized two other types of photophores, Type Alpha

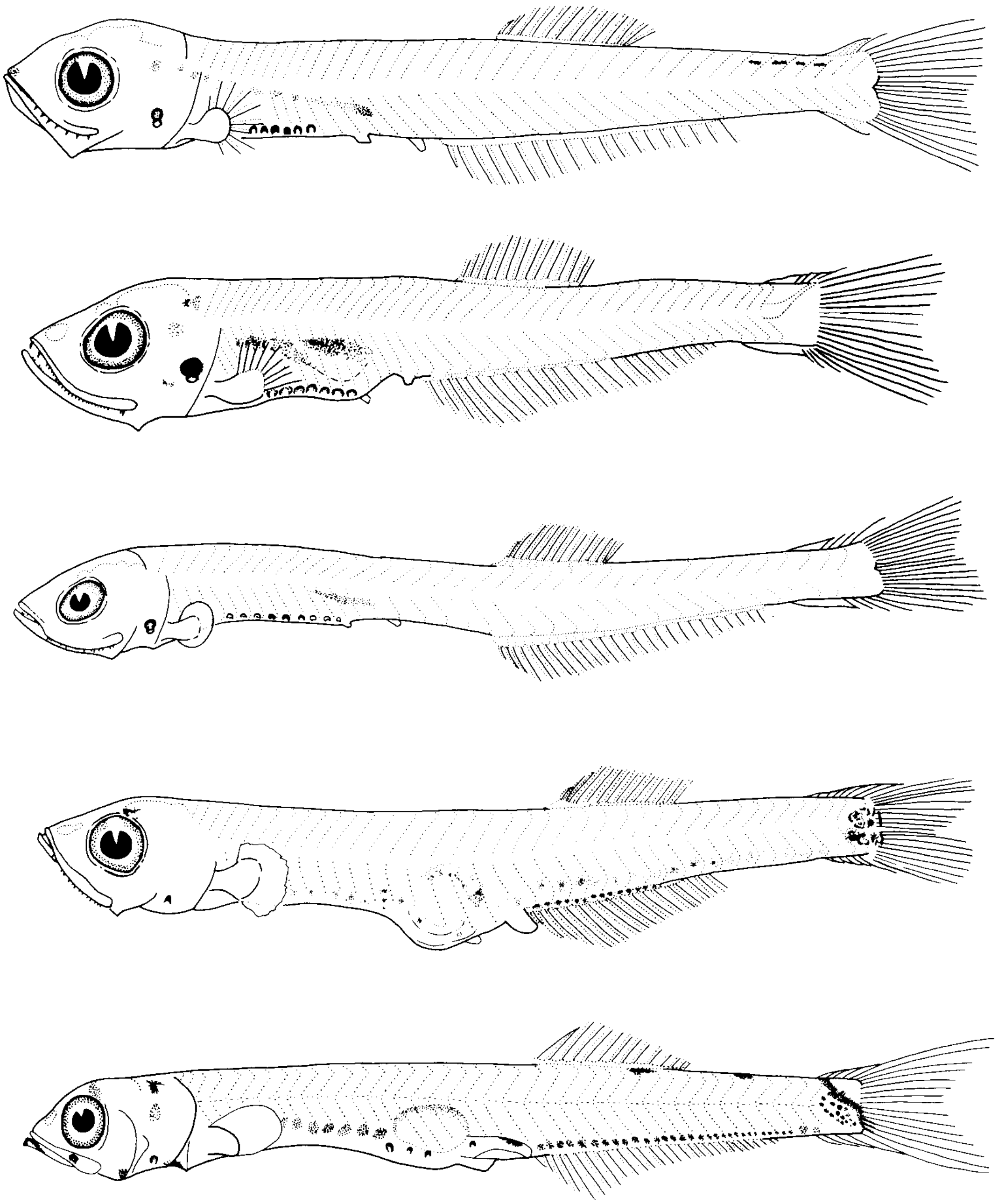


Fig. 101. Lateral view from top to bottom: *Gonostoma bathyphilum* 11.0 mm SL modified after Ahlstrom (1974); *Gonostoma elongatum* 9.8 mm SL modified after Ahlstrom (1974); *Gonostoma ebelingi* 15.0 mm SL modified after Ahlstrom (1974); *Gonostoma atlanticum* 12.0 mm SL modified after Ahlstrom (1974); *Gonostoma denudatum* 20.7 mm SL modified after Sanzo (1931d).

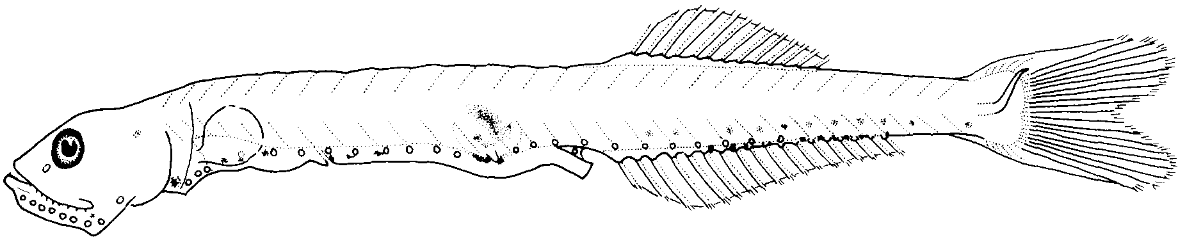


Fig. 102. *Cyclothone signata* 9.0 mm SL, drawn by H. Orr.

and Type Gamma, as being more specialized. This recognition, although not stated by these authors, is based on a concept that Types Alpha and Gamma photophores of some stomiiformes appear to be elaborations of Type Beta photophores. In other words, their particular features appear to be developmental terminal additions to Type Beta photophores and are therefore available for use as synapomorphies for stomiiform subgroups. Although more detailed analyses of these features are needed, for the sake of discussion we here accept that Type Beta photophores are primitive for stomiiforms.

Weitzman (1974:338), on the basis of outgroup comparison (not described or discussed in his text), considered four proximal pectoral-fin radials to be primitive for stomiiforms, their reduction to three or fewer to be specialized. We see no reason to change that analysis. Thus three or fewer proximal pectoral-fin radials are available as synapomorphous characters for stomiiform subgroups.

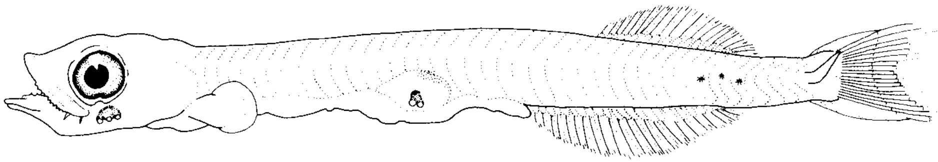
Ahlstrom (1974:660) described what can be labeled as "white" photophore development in which most, or at least the ventral series of photophores, are "laid down initially during a white photophore stage [before black pigment develops] and only a few photophores are late forming." One form or another of "white" photophore development is common to all stomiiforms except those including the gonostomatid genera *Bonapartia, Margrethia,* and *Gonostoma,* and the sternoptychids of Weitzman (1974). Members of these gonostomatid and sternoptychid genera have a protracted metamorphosis from the larval stage as well as a gradual, more extended photophore formation. This latter type of photophore development appears to be an elaboration of "white" photophore development and thus we consider white photophore development primitive with respect to the more complicated forms having prolonged photophore development. Again, much information of an anatomical and developmental nature remains to be gathered from the process of photophore development.

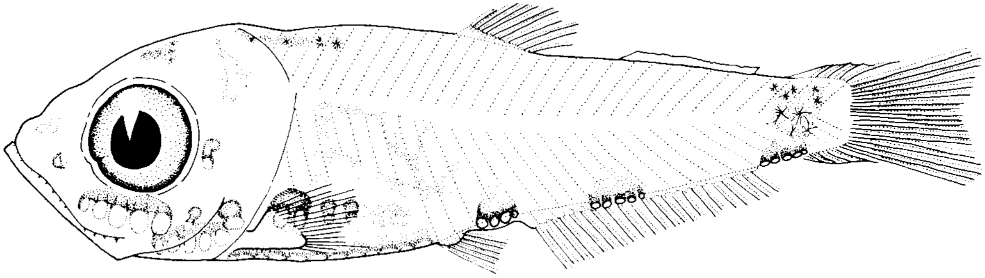
If "white" photophore development and Type Beta photophores are primitive in regard to stomiiform subgroups and therefore unavailable as synapomorphies for stomiiform subgroups, then the conflict regarding the distribution of characters among taxa between Ahlstrom (1974) and Weitzman (1974) disappears in a phylogenetic analysis by somewhat altering certain of the groups of both authors as follows.

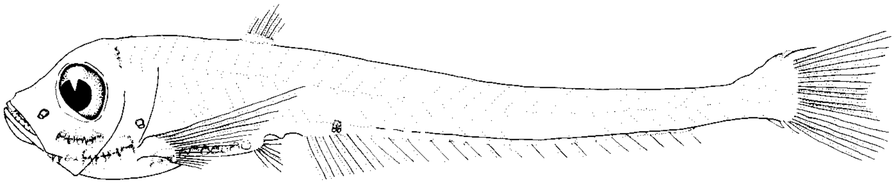
In our tentative scheme of relationships, Weitzman's Sternoptychidae and Ahlstrom's Group (2) genera (Ahlstrom, 1974: 671), *Bonapartia, Margrethia,* and *Gonostoma,* the Gonostomatidae in the strictest sense, are united by a synapomorphy consisting of a specialized form of prolonged metamorphosis and photophore development described by Ahlstrom (1974: 660–661). See also Tables 52–54 herein. These three gonostomatid genera and *Cyclothone* apparently share derived characters of the jaws and associated head parts which will be explained in a later contribution. These four genera retain the primitive Type Beta photophores, a character relating stomiiforms only at the ordinal level. In our opinion these four genera constitute the Gonostomatidae and *Cyclothone* may have lost prolonged photophore development through paedomorphic reversal associated with the small size of most of its members, a situation needing further study.

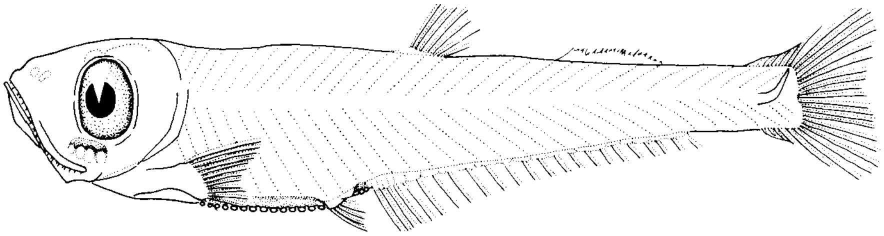
The Sternoptychidae have specialized Type Alpha photophores and the several other synapomorphies listed by Weitzman (1974:446–448). In addition they apparently share a unique photophore growth pattern previously unrecorded. One of us (Weitzman) has been studying photophore development in relation to phylogenetic studies in stomiiforms and has found that each cluster or group of photophores of the sternoptychids appears to develop by budding from one single photophore rather than by fusion at a later growth stage of separately developed photophores. This is a terminal developmental addition in photophore ontogeny and both outgroup comparison and developmental information indicate that this pattern of photophore formation is a specialization in comparison to the simpler appearance of single, separate body photophores (usually one per scale in any given series found in other stomiiforms). This growth character appears to be present in all sternoptychid genera for which we have developmental information. It is therefore a likely synapomorphy for the group.

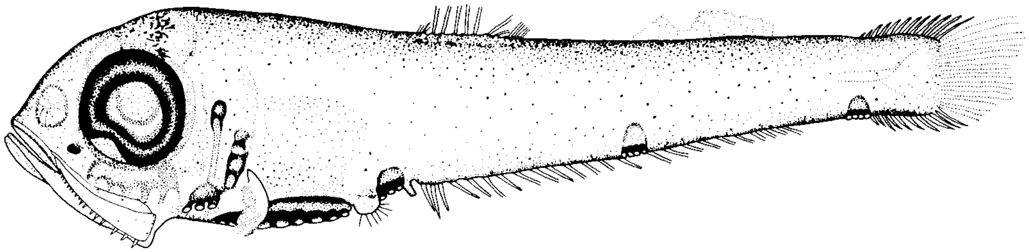
Manducus (based on the type species, *Gonostoma maderense* Johnson) is a primitive stomiiform, having ordinal-level characters with no known specialized characters except the absence of an adipose fin and a short neural spine on the preural centrum. The latter may be a primitive rather than a specialized stomiiform feature. *Diplophos* (based on the type species *Diplophos taenia* Günther) appears to have a transitional stage pectoral radial morphology between *Manducus* on the one hand and the Photichthyidae of Weitzman (1974) (an ill-defined group) and the Stomiidae on the other. In *Manducus* the cartilages and bones of proximal pectoral-fin radials III and IV remain separate whereas *Diplophos* has the cartilages, but not the bones, of the two elements fused, Fink and Weitzman (1982:65–67). In the "photichthyids" and stomiids the cartilages and bones of the two medial pectoral-fin radials are fused. This represents the terminal condition in the transition series except that in some genera there is a reversal of radial numbers and in *Eustomias* there occurs a further specialized, reduced pectoral-fin radial

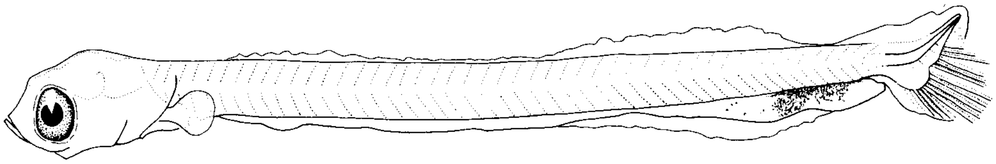












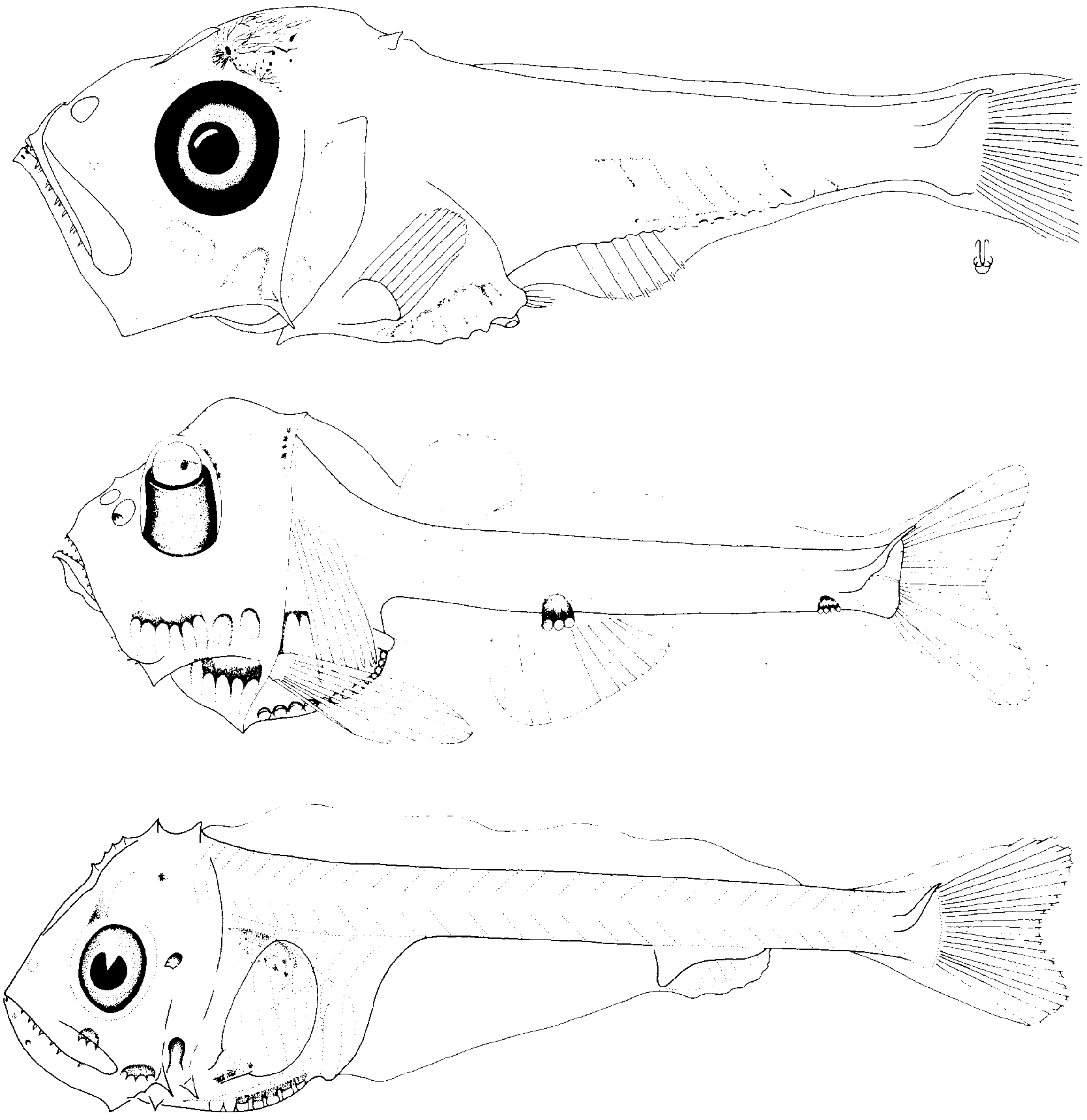


Fig. 104. Lateral views from top to bottom: *Polyipnus polli* 5.2 mm SL R/V GERONIMO Cr. 2, Sta. 155, 05°28′S, 01°120′E, August 21, 1963, drawn by J. C. Javech; *Argyropelecus hemigymnus* 7.8 mm SL modified after Sanzo (1931d); and *Sternoptyx* sp. 8.8 mm SL, drawn by H. C. Orr.

←

Fig. 103. Lateral views from top to bottom: *Araiophos eastropas* 8.8 mm SL modified after Ahlstrom and Moser (1969); *Maurolicus muelleri* 10.8 mm SL modified after Ahlstrom (1974); *Danaphos oculatus* middle metamorphosis modified after Ahlstrom (1974); *Valenciennellus tripunctulatus* middle metamorphosis modified after Ahlstrom (1974); *Argyripnus atlanticus* 18.7 mm SL modified after Badcock and Merrett (1972); and maurolicine Alpha 7.5 mm SL modified after Ahlstrom (1974).

condition. The "photichthyids" and stomiids have specialized Type Gamma photophores, although it is not known that all genera in these groups have Type Gamma photophores; this is a problem for further investigation. *Manducus* and *Diplophos* retain Type Beta photophores and all of these fishes apparently retain "white" photophore development of one kind or another. These two characters are only useful at the ordinal level as synapomorphies. Again, further research on "white" photophore formation is needed since there appears to be more than one form of this development.

The monotypic *Triplophos* may or may not be related to *Manducus* and/or *Diplophos. Triplophos* has a variety of derived features not shared by *Manducus* or *Diplophos.* However, this tells us nothing about its possible relationships with these genera. *Triplophos* has four proximal pectoral-fin radials but with some reduction in radial IV, Type Beta photophores, and probably "white" photophore development, the last two characters synapomorphous only at the ordinal level. Four pectoral-fin radials are not a synapomorphy for stomiiforms at any level since the feature is found in most teleost outgroups. *Triplophos* appears to be a primitive stomiiform with certain autapomorphic features associated with an elongate body. Its relationships are uncertain and there may be indications in the head and pectoral girdle anatomy of a relationship with certain photichthyid genera. The problem needs much study.

Cyclothone retains Type Beta photophores and "white" photophore development but has its own specialized features such as only one pectoral-fin radial. It has a modified head and jaws, which resemble and are, in our opinion, synapomorphous with those of *Gonostoma.* The single pectoral-fin radial might be thought of as a terminal stage in a transition series from *Manducus* (with four pectoral-fin radials) to *Diplophos* to some members of the "Photichthyidae" and then to *Cyclothone.* However, *Cyclothone* does not have specialized Type Gamma photophores of the "photichthyid" genera. The phylogenetic relationships of *Cyclothone* may not be certain as yet, but in many respects it bears a resemblance to the three gonostomatid genera and we favor its placement with these genera. See also discussion above.

Although we have perhaps resolved the differences between Ahlstrom (1974) and Weitzman (1974), we have not achieved a useful phylogeny of most stomiiform groups. Rather, we have attempted to outline certain suggested hypotheses of relationships to be investigated in the future with additional data. Adult morphological data of the kind used by Weitzman to define and relate the sternoptychid genera are available in abundance and may be useful for other stomiiform groups. A closer look at growth stages with the specific purpose of looking for possible developmental specializations and terminal additions to characters found in outgroups should greatly aid in delineating relationships among the stomiiform genera. However, problems associated with a high percentage of homoplasy can be expected for some groups. The answers to problems of stomiiform interrelationships will not come easily.

Consideration of certain features is in order. For example, larvae of *Diplophos* superficially resemble those of *Chauliodus* with their prolonged development to a large larval size and great elongation with bodies that are circular in cross section. Are these convergent larval specializations or primitive stomiiform features found only in certain stomiiform genera? The ventral pigmentation on the body of developing *Diplophos* resembles that of developing paralepidids and myctophoids. Is this a primitive stomiiform feature of *Diplophos* shared with certain stomiiform outgroups or a gross convergence of pigment patterns?

Woodsia and *Ichthyococcus* share with certain stomiid genera (for example, *Eustomias*) such developmental features as elongate pectoral-fin rays, trailing guts, pigmentation patterns, and bodies with a circular cross section. Some, if not all, of these may be shared larval specializations. But again, independent appearance of these characters indicated by a high degree of homoplasy may be a vexing problem. Larvae of other genera such as *Vinciguerria, Pollichthys,* and *Cyclothone* have body shapes and certain other features that closely, but presumably superficially, resemble those of clupeoid larvae. Detailed comparisons of these similarities may possibly distinguish between homology and convergence among these taxa.

In summary, a future phylogenetic analysis based on much additional data may clear up many of the problems of stomiiform generic relationships. However, at present we are left with numerous phylogenetic problems and assignment of certain genera to family-level groups at this time would be misleading. The above analysis retains Weitzman's Sternoptychidae. It restricts the Gonostomatidae to the genera *Bonapartia, Margrethia,* and *Gonostoma,* and we recommend the inclusion of *Cyclothone.*

The other groups of non-stomiid stomiiforms remain unclear as to family relationships. We agree with Fink and Weitzman (1982) that *Manducus* and *Diplophos* are primitive stomiiforms, but we cannot provide a stable classification for *Manducus, Diplophos,* and *Triplophos. Manducus* and *Diplophos* might seem to be sister taxa because of their similarity of appearance. However, they share no known specialized character or characters that would unite them as a stomiiform subgroup except the absence of an adipose fin and possibly a short neural spine on the preural centrum. Currently all their other shared characters seem primitive for stomiiforms. Further analysis of this situation is needed.

Triplophos is again very much like a primitive stomiiform in its head especially, but it has a number of specialized stomiiform features as listed by Grey (1964:106) and may show some relationship to some of the "photichthyid" genera.

That the genera classified in the "Photichthyidae" by Weitzman (1974) form some kind of related group seems reasonable. However, relationships among these genera are not known. That these "photichthyid" genera are related to *Diplophos* is possible, and that the stomiids are related to the "photichthyids" is, in our view, very probable. The larval specializations of *Woodsia* and *Ichthyococcus* noted above, may be important here because they may be synapomorphies relating these genera to the stomiids.

Until the developmental and adult morphological features of many stomiiform genera are analyzed in detail, certain aspects of their developmental stages outlined, and detailed outgroup analysis performed on all putatively useful characters, we can make no certain predictions about relationships and classification.

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