The Diverse Patterns of Metamorphosis in Gonostomatid Fishes – An Aid to Classification

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The gonostomatid lightfishes rank second only to myctophid lanternfishes in abundance in the sea. The gonostomatid genus *Cyclothone* has been singled out as the most abundant group of fishes in the ocean. These observations were based on abundance of adults in mid-water trawl hauls. If abundance is based on larvae, the gonostomatid genus *Vinciguerria* could be the most numerous group of fishes in the ocean. Without attempting to decide whether *Cyclothone* or *Vinciguerria* ranks first in abundance, we can assume that the gonostomatids obviously are an important group of oceanic fishes.

Grey (1964), in her impressive contribution on gonostomatid fishes, recognized 21 genera as valid, with between 52 to 55 valid species. A few species subsequently have been added and a few synonymized, bringing the number of species close to 60. Weitzman (in press) will reduce the number of genera to 20 (pers. comm.). The Gonostomatidae are closely related to the hatchetfishes, family Sternoptychidae; the most recent review of the latter family was made by Baird (1971).

Life histories have been published for 12 of the 20 genera of gonostomatid fishes and for slightly more than a third of the species. In addition to the published record I have larval series for an additional 3 genera and 9 species.

The larvae of Gonostomatidae constitute a moderately homogeneous group. By this I mean that it is not difficult to identify larvae to the family level despite differences noted below. About half the known gonostomatid larvae have moderate to fairly heavy pigmentation that aids in identification. The gut (digestive tract) is more variable in length between larvae of different genera of gonostomatids than perhaps any other family of fishes. It ranges from fairly short, as in *Danaphos*, to a full 95% of the standard length, as visable in an interesting *Maurolicine* larva I will discuss later; occasionally the gut can be trailing, as in *Ichthyococcus*. Gut length is even shorter in the sternoptychid genus *Sternoptyx*. Eyes in larvae are either round or narrowed; but when narrowed they lack the specializations found in the eyes of various myctophid larvae. The most strikingly narrowed larval eyes are found in the sternoptychid genus *Argyropelecus*.

The anal fin in gonostomatids is usually long, occupying most of the tail portion of the body. The shorter dorsal fin, however, is variously placed in relation to the anal. It may completely precede the anal, as in *Danaphos* or *Woodsia*; it may partly precede the anal as in *Vinciguerria* or *Maurolicus*; the origin of the dorsal may be opposite the origin of the anal as in *Cyclothone*; or the anal origin may precede the dorsal by several rays, as in *Gonostoma* or *Araiophos*. In the majority of gonostomatid larvae the dorsal and the anal fins form in about the same relative positions they will retain in later life - but there are interesting exceptions. These are associated with larval forms with relatively long intestines in which the anus shifts anteriorward during metamorphosis, as does the anal fin relative to the dorsal.

Grey (1964) illustrated such a shift in *Pollichthys mauli*, and a marked shift must occur in an interesting *maurolicine* larva that is discussed later.

The caudal fin of gonostomatids is interesting in several respects. The principal caudal rays are invariably 19, a character shared with most salmoniform fishes. The bones that support the principal rays, however, can retain the primitive complement of 4 superior and 3 inferior hypurals as in *Gonostoma* or *Diplophos*, be variously reduced as in *Vinciguerria* (3 + 2) or *Danaphos* (3 + 1) to only 1 superior and 1 inferior hypural as in *Cyclothone* or *Araiophos*, or achieve the ultimate reduction to a single plate in the sternoptychid genus *Sternoptyx*. Similarly epurals can retain the primitive complement of 3, or be variously reduced to none. In no other group of fishes has such a variable pattern of reduction of caudal supporting bones been observed. In the 6 other stomiatoid families of fishes, for example, hypurals are stabilized at 3 superior and 3 inferior plates. In most fishes the procurrent C rays are about equal in number, both in the dorsal group and in the ventral, but in various gonostomatids-sternoptychids the ventral group is reduced in number of rays relative to the dorsal - obviously to accommodate the posteriormost photophores of the AC group. Among the genera with a reduced ventral complement of procurrent caudal rays are *Vinciguerria, Polymetme, Maurolicus, Danaphos,* and *Argyropelecus*; among the genera in which no such reduction occurs are *Cyclothone, Diplophos, Araiophos,* and *Sternoptyx*.

Although larvae of gonostomatids and sternoptychids exhibit marked variability in certain characteristics such as gut length, eye shape, pigmentation and fin position, none of these is of primary value in tracing relationships among genera and species. The patterns of photophore development, during the larval and metamorphic stages and specialization in photophore groups in adults, constitute the most trenchant characteristics for showing such relationships. The notations used to designate photophores follow Grey (1964), with the exception that her IV group is divided into IP + PV groups.

Before discussing photophore information in larval and metamorphic stages, I will briefly characterize photophore groups in adults. Most photophores in gonostomatids are in a ventral series usually extending along the length of the body from symphysis to base of caudal. In addition, photophores are present between branchiostegal rays (6 or more pairs per side), on the head and operculum (3 to 5 pairs), and usually a lateral body series (occasionally several lateral series). In the majority of gonostomatid genera (13) all photophores remain individually separate, but in the other 7 genera some or most of the photophores can be variously clustered into groups with common bases. A similar pattern of clustered photophores is found in the 3 sternoptychid genera.

In most families of stomiatoid fishes, photophores form simultaneously during a relatively brief metamorphic period. They form initially as unpigmented organs and subsequently acquire pigment and structure. This is the pattern of formation, for example, in the families Stomiatidae, Chauliodontidae, Melanostomiatidae, etc.; it is also found in some genera of gonostomatids.

In several genera of gonostomatids, for example *Vinciguerria* and *Cyclothone*, most photophores are laid down initially during a white photophore stage, and only a few photophores are late forming. More commonly, most ventral photophores form simultaneously during a white photophore stage; the lateral photophores form later and usually gradually.

This is the situation in *Ichthyococcus*, *Pollichthys*, and *Diplophos*. All genera with clustered photophores and at least three genera with single photophores (*Gonostoma*, *Margrethia*, and *Bonapartia*) have a protracted metamorphosis with gradual formation of photophores. Even when photophore formation is gradual, each addition is initially unpigmented and then becomes pigmented. Recent additions among pigmented photophores are usually smaller than those formed earlier, hence easily recognized.

The sequence of photophore formation has been as well documented for *Vinciguerria* as for any gonostomatid genus. Developmental series have been described for the 4 recognized species. Sanzo (1913b) showed from life-history studies that 2 species of *Vinciguerria* in the Mediterranean could be distinguished as larvae - *V. attenuata* and *V. poweriae*. Jespersen and Taning (1926) provided additional life-history information for these species and for *V. nimbaria* (as *V. sanzoi*). Ahlstrom and Counts (1958) described the life history of *V. lucetia* and provided information on *V. nimbaria* and *V. poweriae* from the eastern North Pacific; Silas and George (1969) provided additional information concerning development of *V. nimbaria*. The developmental pattern of all 4 species is strikingly similar.

At first formation, photophores are colorless in *Vinciguerria*, but they soon become pigmented. Most photophores appear simultaneously except for 3 to 7 pairs (Fig. 1A).

In *V. lucetia* the late-forming photophores are invariably the following:

A. The upper opercular pair of photophores.
B. The symphysial pair under the lower jaw.
C. A median pair of photophores of the AC group.
D. Two to 4 pairs of lateral photophores of the posterior lateral group.

Only 2 of the 4 recognized species of *Vinciguerria* develop a symphysial pair of photophores; except for this, the late-forming photophores in all 4 species are as listed above, the number of late-forming lateral photophores is reduced to 1 or 2 pairs in *V. poweriae*.

Even though the metamorphic period is relatively short in *Vinciguerria*, Ahlstrom and Counts (1958) indicated a natural division into 3 stages: 1. pro-metamorphosis, the white photophore stage, 2. mid-metamorphosis, when marked changes in body form occur in addition to the development of photophores into functional organs and the formation of several late-forming photophores, and 3. post-metamorphosis during which photophores formation is completed and juvenile body form attained. All stages are commonly taken together in plankton haul sampling no deeper than 200 m.

In *Cyclothone*, all ventral photophores are laid down simultaneously as white stage photophores, and on some species most lateral photophores as well. Developmental series have been described for two species of *Cyclothone*, *C. braueri*, and *C. pygmaea* by Jespersen and Taning (1926) and possibly *C. atraria* (Mukhacheva, 1964 as *C. microdon*). In addition we have developmental series for *C. acclinidens*, *C. signata*, and *C. alba*. Body form and pigmentation are strikingly similar in *Cyclothone* larvae of the various species, which complicates establishing life-history series in this most speciose of gonostomatid genera. Adult taxonomy has recently been clarified by Mukhacheva (1964) and Kobayashi (1973); 12 species are now recognized. Larvae of *Cyclothone* are rather shallowly distributed - i.e. they occur principally in the upper mixed

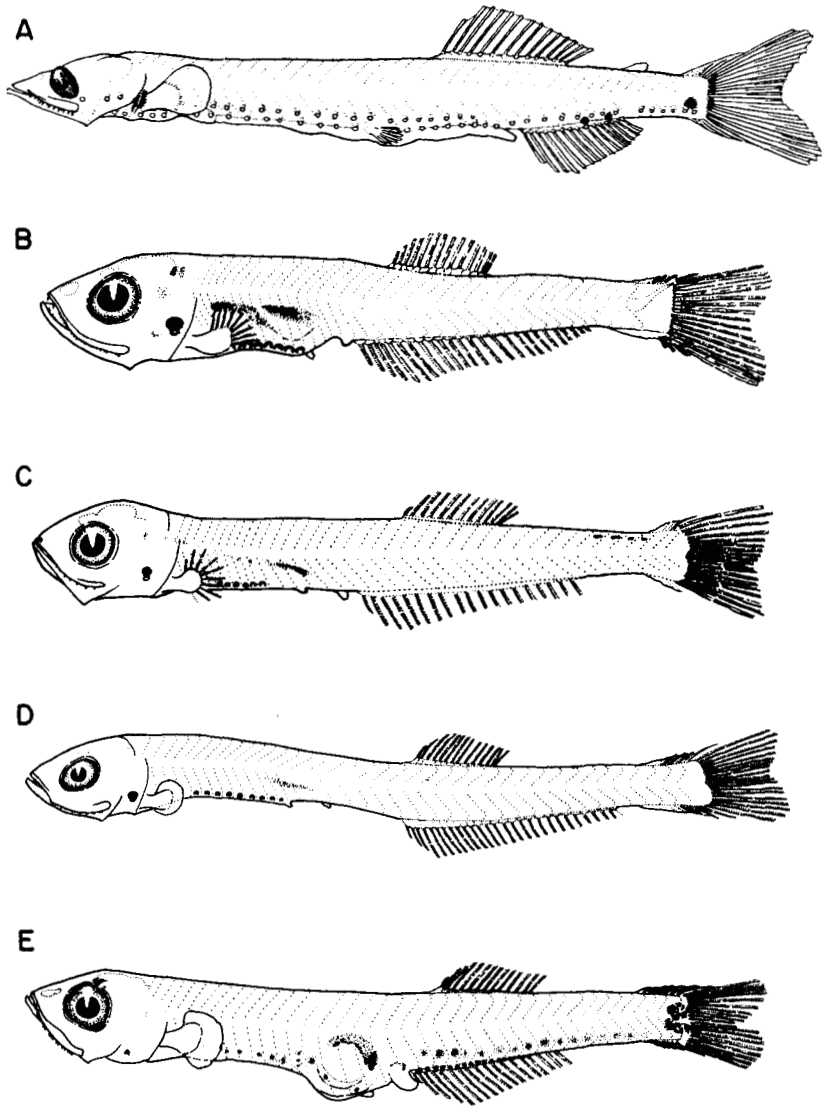

Fig. 1. Larvae and metamorphosing specimens of gonostomatids. (A) *Vinciguerria lucetia*, 15.0 mm, pro-metamorphic stage (from Ahlstrom and Counts, 1958). (B) *Gonostoma elongatum*, 9.8 mm, early metamorphosis. (C) *G. bathyphilum*, 11.0 mm, early metamorphosis. (D) *G. ebelingi*, 15.0 mm, early metamorphosis. (E) *G. atlanticum*, 12.0 mm, late larva

layer (Ahlstrom, 1959) and remain in this depth zone through the pro-metamorphic or white stage of photophore formation; they move to deeper levels to complete photophore formation. Later metamorphic stage specimens of *Cyclothone* are never taken in plankton collections made within the upper 200 m. It should be emphasized that the white photophore stage in *Cyclothone* is strikingly similar to that observed in *Vinciguerria*.

Larvae of *Ichthyococcus* develop more specialized larval characteristics than other gonostomatids, including an elongated ray on the lower part of the pectoral, reminiscent of similar pectoral development on larvae of the myctophids *Loweina* and *Tarletonbeania* (Moser and Ahlstrom, 1970), and a trailing gut. Information on the number of photophore formed initially in *Ichthyococcus* is somewhat inconsistent among authors (Sanzo, 1913a, 1930; Jespersen and Taning, 1926; Grey, 1964) but most photophores of the ventral group form simultaneously as unpigmented "white" photophores, whereas the lateral series forms latter. A 20.3 mm pro-metamorphic specimen of *I. ovatus* collected near Hawaii had 12 BR (definitive), 8 IP (definitive), 17 PV (definitive), 9 VAV (definitive), and 8 + 3 AC (1 or 2 lacking) and no lateral photophores. The AC photophores were divided into 2 groups, a larger anterior group and a posterior group of 3, with 1 or 2 photophores lacking between the 2 groups. A mid-metamorphic specimen illustrated in Jespersen and Taning (1926) has a less complete series of AC (7 + 3), although 13 pairs were developed in the lateral series. Jespersen and Taning indicated that the last photophores to form were the upper OP, posterior photophores of the lateral series, and AC photophores between the anterior and posterior groups. Marked changes in body proportions, particularly a striking increase in body depth, occur during metamorphosis of *Ichthyococcus*. Although metamorphosis is more gradual than in *Vinciguerria* or *Cyclothone*, it is basically similar.

Grey (1964, Fig. 28) illustrates 2 metamorphic-stage specimens of *Pollichthys mauli* of about equal size (16-17 mm), but at different stages of development. At first, I found these illustrations disturbing. The termination of the gut and origin of the anal fin appeared to be too far back on the body on the larger but less advanced specimen. I now know the reason for this: in various gonostomatids the gut length (i.e. snout – anus length) shortens during metamorphosis and in some the origin of the anal fin moves forward relative to the origin of the dorsal fin. This was happening in *Pollichthys* between the 2 metamorphic stages illustrated by Grey.

A less complete complement of photophores is laid down initially than in the preceding genera. Not only is the lateral group of photophores late forming, but the ventral AC group is less complete. The pattern of AC development is strikingly similar to the patterns to be discussed for *Gonostoma* and *Margrethia*. The two posterior AC photophores develop independently of the main group of AC photophores; in the latter the middle photophores develop initially and are added to both anteriorly and posteriorly until the complete complement is formed. The more advanced stage illustrated by Grey has the ventral and head photophores complete, but has only 6 of the lateral group of photophores which will number 19-21 when complete. I have examined post-metamorphic stage specimens of *Pollichthys*, but not the earlier metamorphic stages.

Diplophos has the most elongate larva among gonostomatids, and attains the largest size before transformation (ca. 45-50 mm). Developmental stages of *D. taenia* were described by Jespersen and Taning (1919). Although the majority of ventral photophores form simultaneously in *Diplophos taenia*, few series are actually complete. For example, on a 44.2 mm transforming specimen, the isthmal photophores were incomplete anteriorly, the anterior VAV photophore was small and barely formed; posterior AC group was incomplete. However, the two posteriormost photophores of the AC group were well formed and separate from the main group of AC photophores. The lateral series was partly formed, 25 + 8 photophores, but several anterior photophores were lacking as well as most photophores above the VAV and AC ventral groups. One

photophore of the lateral midline group was formed - the posteriormost photophore of this group, which forms far out on the caudal fin (about 2 mm from the caudal base). A 46 mm specimen had midline photophores formed (87 + 1) but still lacked posterior photophores in the lateral group. Even on juveniles this lateral series is often incomplete.

A developmental feature shared by the above genera is that most or all ventral photophores form simultaneously as white stage photophores. In none of these genera are all photophores formed initially, but the number of late-forming photophores are usually the following: OA series of lateral photophores of which some or all are late-forming; AC (anal-caudal ventral series) which usually form as 2 separate groups with 1 to several photophores lacking (*Cyclothone*, an exception); OP photophores, of which the upper pair is invariably late-forming; and SO photophores are often the last to form on species possessing this pair.

Larvae and pro-metamorphic specimens of Atlantic material tentatively identified as *Polymetme*, have most of the ventral photophores formed, much in *Ichthyococcus*. Larval stages, up to ca. 16 mm are known for *Woodsia nonsuchae* and *Yarrella argenteola*, but not metamorphosing specimens. For both, metamorphosis is assumed to be similar to *Ichthyococcus*. Developmental stages are unknown for *Triplophos* and *Photichthys*.

The genera of gonostomatids-sternoptychids with a protracted metamorphosis and gradual formation of all body photophores can be broken down into 3 clusters of genera:

1. Genera with all photophores remaining individually separate, but with a protracted metamorphosis: *Gonostoma*, *Bonapartia*, and *Margrethia*.

2. *Maurolicus* and 6 related genera having photophores in clusters with common bases: *Danaphos*, *Valenciennellus*, *Araiophos*, *Argyripnus*, *Sonoda*, *Thorophos*, and *Neophos*.

3. The 3 genera of the family Sternoptychidae: *Sternoptyx*, *Argyropelecus*, and *Polyipnus*.

I will deal first with the group that has the least specialized photophores:

Gonostoma, *Bonapartia*, and *Margrethia*. All 3 genera lack photophores on the isthmus, and the lateral (OA) series of photophores is lacking on *Bonapartia* and *Margrethia*.

Developmental series have been described for 3 species of *Gonostoma*: *G. denudatum* (Sanzo, 1912), *G. elongatum* (Jespersen and Taning, 1919 as sternoptychid larva B; Grey, 1964 as *G. elongatum*) and *G. gracile* (Kawaguchi and Marumo, 1967), and for *Bonapartia pedaliota* (Jespersen and Taning, 1919; Grey, 1964), and *Margrethia obtusirostra* (Jespersen and Taning, 1919; Grey, 1964). I have been fortunate in obtaining larvae and/or metamorphosing specimens of the 3 remaining species of *Gonostoma*: *G. atlanticum*, *G. bathyphilum* and *G. ebelingi*, hence developmental stages are known for all species of this group.

Gonostoma appears to be the pivotal genus with respect to photophore development. Among species of *Gonostoma*, photophores may be formed gradually over a rather extended size range as in *G. elongatum* (Fig. 1B), *G. denudatum*, *G. bathyphilum* (Fig. 1C), and probably *G. ebelingi* (Fig. 1D) - or somewhat more rapidly as in *G. gracilis* and *G. atlanticum* (Fig. 1E). The forms with gradual development are closely allied in development to *Bonapartia* and *Margrethia*, as well as to the Maurolicine and sternoptychid genera. The gradual formation of photophores during a pro-

tracted metamorphosis is a major evolutionary trend first evidenced in *Gonostoma*.

The OP_3 pair of photophores is the first to form in all 6 species of *Gonostoma* as well as in *Margrethia* and *Bonapartia*. The next photophores to form (1 or several) are in the PV series, but otherwise the sequence is various, as among the above species (Table 1).

The sequence of photophore formation is contrastingly different in two species of *Gonostoma* with a protracted metamorphosis - *G. denudatum* and *G. elongatum*. In the latter the metamorphosis stage extends from about 6.0 mm to 22.5 mm. Although photophores form gradually in all groups, the sequence among photophore groups is as follows in *G. elongatum*: OP, PV, BR, VAV, ORB and AC, OA and SO. The addition of photophores to the AC group occurs only after most PV and VAV photophores are formed; the initial photophore to form is an inner photophore of the anterior AC group. In contrast, photophores form much later on *G. denudatum* (between ca. 18-34+ mm) and in a different sequence: OP, PV, posterior AC group, BR and VAV, anterior AC group, ORB and OA, SO. Photophores begin forming in the posterior AC group immediately after the first PV photophore is laid down. When photophores are formed in the anterior AC group the 3rd or 4th is laid down first and additional photophores are added both anteriorly and posteriorly.

Metamorphosis in *Margrethia obtusirostra* occurs gradually between about 5.8 to 19.0 mm; photophores are added in the following sequence: OP, PV, VAV and AC (both groups), BR, ORB, and SO. Metamorphosis in *Bonapartia pedaliota* according to Grey (1964) occurs between ca. 9 to 25 mm and is rather similar in sequence to *G. elongatum*.

Although the first few photophores are laid down gradually in *Gonostoma atlanticum*, most of the ventral photophores are laid down as a group. The same general pattern of photophore formation has been described for *Gonostoma gracile* (Kawaguchi and Marumo, 1967). The development of ventral photophores in these two species contrasts sharply with the patterns described above. The lateral series of photophores are laid down after the ventral, much as in *Pollichthys* or *Ichthyococcus*.

Among Maurolicine genera and species rather complete developmental series are known for *Maurolicus mulleri* (Holt and Byrne, 1913; Jespersen and Taning, 1926; Sanzo, 1931; Okiyama, 1971), *Valenciennellus tripunctulatus* (Jespersen and Taning, 1919; Grey, 1964), and *Danaphos oculatus* (original) and less complete series for *Araiophos eastropas* (Ahlstrom and Moser, 1969) and *Argyripnus atlanticus* (Badcock and Merritt, 1972). Information on sequence of photophore formation is contained in Table 2.

The life-history stages are best known for *Maurolicus mulleri* (Fig. 2A) - a fascinating species from egg to adult. Photophores are precociously laid down in this species on larvae as small as 5.5 mm. The first to form are branchiostegal photophores, followed soon by PV photophores. The OP_3 pair form as early as 6.7 mm, the ORB pair soon after (6.9 mm), IP and AC photophores begin to form by 7.5 mm, VAV by 8.6, and OA by 9.0 (see Table 2). Photophore formation is complete by 19.0 mm or sooner. The AC photophores in *Maurolicus* are divided into 3 groups consisting of: an anterior single photophore, a large middle cluster (13-14 photophores), and a posterior cluster (ca. 8 photophores). The first AC photophores to form are in the large middle cluster, but soon thereafter they also form in the posterior cluster. The early forming photophores are in the middle of each cluster and photophores are added in both directions. This pattern appears to be similar to that described for *Margrethia* and *Bonapartia*.

Table 1. Sequence of photophore formation in *Gonostoma, Bonapartia,* and *Margrethia*

		ORB	OP	SO	BR	PV	VAV
Gonostoma elongatum	adult	1	3	1	9	15	(4)-5
	6.0	0	1	0	0	0	0
	7.5	0	1	0	0	5	0
	10.2	0	1	0	2/1	10	2
	13.0	0	1	0	2	11	3
	14.0	1	1	0	2	11	2/3
	16.7	1	1	0	3	11	4
	22.5	1	3	1	9	15	5
Gonostoma denudatum	adult	1	3	1	9	15-16	5
	18.25	0	1	0	0	1	0
	19.0	0	1	0	0	2	0
	20.75	0	1	0	1	3	1
	24.75	0	1	0	3	6	3
	29.65	0	2	0	5	14	5
	34.0	1	3	0	9	16	5
	39.0	1	3	1	9	16	5
Gonostoma gracile	adult	1	2	1	9	13-15	4-5
	15.5-17.0	0	1	0	0	0	0
	20.0	1	2	1	2	13	5
	22.0	1	2	1	9	14	4
Gonostoma ebelingi	adult	1	2	1	9	15	10
	13.8	0	1	0	0	7	0
	15.0	0	1	0	0	9	0
Gonostoma bathyphilum	adult	1	2		9	11-12	4-5
	11.0	0	1	0	0	5	0
	14.8	1	1	0	4	10	2
Gonostoma atlanticum	adult	1	2	1	9	15-16	5
	12.0		1				
	13.0	0	1	0	0	1	0
	14.5	0	1	0	0	2	0
	18.8	1	2	0	9	16	5
Margrethia obtusirostra	adult	1	3	0	9-12	13-15	4
	5.8	0	1	0	0	2	0
	6.4	0	1	0	0	6	2
	8.0	0	1	0	2	10	4
	11.3		2	0	6	14	4
	15.0	1	3	0	9	14	4
Bonapartia pedaliota	adult	1	3	1	11-13	14-15	5-(6)
	9.5	0	1	0	2	3	0
	12.0	0	1	0	4	5	2
	14.0	1	1	0	5	10	4
	16.0	1	1	0	6	11	5
	23.0	1	3	0	11	14	5

Table 1. (continued)

AC	OA + ODM	Source
21-23	13-15	Grey 64
0	0	Orig
0	0	Orig
0	0	Orig
0	0	Orig
1+	0	Grey
1+	0	J & T 19
22	13	Grey 64
17-20	13-15	Grey 64
0	0	Sanzo 12
+2	0	Sanzo 12
+3	0	Sanzo 12
3 + 3	0	Sanzo 12
11 + 3	0	Sanzo 12
15 + 5	13	Sanzo 12
15 + 5	13	Sanzo 12
17-19	11-12 + 6-7	K & M 67
0	0	K & M 67
17	0	K & M 67
18	12 + 4	K & M 67
19	21	Grey 64
0	0	Orig
0	0	Orig
20-21	14	Grey 64
0	0	Orig
0	0	Orig
19	13	Grey 64
		Orig
0	0	Orig
0	0	Orig
19	0	Orig
13-14 + 3-4	0	Grey 64
0	0	Orig
1 + 2	0	Orig
1 + 2	0	Orig
5 + 3	0	Orig
11 + 4	0	Orig
16-18 + 2-3	0	Grey 64
0	0	Grey 64
0	0	Grey 64
3 + 1	0	Grey 64
5 + 2	0	J & T 19
14 + 2	0	Grey 64

Table 2. Sequence of photophore formation in *Maurolicus muelleri* and allied maurolicine genera

		ORB	OP	SO	BR	IP	PV	VAV	AC	OA	Source
Maurolicus muelleri	adult	1	3	1	(6)	(6)	(12)	(6)	1 + (13/14) + (8)	(2) + 7	Orig
	5.5	0	0	0	(1/2)	0	0	0	-0-	-0-	Orig
	6.2	0	0	0	(2)	0	(2)	0	-0-	-0-	Orig
	6.5	0	0	0	(2)	0	(4)	0	-0-	-0-	Orig
	6.7	0	1	0	(3)	0	(5)	0	-0-	-0-	Orig
	6.9	1	1	0	(4)	0	(8)	0	-0-	-0-	Orig
	7.5	1	1	0	(4)	1	(9)	0	0 + (2) + 0	-0-	Orig
	8.6	1	2	0	(5)	(3)	(12)	(2)	0 + (3) + (3)	-0-	Orig
	9.0	1	2	0	(5)	(3)	(11)	(2)	0 + (3) + (3)	1	Orig
	9.7	1	3	0	(5)	(5)	(11)	(3)	0 + (4) + (6)	(2) + 1	Orig
	10.8	1	3	0	(6)	(5)	(12)	(4)	0 + (5) + (6)	(2) + 2	Orig
	13.5	1	3	0	(6)	(6)	(12)	(6)	0 + (9) + (7)	(2) + 6	Orig
Danaphos oculatus	adult	1	3	0	(6)	(3) + (4)	(11)	(5)	(3) + 16 + (4) + 1	6	Orig
	16.5	0	0	0	(2)	-0-	0	0	-0-	0	Orig
	16.5	0	0	0	(3)	-0-	(3)	0	-0-	0	Orig
	19.2	0	0	0	(4)	-0-	(10)	0	-0-	0	Orig
	21.0	1	1	0	(5)	(2) + (4)	(10/11)	0	(2) + 0 + 0 + 0	0	Orig
	21.3	1	1	0	(4/5)	(3) + (4)	(10)	0	(3) + 0 + (2) + 0	0	Orig
	21.8	1	2	0	(5)	(3) + (4)	(11)	(2)	(3) + 8 + (4) + 0	2	Orig
	24.2	1	2	0	(6)	(3) + (4)	(11)	(2)	(3) + 9 + (4) + 0	2	Orig
Valenciennellus tripunculatus	adult	1	3	0	(6)	(3) + (4)	(16-17)	(4-5)	(3) + (3) + (3) + (2) + (4)	(2) + 3	Grey 64
	8.6	0	0	0	(3)	-0-	(3)	0	-0-	-0-	Orig
	9.5	0	0	0	(4)	-0-	(6)	0	-0-	-0-	Orig
	12.0	0	0	0	(4)	-0-	(13)	(2)	-0-	-0-	Orig
	13.2	0	0	0	(4)	-0-	(14)	(3)	-0-	-0-	Orig
	17.0	1	2	0	(4-5)	(3) + (4)	(15)	(5)	(3) + (3) + 0 + (3) + (4)	(2)	Grey 64
Araiophas eastropas	adult	1	1	0	(6)	(2)	(3) + 3-4 + (2)	(3)	(2) + 2 + (2)	no	A & M 69
	11.2	0	0	0	(3)	0	(2)	0	-0-	-	A & M 69

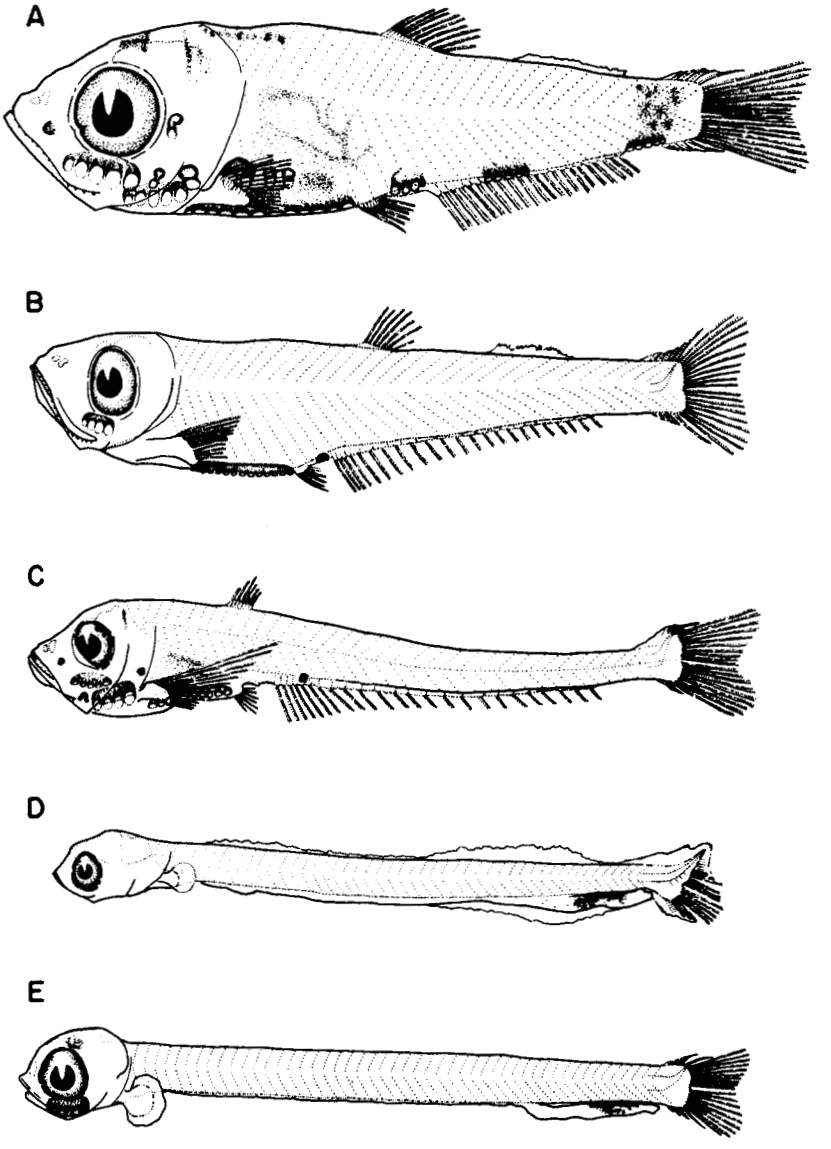

Fig. 2. Larvae and metamorphosing specimens of gonostomatids. (A) *Maurolicus muelleri*, 10.8 mm, middle metamorphosis. (B) *Valenciennellus tripunctatus*, middle metamorphosis. (C) *Danaphos oculatus*, middle metamorphosis. (D) Maurolicine alpha - 7.5 mm larvae. (E) Same, 16.0 mm, early metamorphosis

The initiation of photophore formation on *Valenciennellus tripunctulatus* is not quite as precocious as in *Maurolicus*: BR and PV photophores were first observed on 8.6 mm larvae. The sequence also is different: the VAV photophores form relatively much sooner and the AC group much later (Fig. 2B). These differences in sequence facilitate identification.

Larvae of *Danaphos* and *Valenciennellus* occur together in the eastern Pacific, and small specimens are somewhat similar in appearance. *Danaphos* has a shorter gut; both lack pigmentation (except peritoneal). Hence it is fortunate that *Valenciennellus* begins photophore formation at a relatively small size, whereas *Danaphos* delays photophore formation until about 16.5 mm. As in the preceding 2 genera, photophore formation begins in the BR and PV groups. Thereafter the sequence differs from that in *Maurolicus* and *Valenciennellus*, although it is closer to *Maurolicus* (Fig. 2C).

We have observed only larvae and early transformation-stage specimens of *Araiophos eastropas*. The larvae have a substantially longer gut than the preceding 3 genera (snout-anus in *Araiophos* larvae - 72-79% SL). Metamorphosis beings at about 11.0 mm, with the initial formation of photophores in the BR and PV groups.

The developmental pattern, shared in common by all Maurolicine genera for which metamorphic stages are known, is a gradual metamorphosis with the initial formation of photophores in the BR and PV groups.

I am illustrating two sizes of a fascinating Maurolicine larvae that I call simply "alpha" (Fig. 2D, E). The eye is large, to the point of dominating the head; the gut is exceptionally long for a gonostomatid larva (ca. 95% SL). The posterior portion of the gut is becoming detached from the body in the larger specimen, undoubtedly to accommodate the anal fin which hasn't yet begun to develop. However, the branchiostegal photophore group is complete - a cluster of 6 branchiostegal photophores with a common base. No other photophores have formed. The number of myomeres is in the mid-40's. The larva is obviously of a primitive Maurolicine gonostomatid. Among described species only *Neophos nexilis* Myers has this number of vertebrae (44-45, S. Weitzman, pers. comm.). If not this, it represents an undescribed form.

Inasmuch as the Maurolicine genera are as closely related to the Sternoptychidae as to the gonostomatid with separate photophores, I will give a little information on the sequence of photophore formation in *Sternoptyx diaphana* and *Argyropelecus lychnus*.

The first photophore pair to form in *Sternoptyx* is the subopercular pair (OP_3). This is soon followed by BR, and then both PV and IP photophores. The lateral (suprapectoral) photophores begin forming before the AC photophores. Marked changes occur in body depth and form during transformation which occurs over a relatively short size range, as measured by SL.

I have not been as successful with transforming specimens of *Argyropelecus lychnus* in tracing the sequence in which photophores form. When I have found transforming specimens, a number of photophores were already developed. The BR and IP groups form their full complement of photophores before the PV group and the AC photophores begin to form before the VAV group.

In my attempt to coordinate what is known concerning metamorphic patterns, I have separated the gonostomatids-sternoptychids into 4 groups of genera.

Group A. Genera in which most or all ventral photophores are laid down initially during a pro-metamorphic (white photophore) stage and which have all photophores separate - *Vinciguerria, Cyclothone, Ichthyococcus, Pollichthys, Diplophos,* and presumably *Woodsia, Yarrella,* and *Polymetme.*

Group B. Genera with a gradual, protracted metamorphosis, with all photophores remaining individually separate and initial photophore formation in OP and PV groups - *Gonostoma, Bonapartia,* and *Margrethia.*

Group C. Genera having some or most photophores in clusters with common bases, a gradual, protracted metamorphosis, with initial photophore formation in BR and PV groups - *Maurolicus, Valenciennellus, Danaphos, Araiophos, Argyripnus,* and presumably *Thorophos, Neophos,* and *Sonoda.*

Group D. More highly specialized fishes having most photophores in clusters with common bases; they have a gradual, protracted metamorphosis with striking changes in body form - sternoptychid genera *Sternoptyx, Argyropelecus,* and *Polyipnus.*

The triad of genera in group B is a closely knit assemblage, with *Gonostoma* the pivotal genus. Metamorphosis among the 6 species of *Gonostoma* shows much greater diversity than among species of other genera, as for example *Vinciguerria* or *Cyclothone.* As pointed out earlier, all species of *Gonostoma* first form the OP_3 pair and 1 to several PV pairs before forming other photophores; thereafter the patterns diverge. Most of the photophores of the ventral series are laid down fairly rapidly in *G. gracile* and *G. atlanticum* - features that ally this pair of species to the genera included in group A. The species of *Gonostoma* with a protracted metamorphosis, as for example *G. elongatum* and *G. denudatum,* share developmental features with the Maurolicine genera (group C).

Certain developmental patterns are common to all 4 groups, and to me the most striking of these is the pattern of photophore formation within the AC group. During formation of these photophores there is usually a sharp separation into 2 groups - a posterior group of 2 or more AC photophores separate from the main AC group. In the anterior AC group, 1 or several of the inner photophores develop initially and are added to both anteriorly and posteriorly. When the posterior group contains 3 or more photophores, they form similarly; eventually the 2 groups may unite. This pattern of AC development is found in *Pollichthys, Ichthyococcus,* and *Diplophos* in group A, in several species of *Gonostoma* (example *G. denudatum*), as well as *Bonapartia* and *Margrethia* in group B, and in a modified form among Maurolicine (group C) and Sternoptychidae (group D) genera, i.e. separation in 3 or more AC groups, each with an inner to outer sequence of photophore formation.

Although *Gonostoma* is considered the pivotal genus, with developmental patterns that show relationships to both the Maurolicine line and the genera in group A; I consider it closer to the genera in group A. There are objections to considering it as basic stock from which the other lines could be derived.

First of all there is the problem of isthmal photophores; these are lacking in *Gonostoma-Margrethia-Bonapartia* but developed in all Maurolicine genera, and in all genera of group A except *Cyclothone.* It is more logical to derive both lines from an ancestor that possessed this group of photophores than from one that lacked it. There is the additional problem of separate photophores vs. clustered photophores when relationships with Maurolicine genera are considered. We are also confronted with the fact that in some larval characteristics, such as

gut length, several Maurolicine genera appear to be more primitive than *Gonostoma*. Undoubtedly the divergence between species with single vs. clustered photophores came early in the evolution of gonostomatid-like fishes.

Bassot (1966, 1970) used the structure of light organs to trace evolutionary lineages among stomiatoid fishes. He described 3 types of light organs, the most primitive type was found in *Gonostoma, Bonapartia, Cyclothone*, and *Diplophos (Manducus)*; a distinctively different type in Maurolicine and sternoptychid genera; and third type in *Vinciguerria, Ichthyococcus, Yarrella* and in most stomiatoids (*Chauliodus, Stomias*, etc.). His findings based on light organs are in general agreement with the groups discussed above, except for placement of 2 genera - *Cyclothone* and *Diplophos*.

The question arises as to the relation of the Maurolicine genera to the three genera of sternoptychids. The latter show more marked specializations in both larval and adult characters: they are a more specialized group than the Maurolicine genera. The two assemblages have several important characters in common: clustered photophores, a protracted metamorphic stage, and similar structure of light organs. The Maurolicine genera certainly are as closely related to the sternoptychids as to other genera of gonostomatids. The present separation of the two groups into separate families is artificial. If the sternoptychids are combined with the gonostomatids, the former would have priority as the family name. I personally favor the inclusion of all gonostomatid-sternoptychid fishes in a single family. If divisions are to be made within the family, the genera with clustered photophores would constitute one subfamily, those with separate photophores the other. I find the genus *Gonostoma* too ambivalent in developmental patterns to separate it sharply from other gonostomatid genera with separate photophores.

SUMMARY

The gonostomatid light fishes rank second only to myctophid lantern fishes in abundance in the sea. The family is made up of 20 genera and approximately 60 species, all possessing photophores. Photophore patterns have been used as a primary character in adult taxonomy. The diversity of patterns of photophore acquisition - ranging from most photophores being formed simultaneously to a gradual formation of photophores during a protracted metamorphosis - is used to trace relationships among gonostomatid genera. On the basis of metamorphic patterns, the gonostomatid genera fall into three groups. One group includes genera in which most or all ventral photophores are laid down initially during a "white" photophore stage and which have all photophores individually separate (*Vinciguerria, Cyclothone, Ichthyococcus*, etc.). The second group includes genera with a gradual, protracted metamorphosis, but with all photophores individually separate (*Gonostoma, Bonapartia*, and *Margrethia*). The third group includes genera having some or most photophores in clusters with common bases which are laid down gradually during a protracted metamorphosis (*Maurolicus, Valenciennellus, Danaphos, Araiophos*, etc.). *Gonostoma* is considered the pivotal genus with developmental patterns that show relationships to the other two groups. It is pointed out that the third group is as closely related in developmental pattern to the sternoptychids as to other genera of gonostomatids, and that the two families should be combined into a single family.

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REFERENCES

Ahlstrom, E.H., 1959. Vertical distribution of pelagic fish eggs and larvae off California and Baja California. Fish. Bull., U.S., 60, 107-146.

Ahlstrom, E.H. and Counts, R.C., 1958. Development and distribution of *Vinciguerria lucetia* and related species in the eastern Pacific. Fish. Bull., U.S., 58, 363-416.

Ahlstrom, E.H. and Moser, H.G., 1969. A new gonostomatid from the tropical eastern Pacific. Copeia (3), 493-500.

Badcock, J.R. and Merritt, N.R., 1972. On *Argyripnus atlanticus*, Maul 1952 (Pisces, Stomiatoidei), with a description of post-larval forms. J. Fish. Biol., 4, 277-287.

Baird, R.C., 1971. The systematics, distribution, and zoogeography of the marine hatchetfishes (family Sternoptychidae). Bull. Mus. Comp. Zool., Harvard Univ., 142 (1), 128 p.

Bassot, Jean-Marie, 1966. On the comparative morphology of some luminous organs. In: Frank H. Johnson and Yata Haneda (eds.) Bioluminescence in Progress. Princeton University Press, 557-610 pp.

Bassot, Jean-Marie, 1970. Structure and evolution of the light organs of stomiatoid fish. In: The world ocean. Joint Oceanography Assembly, Tokyo, 13-25 September 1970. Contribution in Biological Oceanography, mimeo, 4 pp.

Grey, Marion, 1964. Family Gonostomatidae. In: Fishes of the western North Atlantic, 78-240. Mem. Sears Found. Mar. Res. 1, part 4.

Holt, E.W.L. and Byrne, L.W., 1913. Sixth report on the fishes of the Irish Atlantic Slope. Fisheries, Ireland, Sci. Invest. (1912), I, 27 pp.

Jespersen, P. and Taning, A. Vedel, 1919. Some Mediterranean and Atlantic Sternoptychidae. Preliminary note. Saertryk af Vidensk. Medd. fra Dansk naturh. Foren., 70, 215-226.

Jespersen, P. and Taning, A. Vedel, 1926. Mediterranean Sternoptychidae. Rep. Danish Oceanogr. Exped. 1908-1910, col. 2 (Biology) A, 12, 1-59.

Kawaguchi, K. and Marumo, R., 1967. Biology of *Gonostoma gracile* (Gonostomatidae) 1. Morphology, life history and sex reversal. Inform. Bull. Planktol. Japan, Commem. Dr. Y. Matsue, 53-69.

Kobayashi, B.N., 1973. Systematics, zoogeography, and aspects of the biology of the bathypelagic fish genus *Cyclothone* in the Pacific Ocean. Thesis, Univ. of Calif., Scripps Inst. Oceanogr.

Moser, H.G. and Ahlstrom, E.H., 1970. Development of lantern fishes (family Myctophidae) in the California Current. Part 1. Species with narrow-eyed larvae. Bull. Los Angeles County Mus. Nat. Hist. Sci. 7, 145 pp.

Mukhacheva, V.A., 1964. The composition of species of the genus *Cyclothone* (Pisces, Gonostomatidae) in the Pacific Ocean. Trudy Inst. Okeanol. Akad. Nauk SSSR 73: 93-138 (Eng. trans. from Russ. in Isreal program for scient. trans., 1966, IpST Cat. No. 141).

Okiyama, Muneo, 1971. Early life history of the gonostomatid fish, *Maurolicus muelleri* (Gmelin), in the Japan Sea. Bull. Jap. Sea. Reg. Fish. Res. Lab., 23, 21-52.

Sanzo, Luigi, 1912. Comparsa degli organi lummosi in una serie di larve di *Gonostoma denudatum* Raf. R. Comitato Talassografico Italiano Mem., 9, 22 pp.

Sanzo, Luigi, 1913a. Larva di *Ichthyococcus ovatus*. R. Comitato Talassografico Italiano Mem., 27, 6 pp.

Sanzo, Luigi, 1913b. Stadi post-embrionali di *Vinciguerria attenuata* (Cocco) e *V. poweriae* (Cocco) Jordan ed Evermann. R. Comitato Talassografico Italiano Mem., 35, 7 pp.

Sanzo, Luigi, 1930. Uova, sviluppo embrionale, stadi larvali, post-larvali e giovanili de Sternoptychidae e Stomiatidae. 2 *Ichthyococcus ovatus*. R. Comitato Tallasografico Italiano Monogr., 2, 69-119.

Sanzo, Luigi, 1931. Uova, larvae e stadi giovanili di Teleostei. Sottordine: Stomiatoidei. Fauna e Flora del Golfo di Napoli, Monogr. 38: 42-92.

Silas, E.G. and George, K.C., 1969. On the larval and postlarval development and distribution of the mesopelagic fish *Vinciguerria nimbaria* (Jordan and Williams - family Gonostomatidae) off the west coast of India and the Laccadive Sea. J. Mar. Biol. Ass. India 11 (1, 2), 218-250.

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