

RELATIONSHIPS OF ATHERINOMORPH FISHES (TELEOSTEI)

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ABSTRACT

Atherinomorphs have been recognized since 1964 as a group of teleost fishes comprising silversides, phallostethids, killifishes, ricefishes, halfbeaks, needlefishes, flying fishes, and sauries. Atherinomorphs are diagnosed as monophyletic by derived characters of the testis, egg, reproductive behavior, circulatory system, ethmoid region of the skull, gill arches, pelvic girdle, jaw musculature, olfactory organ, and inferred reductions in the infraorbital series and some other bones. Monophyly of killifishes (Cyprinodontiformes), ricefishes and exocoetoids (Beloniformes), and Division II atherinomorphs (Cyprinodontiformes plus Beloniformes) is well-supported. Atherinoids (silversides plus phallostethids) are considered paraphyletic. One cladistic interpretation of character distribution among selected ctenosquamate teleosts supports the hypothesis that atherinomorphs are the sister group of some or all paracanthopterygian fishes. However, corroboration of an atherinomorph sister group, and modification of atherinomorph membership, requires more precise definition of derived characters (i.e., better statement of homology) and continued surveys of characters, such as testis structure, in outgroup taxa.

The Atherinomorpha, comprising teleost fishes commonly known in English as silversides, phallostethids, killifishes, halfbeaks, needlefishes, flying fishes, and sauries, were first recognized and classified by Rosen (1964; Table 1) as the order Atheriniformes. The over 1,000 species (Nelson, 1984) are widely distributed in an array of pantropical and pantemperate, freshwater and marine, habitats. Most atherinomorphs are relatively small (less than 100 mm SL) surface feeding estuarine or coastal fishes. Many can survive extremes of temperature and salinity (Rosen, 1973a; Parenti, 1981; Meffe and Snelson, 1989).

Prior to the concept of an Atherinomorpha, close relationship between cyprinodontiforms and percopsiforms and/or amblyopsiforms was supported by Berg (1940), Woods and Inger (1957), and Gosline (1962), among others. Rosen (1964) argued against a close relationship between cyprinodontiforms and paracanthopterygians, including amblyopsiforms. I believe his intent was to remove paracanthopterygians from consideration as close relatives of cyprinodontiforms and to justify a close relationship among atherinoids, exocoetoids, and cyprinodontiforms, making up his new order, Atheriniformes.

Gosline (1962, 1963) and Rosen (1962, 1964) disagreed because Gosline supported cyprinodontiform/amblyopsiform and mugiloid/atherinoid sister group relationships. Gosline did not support a monophyletic Atherinomorpha, in part because atherinoids and mugiloids share some derived characters, such as the I,5 pelvic-fin ray formula (Gosline, 1963). However, some cyprinodontiforms have the I,5 pelvic-fin ray formula (e.g., *Pantodon*; Whitehead, 1962); whereas others, such as New World rivulids, may have seven or eight pelvic-soft rays (Parenti, 1981). It is not parsimonious to reject atherinomorph monophyly on the grounds that atherinoids and percopsiforms have a pelvic spine.

Freihofer (1972) reviewed statements of Gosline (1962, 1963) and Rosen (1962, 1964) on relationships among these taxa and recognized a monophyletic Atherinomorpha (then the order Atheriniformes). He came to no firm conclusions on higher classification (Freihofer, 1972: fig. 11), but argued that his restricted paracanthopterygians, atherinomorphs, and mugiloids were all descended from a percopsiform-like ancestor. In other words, Freihofer considered percopsiform

Table 1. Classification of Atherinomorph fishes of Rosen (1964), with common names of each higher category

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|--|
| Order Atheriniformes |
| Suborder Exocoetoidei (halfbeaks, flying fishes, needlefishes and sauries) |
| Suborder Cyprinodontoidei |
| Superfamily Adrianichthyoidea (ricefishes) |
| Superfamily Cyprinodontoidea (killifishes) |
| Suborder Atherinoidei (silversides and phallostethids) |

fishes as possibly plesiomorphic to a larger group that includes atherinomorphs, mugiloids, and the remaining Paracanthopterygii.

Rosen and Parenti (1981) followed Rosen (1964, 1973b) and hypothesized that atherinomorphs and percomorphs are sister taxa. Despite their use of a putative synapomorphy—presence of an interarcual cartilage—that has been shown to be more widely distributed (Travers, 1981), this sister group relationship has been incorporated uncritically into phylogenetic systematic summaries of higher teleost classification (Fig. 1A; see Lauder and Liem, 1983; Nelson, 1989; Patterson and Rosen, 1989). Acceptance of an atherinomorph/percomorph sister group relationship has affected polarity decisions in phylogenetic systematic analyses of ctenosquamates. For example, Rosen and Parenti (1981) ignored paracanthopterygians in their survey of dorsal gill arch bones and cartilages in acanthomorphs, and neglected to mention that a large fourth epibranchial bone is present in atherinomorphs and plesiomorphic paracanthopterygians.

Rosen's (1964) diagnosis of atherinomorphs included synapomorphies such as single or double dislike mesethmoid ossifications (Tigano and Parenti, 1988), separation of afferent and efferent circulation during development (White et al., 1984), and reduction in number of infraorbital bones, as well as symplesiomorphies. Rosen and Parenti (1981) reconsidered atherinomorph monophyly and reviewed evidence for relationships among included taxa. One change in higher classification was formal recognition of adrianichthyoids (ricefishes) as plesiomorphic beloniforms, rather than as cyprinodontiforms, with which they had been long associated (see Table 2 for comparison of Rosen and Parenti's, 1981 and Parenti's, 1984 classification with that of Rosen, 1964). A second change in classification reflected identification of atherinoids as paraphyletic and rejected a named higher category for them.

Collette (1984) and Collette et al. (1984) recognized a monophyletic Atherinomorphs and summarized evidence for a monophyletic Beloniformes which comprised ricefishes as well as halfbeaks, needlefishes, flying fishes, and sauries, following Rosen and Parenti (1981). Cyprinodontiform monophyly is well-supported and currently non-controversial (Parenti, 1981; Able, 1984); additional diagnostic cyprinodontiform characters are discussed below.

Rosen and Parenti (1981: 21) proposed four characters to support the sister group relationship of Cyprinodontiformes and Beloniformes (Table 2): absence of a second infraorbital bone; first epibranchial bone with an expanded base and no separate uncinat process; absence of the first pharyngobranchial bone; and the second and third epibranchial bones noticeably smaller than first and fourth. The last character is more appropriately treated as a synapomorphy of Beloniformes in which the state is unambiguously present. Aplocheiloid killifishes have four epibranchial bones approximately equal in length (Rosen and Parenti, 1981:

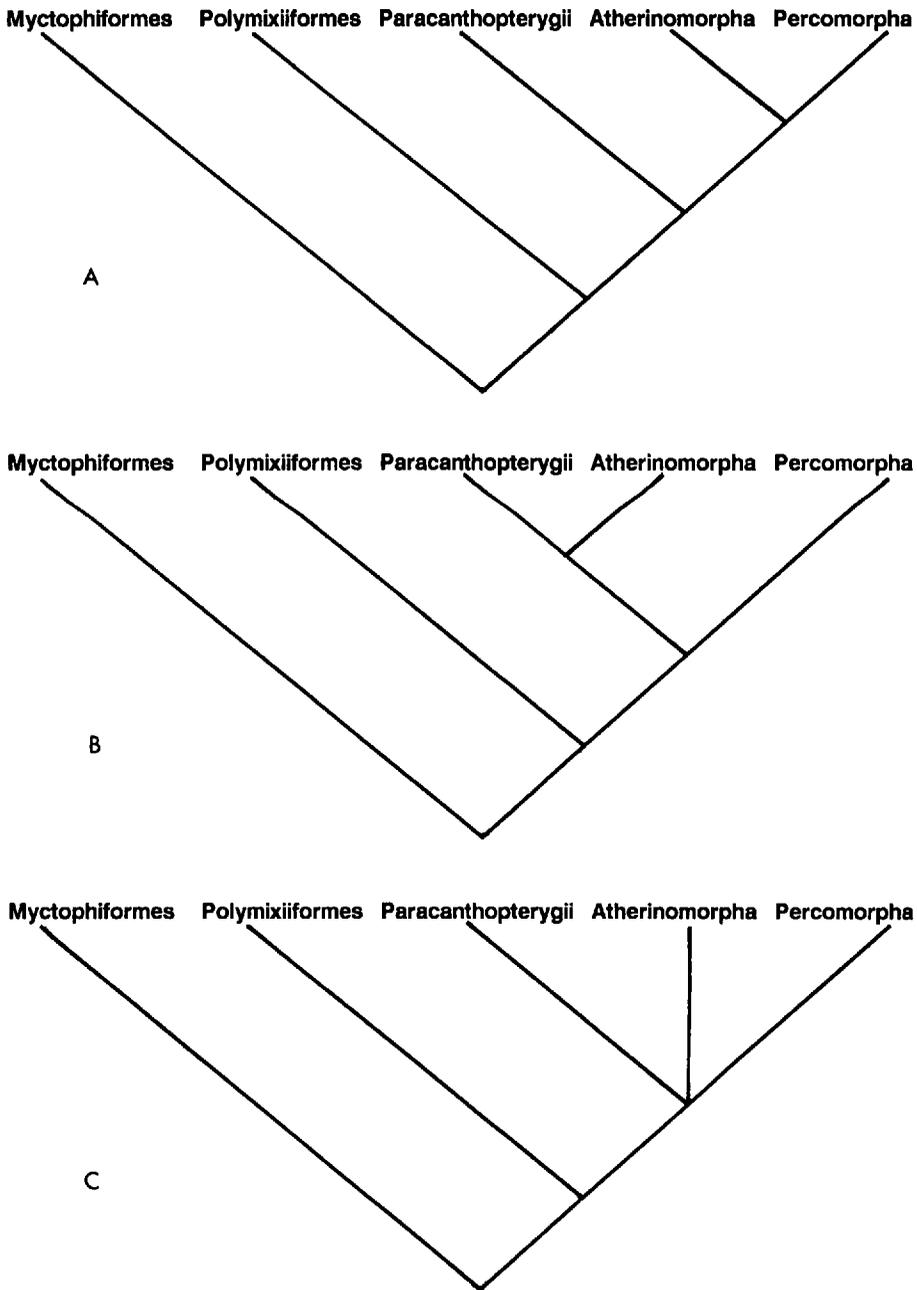


Figure 1. Three possible solutions to relationships among ctenosquamates: A. Atherinomorpha and Percomorpha as sister taxa; B. Atherinomorpha and Paracanthopterygii as sister taxa; C. unresolved relationships among Atherinomorpha, Paracanthopterygii, and Percomorpha. Monophyly of all groups is not implied. See text for discussion.

fig. 10). To the three remaining synapomorphies, White et al. (1984) added fin rays present at hatching. Here, I recognize a fifth synapomorphy, loss of the spinous first dorsal fin that is plesiomorphically present in atherinoids.

White et al. (1984) supported monophyly of atherinoids, their Atheriniformes; whereas, Parenti (1984, 1989) followed Rosen and Parenti (1981) and rejected

Table 2. Classification of Atherinomorph fishes (following Rosen and Parenti, 1981; Parenti, 1984), with equivalents in other classifications

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|---|
| Series Atherinomorpha [=Atheriniformes of Rosen, 1964] |
| Division I [=Atherinoidei of Rosen, 1964; Atheriniformes of White et al., 1984] |
| Family Bedotiidae |
| Family Melanotaeniidae |
| Family Pseudomugilidae |
| Family Telmatherinidae |
| Family Atherinidae |
| Family Notocheiridae (includes Isonidae) |
| Superfamily Phallostethoidea |
| Family Phallostethidae |
| Family Dentatherinidae |
| Division II [not recognized by Rosen, 1964] |
| Order Cyprinodontiformes [=Cyprinodontoidea of Rosen, 1964] |
| Order Beloniformes [not recognized by Rosen, 1964] |
| Suborder Adrianichthyoidei [=Adrianichthyoidea of Rosen, 1964] |
| Suborder Exocoetoidei |

atherinoid monophyly. Systematic analyses of some parts of atherinoids have been published during the past decade, viz. Old World silversides (Allen, 1980; Ivantsoff et al., 1987; Saeed et al., 1989; Stiassny, 1990), phallostethids (Parenti, 1984, 1986a, 1986b, 1989), and New World silversides (White, 1985; Chernoff, 1986). A comprehensive phylogenetic systematic analysis of Old and New World atherinoids, and an investigation of their relationships to other atherinomorphs, remains a critical omission within atherinomorph systematics.

Three questions of atherinomorph higher classification were unanswered or only insufficiently addressed by Rosen and Parenti (1981): 1) what derived characters support atherinomorph monophyly; 2) what are relationships among atherinoid fishes, the silversides and phallostethids; and 3) what is the sister group of atherinomorphs? My purpose here is to address these three questions, emphasizing the first, atherinomorph monophyly. Rosen and Parenti (1981) assumed atherinomorph monophyly and discussed briefly diagnostic or synapomorphic characters as part of an introduction to their gill arch survey. However, monophyly of any taxon can always be re-evaluated, and statement of monophyly should be justified before relationships among atherinomorph subgroups are considered. The two other questions, atherinoid diagnosis and an atherinomorph sister group, are considered here, but given less attention because broad character surveys, beyond the scope of this review paper, are required to answer them. This contribution points out problems in character interpretation and suggests characters that should be investigated.

Evidence for statements of relationship comes principally from descriptions of reproductive biology (e.g., by Grier and co-workers), as well as a survey of caudal-, dorsal-, and pelvic-fin anatomy and development. I have relied on other phylogenetic systematic analyses of ctenosquamate fishes (Rosen, 1973b, 1985; Johnson, 1984, 1986; Stiassny, 1986, 1990; Patterson and Rosen, 1989) for choices of, and states of some characters in, outgroup taxa.

MATERIALS AND METHODS

The following cleared and stained or alcohol material was examined. Just the genus is given in the text if a particular character state is present in all specimens of each species of that genus examined. Otherwise, more information, such as species and/or catalog number or size of specimen(s) in mm

Standard Length (SL), is provided. Size of specimens is a range of SL. Number of specimens following a catalog number refers to alcohol-preserved material, unless specified as cleared and stained. Cleared and counterstained specimens were stained with alcian blue for cartilage and alizarin red for bone, following Dingerkus and Uhler (1977). Additional cleared and solely alizarin stained preparations are housed in the USNM. Institutional abbreviations follow those in Leviton et al. (1985). CMK is the collection of Maurice Kottelat, Zoologische Staatssammlung, Munich.

The philosophy of phylogeny reconstruction that I follow, phylogenetic systematics or cladistics, was outlined by Hennig (1966), and developed further by Nelson and Platnick (1981), among others. Monophyletic groups contain all descendants and only descendants of an hypothesized common ancestor and are diagnosed by shared derived characters or synapomorphies. Paraphyletic groups are avoided as unnatural assemblages. Character states are judged as plesiomorphic or apomorphic based on the method of outgroup comparison summarized by Maddison et al. (1984).

Ctenosquamata (sensu Rosen, 1973b)

Myctophiformes

Myctophum obtusirostris, AMNH 29140SW: 4, 39.0–70.0 mm, cleared and counterstained.

Polymixiiformes

Polymixia lowei, USNM 308378: 1, 70.0 mm, cleared and counterstained, 1, 65.0 mm, hemisectioned of which part is cleared and counterstained.

Percopsiformes

Percopsis omiscomaycus, USNM 308216: 10, 25.5–62.2 mm; USNM 308217: 5, 24.4–35.7 mm, cleared and counterstained; USNM 179711: 5, 62.6–79.6 mm, cleared and stained solely with alizarin.

Percopsis transmontana, UW 19764: 2, 44.0–47.0 mm, cleared and counterstained.

Amblyopsiformes

Aphredoderus sayanus, USNM 217374: 6, 34.3–40.0 mm, cleared and counterstained, 2, 35.4–36.3 mm, cleared and stained solely with alizarin.

Chologaster cornuta, USNM 177924: 3, 27.6–30.0 mm, cleared and stained solely with alizarin; USNM 237005: 4, 12.6–26.6 mm, cleared and counterstained.

Gadiformes

Bathygadus macrops, USNM 202778: 1, 147.0 mm, cleared and stained solely with alizarin.

Brotula multibarbata, USNM 214124: 2, 81.6–117.0 mm, cleared and stained solely with alizarin.

Atherinomorpha

Atherinoids

Bedotiidae

Bedotia sp., USNM 301513: 2, 32.7–37.9 mm, cleared and counterstained.

Rheocles alaotrensis, AMNH 88171: 3, cleared and counterstained; USNM 301512: 2, 35.0–47.0 mm, cleared and counterstained.

Melanotaeniidae

Melanotaenia splendida, USNM 308410: 9, 11.0–22.2 mm, cleared and counterstained.

Pseudomugilidae

Pseudomugil novaeguineae, USNM 217157: 4, 22.0–30.0 mm, cleared and stained solely with alizarin.

Telmatherinidae

Telmatherina ladigesi, CAS 67425: 4, 31.4–38.2 mm, cleared and counterstained.

Atherinidae—Old World

Atherinomorus vaigiensis, USNM 174244: 3, 75.0–76.0 mm, cleared and stained solely with alizarin.

Craterocephalus lacustris, AMS I.18515-001: 5 of 32 radiographed.

Teramulus kieneri, AMNH 88141: 2, cleared and counterstained.

Atherinidae—New World

Labidesthes sicculus, USNM 108573: 16, 53.4–58.0 mm, cleared and stained solely with alizarin.

Membras martinica, USNM 273079: 3, 23.3–27.6 mm, cleared and stained solely with alizarin.

Notocheiridae (includes Isonidae)

Iso sp., USNM 297353: 4, 17.0–25.0 mm, cleared and counterstained.

Dentatherinidae

Dentatherina merceri, USNM 230374: 2, 28.2–29.5 mm, cleared and counterstained.

Phallostethidae

Phenacostethus posthon, USNM 229302: 6, 13.1–17.5 mm, cleared and counterstained.

Phenacostethus smithi, USNM 88667: 4, 5.0–9.0 mm, cleared and counterstained.

Cyprinodontiformes

Aplocheiloidei

Cynolebias whitei, USNM 177530: 4, 24.6–50.8 mm, cleared and stained solely with alizarin.

Cyprinodontoidei

Fundulus heteroclitus, USNM 278883: 1, 40.0 mm, cleared and counterstained.

Beloniformes

Adrianichthyoidei

Horaichthys setnai, USNM 277482: 8, 8.0–17.5 mm, cleared and counterstained; CAS 56255: 4, 16.0–17.5 mm, cleared and counterstained; AMNH 36576SW: 10, 11.0–18.5 mm, cleared and counterstained.

Oryzias profundicola, ZSM/CMK 6485: 1, 45.2 mm, cleared and counterstained.

Oryzias timorensis, ZMA 100.571: 1, 25.7 mm, cleared and counterstained.

Exocoetoidei

Hyporhamphus unifasciatus, USNM 196819: 13, 70.0–81.0 mm, cleared and stained solely with alizarin.

Nomorhamphus sp., USNM 309968: 1, 51.0 mm, cleared and counterstained.

Percomorpha

Beryciformes

Stephanoberyx monae, USNM 208284: 1, 80.0 mm, cleared and counterstained.

Mugiliformes

Mugilidae, USNM 308107: 2 postflexion larvae, approximately 2.5–4.0 mm, cleared and counterstained.

Agonostomus monticola, USNM 73742: 4, 28.0–34.0 mm, cleared and counterstained.

Mugil cephalus, USNM 156159: 4, 20.0–22.7 mm, cleared and counterstained.

Liza vaigiensis, USNM 265614: 3, 11.3–13.3 mm, cleared and counterstained.

Gasterosteiformes

Culaea inconstans, USNM 196818: 4, 34.5–37.0 mm, cleared and stained solely with alizarin.

Perciformes

Centropomus sp., USNM 114415: 1, 74.5 mm, cleared and counterstained.

Elassoma sp., CAS 39451: 1 cleared and counterstained.

Lepomis macrochirus, USNM 287448: 4, 31.0–42.5 mm, cleared and counterstained.

MONOPHYLY OF ATHERINOMORPHA

Here, I propose and discuss 14 diagnostic characters of the Atherinomorpha, sensu Rosen and Parenti (1981). These characters could be considered individually, but I group them into categories for purpose of discussion and also because several, if not all, in each category are correlated functionally as well as phylogenetically.

Cogent characters of atherinomorph monophyly are those of reproduction and development. These characters are convincing because they are unambiguous, i.e., they occur in all atherinomorph taxa so far surveyed, with rare and explained exception, and they are hypothesized to be derived relative to states in outgroup

taxa. Some of these and other characters will possibly be found homologous with character states in other ctenosquamate taxa, thus supporting proposal of an atherinomorph sister group. I discuss character states, when known, in putative atherinomorph sister groups, the mugiloids (following Stiassny, 1990) and paracanthopterygians.

Reproduction and Development. — 1. Testis a restricted spermatogonial type: spermatogonia restricted to distal end of testicular tubules (or lobules).—Grier and co-workers initially reported structure and associated reproductive modifications of an apparently unique testis type within several groups of atherinomorph fishes, including viviparous poeciliids (Grier, 1975a, 1975b) and goodeids (Grier et al., 1978), and oviparous ricefishes (Grier, 1976); in this type spermatogonia are restricted to the distal end of testicular tubules (or lobules). Sperm collect and pass through the efferent duct at the proximal end of the tubule. Grier et al. (1980) and Grier (1981) expanded the survey to include additional atherinomorph and other teleost species, and concluded that a restricted spermatogonial testis is unique to atherinomorphs. Other teleosts surveyed—Esocidae, Salmonidae, Cypriniformes, and Perciformes, including striped mullet, *Mugil cephalus*—have an hypothesized plesiomorphic state of an unrestricted spermatogonial testis in which spermatogonia are distributed throughout the testicular tubules or lobules (Grier et al., 1980: table 1). Knowledge of testis type within paracanthopterygians is limited; an unrestricted spermatogonial, tubular testis has been reported in the Atlantic cod, *Gadus morhua* (Morrison, 1990). A more extensive survey of testis type in paracanthopterygians is planned (Grier and Parenti, in prep.).

The atherinomorph testis has been confirmed subsequently in the ricefish *Horachichthys* (Grier, 1984), the halfbeak *Zenarchopterus* (Grier and Collette, 1987), and five phallostethid species (Grier and Parenti, in prep.), including *Gulaphallus mirabilis* (Grier et al., 1980), and *Phenacostethus smithi* (Munro and Mok, 1990).

Functional significance of the atherinomorph testis is unknown. It occurs in both oviparous and viviparous taxa. The testis produces sperm that are packaged or bundled together, and its presence is correlated with internal fertilization, long developmental period, and other reproductive modifications. Transfer of sperm bundles from male to female, in those species with internal fertilization, occurs via a modified anal fin (e.g., some rivulids, and goodeids, poeciliids, and anablepids; Parenti, 1981), a modified pelvic and part of the pectoral fin (phallostethids; Parenti, 1989), or through a urogenital papilla (hemiramphids; B. B. Collette, pers. comm.).

2. Egg demersal, with several to many short or long chorionic filaments, and several oil globules that coalesce at the vegetal pole.—Kamito (1928) illustrated the egg of the medaka, *Oryzias latipes*, covered with short filaments, and with a single tuft of long filaments. Numerous reports confirm widespread occurrence in atherinomorphs of eggs with chorionic filaments by which they may attach to floating or emergent vegetation (Kulkarni, 1940: fig. 15; Foster, 1968; Able, 1984; Collette et al., 1984; Matarese et al., 1989). Chorionic filaments may be adhesive (Matarese et al., 1989).

White et al. (1984) agreed that atherinomorph fishes have a distinctive egg, but stated that chorionic filaments are absent in the atherinoids *Labidesthes*, *Atherion*, and *Bedotia*. Subsequently, Takita and Nakamura (1986: fig. 1) published a photograph of *Atherion elymus* eggs with well-developed chorionic filaments as well as oil globules. Grier et al. (1990: 222), in their report of internal fertilization in brook silverside, included the observation that *Labidesthes sicculus* “. . . eggs had to be teased apart due to the entanglement of attached filaments.” Eggs removed

from the ovary of a *Bedotia* (USNM 301513) have elongate filaments. Filaments on *Bedotia* eggs have also been confirmed by M. L. J. Stiassny (pers. comm.).

Egg diameter varies from small (0.1 mm) to large (3.0 mm) (Able, 1984). Eggs may be relatively large even in species that mature at a small size, e.g., the poeciliid *Tomeurus gracilis* (Rosen and Bailey, 1963: fig. 7b). Development is usually direct with no pronounced larval stage (White et al., 1984). Hence, individuals are relatively large and well-formed at hatching, and sexual maturity is reached at a relatively young age (see character 4, below).

3. Coupling during mating.—Atherinomorph fishes typically couple during mating (Hubbs, 1919; Breder and Rosen, 1966). Males and females spawn in pairs, head to head, with bodies close together and bent in an S-curve. Correspondingly, internal fertilization and embryo retention, until or close to time of hatching, is widespread (Foster, 1967; Grier et al., 1990). Superfetation, simultaneously developing broods of different ontogenetic stages, is known in poeciliids and hemiramphids (Wourms, 1981).

4. Prolonged developmental period.—Atherinomorph eggs typically hatch 1 to 2 weeks following fertilization; although, some may hatch in as short a period as 4 days (e.g., sheepshead minnow, *Cyprinodon variegatus*), or as long as several months in annual killifishes (Able, 1984). This is in contrast to the inferred plesiomorphic state of relatively rapid developmental period of approximately 2 days in, for example, white mullet, *Mugil curema* (Anderson, 1957), and Pacific sardine, *Sardinops sagax* (Matarese et al., 1989).

Breder (1962) compared development of marine and freshwater fishes, emphasizing that many marine groups have pelagic transparent eggs that hatch a prolarval or larval stage in a few days; whereas, numerous freshwater groups have demersal, heavily pigmented eggs that hatch well-developed free-living young in 7 days or more. However, the environmental (marine versus freshwater) distinction does not hold across phylogenetic lines, as the demersal eggs of the nearly exclusively freshwater ostariophysan fishes hatch in 1 to 2 days (Breder and Rosen, 1966).

Time to hatching can be relatively long in both freshwater and marine paracanthopterygians. Eggs of *Aphredoderus* hatch 6 to 7 days after fertilization (Hardy, 1978). Eggs of walleye pollock, *Theragra chalcogramma*, hatch in 15 days at 5°C, and those of Pacific hake, *Merluccius productus*, hatch in 3.1 days at 16.1°C (Matarese et al., 1989). Seasonal variation in water temperature, dissolved oxygen and other parameters, however, makes homology of this character questionable (Markle and Frost, 1985; D. F. Markle, pers. comm.).

5. Separation of embryonic afferent and efferent circulation by development of heart in front of head.—During atherinomorph ontogeny, the heart is displaced forward on the yolk sac to a position in front of the head, resulting in complete separation of afferent and efferent circulation (Rosen, 1964). In embryos of other fishes, the heart is more posterior, and afferent and efferent circulation are superimposed (see Rosen, 1964; Rosen and Parenti, 1981; White et al., 1984: table 95).

Skull.—6. Ethmoid region of skull with one or two laminar, disclike mesethmoid ossifications.—Rosen (1964) described what he considered to be a unique condition of mesethmoid ossifications to diagnose atherinomorphs: double, rarely single, disclike ossified mesethmoid, the dorsal disc a dermal ossification, the ventral disc a chondral ossification. When just one disc is present, it is the dorsal, dermal bone, never the ventral, chondral bone, as far as known (Tigano and

Parenti, 1988). This is consistent with the observation that the dorsal disc ossifies before the ventral disc during ontogeny. Also, the palatine does not abut the ossified mesethmoid as it does in other neoteleosts, viz. *Agonostomus*, *Percopsis*, *Aphredoderus*, and *Aulopus* (Rosen and Patterson, 1969: fig. 74a).

Johnson (1984) reported the possibly homologous condition of two disclike mesethmoid ossifications in the perciform *Elassoma*. However, the ethmoid regions of *Elassoma* and atherinomorphs differ. The atherinomorph ethmoid region is depressed; the mesethmoid discs lie in roughly the same plane as the dorsoventrally flattened vomer and the parasphenoid (Tigano and Parenti, 1988: fig. 3). The mesethmoid discs, vomer, and parasphenoid of *Elassoma* meet anteriorly at an angle of approximately 45 degrees. This observation is not sufficient to reject homology of the ethmoid region of *Elassoma* and atherinomorphs, but is mentioned so that further descriptions of ethmoid regions may be more detailed.

7. Infraorbital series represented by the lacrimal, dermosphenotic, and two, one, or no anterior infraorbital bones.—Ctenosquamates plesiomorphically have a complete infraorbital series, consisting of a lacrimal, dermosphenotic, and four or more additional canal-bearing infraorbital bones, as in, for example, *Myctophum*, *Percopsis*, *Agonostomus*, and *Polymixia*. Presence of just two infraorbital bones (a lacrimal and a dermosphenotic) was considered diagnostic of atherinomorphs by Rosen (1964). However, this is true only of cyprinodontiforms and beloniforms (Rosen and Parenti, 1981). Atherinoids have, in addition to the lacrimal and dermosphenotic, one or two anterior infraorbital bones (Chernoff, 1986). Some Old World atherinoids, *Telmatherina*, *Melanotaenia*, and *Teramulus*, have well-developed, canal-bearing, second and third infraorbital bones. Inferred loss of the third infraorbital bone reduces the total number of infraorbital bones to three in New World atherinoids, such as *Membras* and *Labidesthes* (Chernoff, 1986), and various other Old World atherinoids, viz. *Rheocles* and *Bedotia* (Stiassny, 1990), and pseudomugilids (Saeed et al., 1989). Thus, reduction to three or less is a synapomorphy of some Old World atherinoids, New World atherinoids, and Division II atherinomorphs. This is in contrast to the interpretation of Chernoff (1986) that three infraorbital bones is diagnostic of New World atherinoids. Number of infraorbital bones is not considered here to diagnose any group of atherinoids.

Fins.—8. Lateral process of pelvic bone and distal end of pleural rib in close association, and, in some taxa, connected via a ligament.—Attachment of the distal end of the ventral elongate, rib-like postcleithrum (postcleithrum 3: Parenti, 1981; Gottfried, 1989) to a pelvic bone via a ligament is widespread in acanthomorph teleosts, viz. *Polymixia*, *Aphredoderus*, *Mugil* (Berg, 1940), *Agonostomus* (Fig. 2A), *Stephanoberyx*, *Liza*, *Centropomus*, and *Lepomis*. In the last two genera, pelvic fins are the farthest anterior; a ligament is perpendicular to the pelvic girdle, a further derived condition within percomorphs.

Atherinomorphs are unique among acanthomorph fishes surveyed in having the lateral process of the pelvic bone in close association with the distal tip of a pleural rib, rather than postcleithrum 3. In Old World atherinoids *Bedotia*, *Rheocles*, *Pseudomugil* (Saeed et al., 1989), *Melanotaenia*, *Atherinomorus*, *Telmatherina*, and the beloniform *Xenopoeilus*, the distal tip of the third or fourth pleural rib is attached laterally to the pelvic bone via a short ligament (Fig. 2B). In all other atherinomorphs examined, pelvic bones are in close association with pleural ribs, but I have seen no ligamentous attachment.

Pelvic fins of *Percopsis* are in a position that may be considered intermediate between posterior extent of the ventral postcleithrum and pleural ribs, and I have

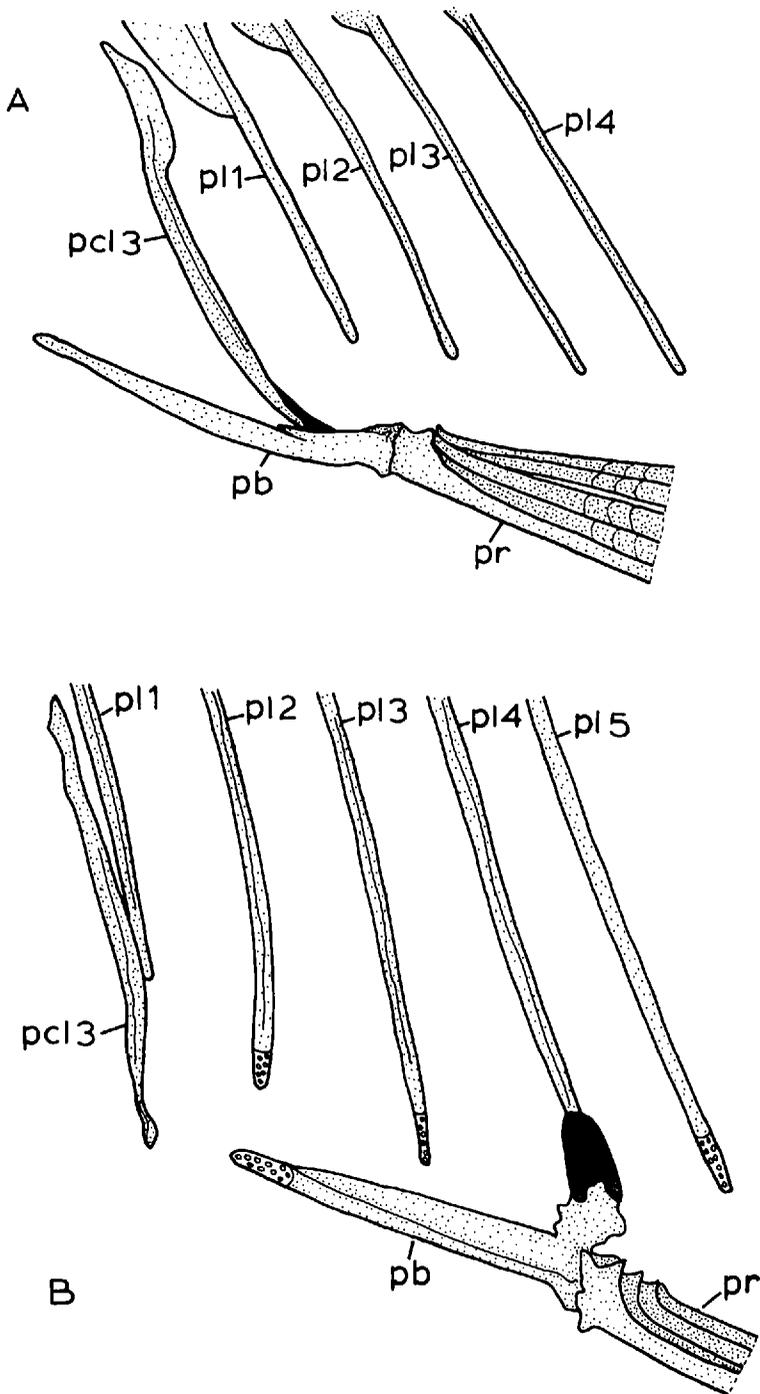


Figure 2. Diagrammatic representation of relative position and attachment of lateral process of pelvic bone to A. ventral postcleithrum in *Agonostomus monticola*, 32.0 mm SL (USNM 73742), B. distal tip of fourth pleural rib in *Bedotia* sp., 37.9 mm SL (USNM 301513). Abbreviations: pb, pelvic bone; pcl 3, ventral postcleithrum; pl 1–5, pleural rib 1–5; pr, pelvic rays. Rest of shoulder girdle and fin rays removed. Bone lightly stippled; ligament densely stippled; cartilage open circles. Anterior to the left.

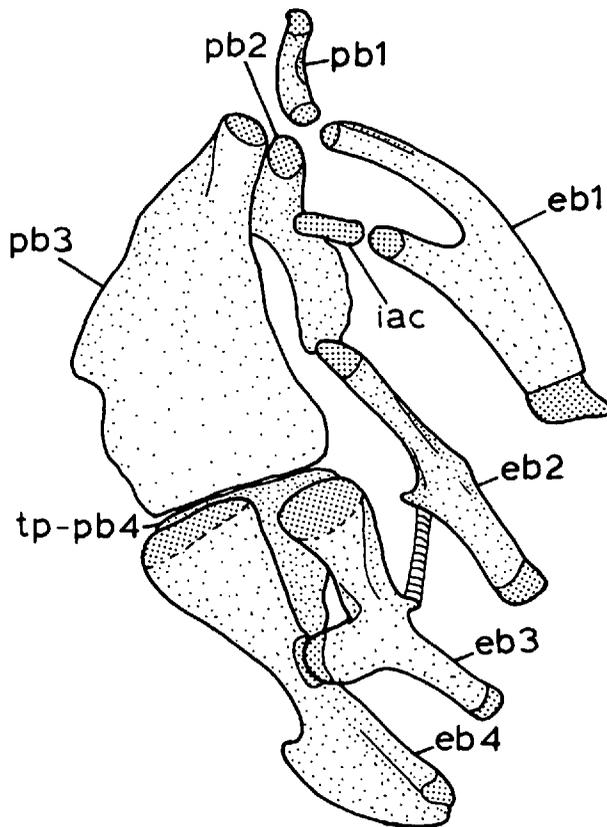


Figure 3. Diagrammatic representation of dorsal portion of gill arches in *Bedotia* sp., 37.9 mm SL (USNM 301513). Abbreviations: eb 1-4, epibranchial bones 1-4; iac, interarcual cartilage; pb 1-4, pharyngobranchial bones 1-4; tp-pb 4, toothplate of fourth pharyngobranchial bone. Observed interarcual ligaments included following Markle (1989). Anterior towards the top.

not identified a pelvic-pleural rib or pelvic-postcleithrum ligament. Amblyopsids *Chologaster* and *Typhlichthys* lack pelvic fins, which are variably present in *Amblyopsis* (Woods and Inger, 1957).

Pelvic bones of *Myctophum* are associated closely with distal tips of pleural ribs and not joined to ribs via a ligament, a condition resembling derived atherinomorph fishes. For now, I hypothesize that this condition is nonhomologous in *Myctophum*, plesiomorphic to *Polymixia* and remaining acanthomorphs (Fig. 1). This interpretation is consistent with the conclusion that overlapping medial processes of pelvic bones, in *Polymixia*, percopsiforms, amblyopsiforms, and some gadiforms (e.g., *Bathygadus*), is plesiomorphic for acanthomorphs. Mugilids, as well as *Elassoma*, share with other perciforms the apparently derived state of pelvic bones sutured along the midline (Stiassny, 1990). Numerous beryciform taxa, such as *Stephanoberyx*, have pelvic bones that overlap in the midline (Zehren, 1979), one of many characters that cause us to question beryciform monophyly and placement of beryciform taxa in the Percomorpha (see Moore, this issue).

9. Supracleithrum reduced or absent.—An elongate supracleithrum is interpreted as plesiomorphic for acanthomorphs because it is present in taxa such as *Poly-*

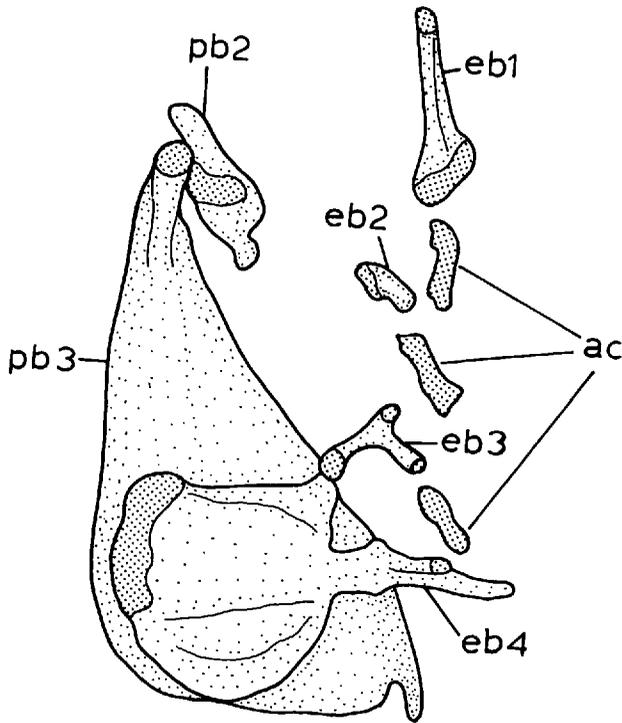


Figure 4. Diagrammatic representation of dorsal portion of gill arches in *Oryzias profundicola*, 45.2 mm SL (ZSM/CMK 6485). Abbreviations as in Fig. 3.

mixia, *Percopsis*, and *Centropomus*. The supracleithrum is reduced to a small, oblong bone in plesiomorphic atherinoids, *Rheocles*, *Telmatherina*, *Bedotia* (see also Rosen, 1964), and plesiomorphic cyprinodontiforms, *Rivulus* (Parenti, 1981: fig. 7d). In other Division II atherinomorphs, the supracleithrum may be absent (*Oryzias* and *Tomeurus*; Parenti, 1981), or indistinguishable from the elongate posttemporal (Old World aplocheiloids; Parenti, 1981: fig. 7c). A distinctive, disclike supracleithrum is possibly diagnostic for Pseudomugilidae (Saeed et al., 1989).

Gill Arches.—10. Dorsal portion of gill arches with a large, fourth epibranchial the prominent supporting bone and no fourth pharyngobranchial element.—A fourth pharyngobranchial cartilage was considered plesiomorphic for acanthopterygians by Rosen and Parenti (1981: figs. 1–5), who proposed absence of a fourth pharyngobranchial element as an atherinomorph synapomorphy. Rosen and Parenti (1981: fig. 4b) found no fourth pharyngobranchial element in the great barracuda, *Sphyaena borealis*. Following the hypothesis of Johnson (1986) that barracudas are plesiomorphic scombroid fishes, absence of this element in atherinomorphs and scombroids is considered homoplastic. Absence of a fourth pharyngobranchial element in atherinomorphs led Langille and Hall (1987: 149) to misidentify the prominent upper pharyngeal toothplates of *Oryzias latipes* as fourth pharyngeal rather than third pharyngeal toothplates, as supported by other interpretations of teleost gill-arch anatomy (Rosen, 1973b; Johnson, 1986; Rosen and Patterson, 1990).

The fourth epibranchial bone is relatively large in atherinoids (e.g., *Bedotia*, Fig. 3) and cyprinodontiforms (Parenti, 1981: figs. 6, 24, 46–50), and huge in

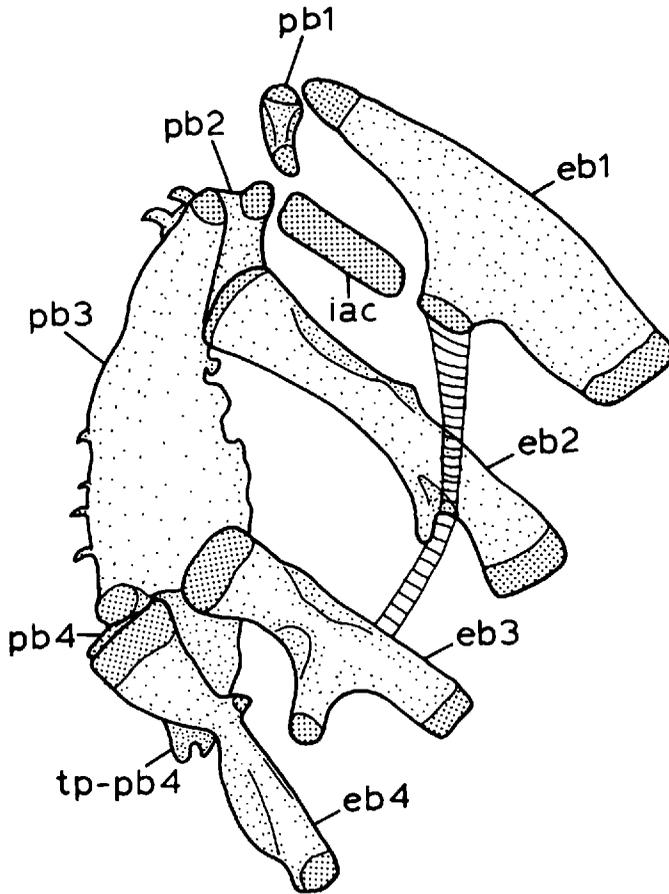


Figure 5. Diagrammatic representation of dorsal portion of gill arches in *Agonostomus monticola*, 32.0 mm SL (USNM 73742). Abbreviations as in Fig. 3.

beloniforms (e.g., *Oryzias*, Fig. 4). This is in contrast to a fourth epibranchial bone that is small relative to epibranchials one through three in other acanthomorphs (e.g., *Agonostomus*, Fig. 5), except amblyopsiforms and percopsiforms. In *Aphredoderus* (Fig. 6) and other amblyopsiforms and percopsiforms (Patterson and Rosen, 1989: fig. 13a–e), the fourth epibranchial bone may be short relative to the first; however, the surface that contacts the fourth and third pharyngobranchial elements is broad. I interpret the large fourth epibranchial bone of atherinomorphs, amblyopsiforms, and percopsiforms as a synapomorphy. The fourth pharyngobranchial element is present or absent in gadiforms (Markle, 1989).

11. Medial hooklike projection and ventral flange on fifth ceratobranchial bone.—Rosen (1964:237) described “. . . a large bony wing ventrally . . .” on the lower pharyngeals (=fifth ceratobranchial bone). Stiassny (1990: fig. 7) illustrated the fifth ceratobranchial bones of the Madagascan silverside, *Rheocles alaotrensis*, in dorsal view, with medial hooklike projections and ventral flanges, each modification enumerated as an atherinomorph synapomorphy. The medial hooklike projection is the insertion site of the fifth adductor and the obliquus dorsalis

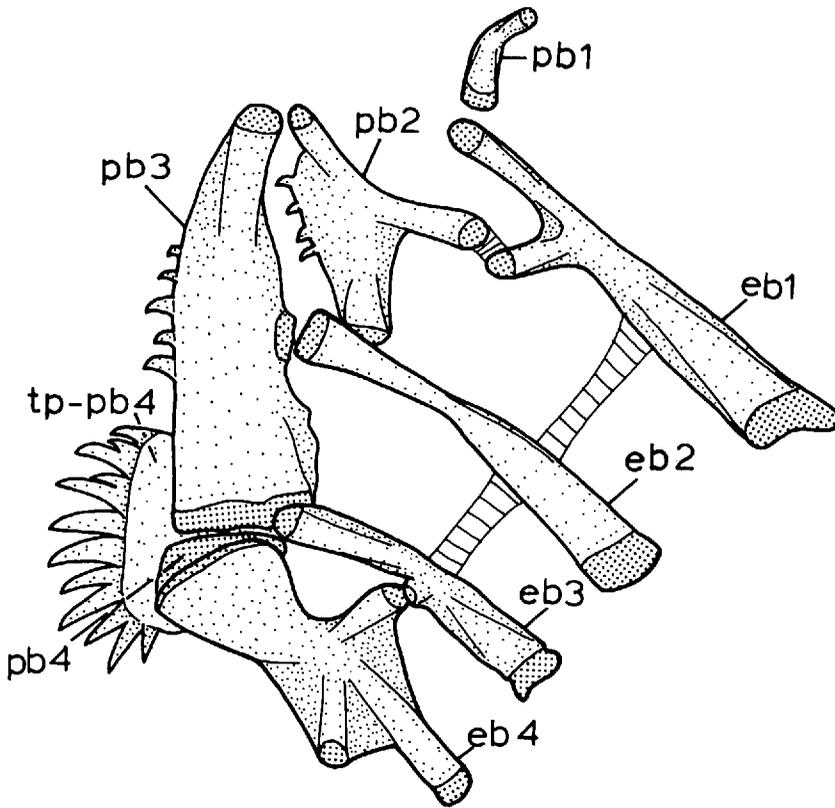


Figure 6. Diagrammatic representation of dorsal portion of gill arches in *Aphredoderus sayanus*, 40.0 mm SL (USNM 217374). Abbreviations as in Fig. 3.

posterior muscles; the ventral flange is site of the tendinous origin of the pharyngo-hyoideus muscle (Stiassny, 1990).

Axial Skeleton. — 12. Supraneural bones absent. — Atherinomorphs have been described as lacking identifiable supraneural (=predorsal; Mabee, 1988) bones (Stiassny, 1990). Three distinct supraneural bones in, for example, *Polymixia* (Patterson and Rosen, 1989: fig. 9a), *Agonostomus*, *Stephanoberyx*, *Culaea*, *Centropomus*, and *Lepomis*, is considered plesiomorphic for acanthomorphs (Johnson, 1984). Paracanthopterygians have one supraneural bone, flat and platelike in percopsiforms (Patterson and Rosen, 1989: fig. 9b, c).

In adult atherinomorphs, e.g., *Hyporhamphus* (Fig. 7A), a distinct rectangular plate extends anterior and posterior to the neural arches of each of the first or second through fifth or higher vertebrae. Neural arches do not necessarily meet in the midline to form a spine. The condition is nearly identical in juveniles as well as adults. In the smallest *Melanotaenia* I examined (11.0 mm SL), the dorsal plates are separate from the neural arches.

In contrast, neural arches of the second through fourth or fifth vertebra of mullets, e.g., *Agonostomus* (Fig. 7B), *Liza*, and *Mugil*, are expanded anterior to the neural spine, much like, but not identical to, the condition illustrated by Carpenter (1990: fig. 8a) in perciform caesionids.

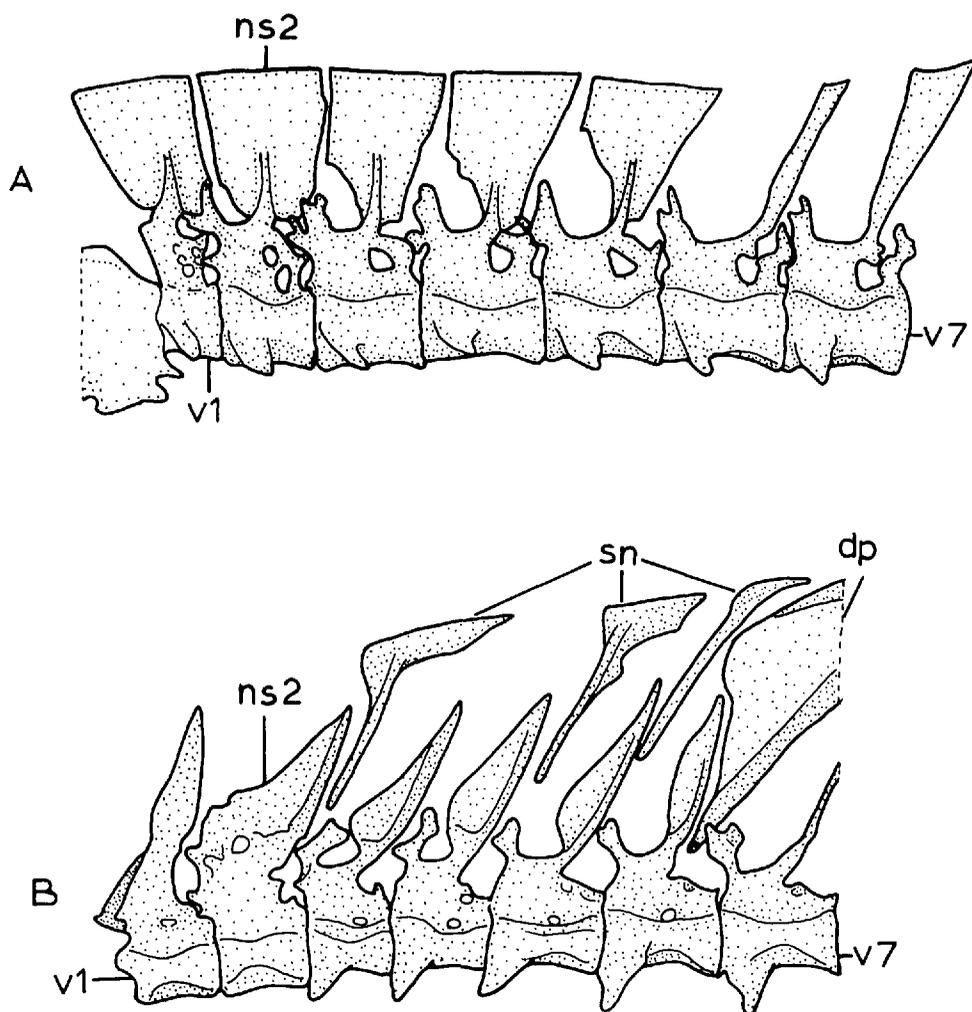


Figure 7. Diagrammatic representation of anterior neural arches in A. *Hyporhamphus unifasciatus*, 81.0 mm SL (USNM 196819), B. *Agonostomus monticola*, 31.0 mm SL (USNM 73742). Abbreviations: dp, dorsal fin pterygiophore; ns 2, neural spine of second vertebra; sn, supraneural bones; v 1, 7, vertebra one and seven. Ribs are removed. Anterior to the left.

Because there may be more than three expanded neural arches in atherinomorphs, I do not interpret that condition as a complex of the "absent" supraneural bones and neural arches. Stiassny (1990) treated absence of supraneural bones as an atherinomorph autapomorphy, and I agree. She also proposed expanded neural arches of anterior vertebrae as a synapomorphy of mugiloids (her Mugilomorpha) and atherinomorphs. The above observations question homology of acanthomorph expanded neural arches.

Jaw Musculature.—13. Superficial (A_1) division of adductor mandibulae with two tendons, one inserting on the maxilla, a second inserting on the lacrimal bone.—Various authors have used modifications of the superficial (A_1) division of the adductor mandibulae as diagnostic of atherinomorphs, although their de-

scriptions differ significantly. Rosen (1964: 234) described what he considered a derived condition of A_1 in atherinomorphs: the maxillary tendon inserts on the posteroventral section of the maxilla, rather than near the maxillo-palatine hinge, as he observed in mugiloids, sphyraenoids, and polynemoids. Alexander (1967: fig. 1a) described two dorsal A_1 tendons: one inserts on the medial face of the first infraorbital (=lacrima) bone, and a second inserts on the posterior arm of the maxilla. Stiassny (1990) clarified distribution of this character in atherinomorphs, reporting both tendons in atherinoids and beloniforms and absence of a tendon to the lacrimal bone in cyprinodontiforms. She interpreted presence of both tendons as an autapomorphy of atherinomorphs, and absence of the tendon to the lacrimal bone an autapomorphy of cyprinodontiforms, and I agree (see Discussion, below).

Olfactory Organ. — 14. Olfactory sensory epithelium arranged in sensory islets. — The teleost olfactory organ typically consists of sensory epithelium folded into a circular or oblong nasal rosette. Olfactory organ shape is variable (Zeiske et al., 1979); however, atherinomorphs share a derived characteristic: sensory epithelium on the nasal lamellae is arranged in so-called sensory islets, individual masses of sensory tissue surrounded by indifferent (nonsensory) tissue (Yamamoto and Ueda, 1979). Yamamoto (1982) reported sensory epithelial patterns in eighty teleost species. All seven atherinomorph species, including representative atherinoids, cyprinodontiforms and beloniforms, have these sensory islets. The islets are found otherwise in one or two but not all species surveyed in the Siluriformes, Gasterosteiformes, Scorpaeniformes, Perciformes and Tetraodontiformes. In contrast, sensory epithelium is distributed continuously on the olfactory lamellae in *Mugil* and *Sphyraena*, as in “. . . the majority of Perciformes” (Yamamoto and Ueda, 1979: 162), and two gadiform and two lophiiform species (Yamamoto, 1982).

Rosen and Parenti (1981) cited method of nasal capsule ventilation as reported by Melinkat and Zeiske (1979) as diagnostic of atherinomorphs. However, unique characteristics of the atherinomorph olfactory organ are here described as structural rather than functional.

RELATIONSHIPS AMONG ATHERINOMORPHA

Rosen and Parenti (1981) characterized atherinoids as paraphyletic in part because of an hypothesized transition series of reduction and loss of the first dorsal fin in atherinomorphs. White et al. (1984) proposed two larval characters to support atherinoid monophyly: dorsal pigmentation pattern and short preanal length through flexion. Parenti (1984) described two transition series that could be analyzed as one, reduction of premaxillary articular process and decoupling of the rostral cartilage from ascending process of premaxilla, to reject atherinoid monophyly. Ivantsoff et al. (1987) could also find no evidence for atherinoid monophyly, but objected to some statements by Parenti (1984) on character homology within atherinomorphs.

Definition and diagnosis of most atherinoid families are unsettled. For example, during the past three decades, *Pseudomugil* has been classified in the Atherinidae (Rosen, 1964), the Melanotaeniidae (Allen, 1980), and the Pseudomugilidae (Saeed et al., 1989). *Pseudomugil helodes*, described in the Melanotaeniidae by Ivantsoff and Allen (1984), will soon be moved to the Telmatherinidae, as reported in Saeed et al. (1989).

Statements on relationships among families are correspondingly vague. Atherinoid families were listed in a classification by Parenti (1984) to reflect a hypothesized sister group relationship between phallostethids and *Dentatherina* (Table 2). It is beyond the scope of this paper to resolve further the relationships among atherinoid families, especially because the monophyly of several is in question. Here, I discuss two characters to illustrate some common obstacles to resolution of phylogenetic relationships of atherinomorphs and other ctenosquamate groups.

First Dorsal Fin.—The plesiomorphic condition of the group comprising paracanthopterygians, atherinomorphs, and percomorphs is a single dorsal fin with anterior thickened spinous rays and posterior segmented branched rays, as in two successive outgroups, *Myctophum* and *Polymixia* (Fig. 1). Supraneural bones number three (Fig. 7B). Two complete dorsal fins, the first spinous and the second with anterior spines and segmented branched rays, characterizes many percomorphs, e.g., *Centropomus*; although degree of separation between fins, and variation in presence and formation of spines confounds determination of polarity of dorsal fin transformation series (Johnson, 1984).

Paracanthopterygians are also notable for extreme variation in dorsal fin morphology. *Aphredoderus* and *Percopsis* are like the plesiomorphic ctenosquamate, having a single dorsal fin with anterior spines. *Percopsis* and *Myctophum* have an adipose fin. The gadiform *Bathygadus* has a single dorsal fin that may be described as having two portions: the first portion with a spine followed by 11 segmented rays, and the second portion with a series of segmented, but spine-like, rays confluent with caudal-fin rays. Dorsal pterygiophores are continuous. In the gadiform *Muraenolepis marmoratus* (Markle, 1989: fig. 13) small rudimentary pterygiophores lie between a small first and the second dorsal fin.

Mugiloids have two dorsal fins, as in *Agonostomus* (Fig. 8A). The first dorsal has four spines, three of which are robust, and no soft rays. The second dorsal has two anterior unbranched rays followed by branched rays and a final unbranched ray. Small separate pterygiophores that have a median shaft, but bear no soft rays or spines, lie between the two dorsal fins.

Inferred plesiomorphic Old World atherinoids, such as *Rheocles*, *Melanotaenia*, and *Bedotia*, have two dorsal fins. In *Bedotia* (Fig. 8B), the first dorsal has five thin spines. Pterygiophores with a distinct, median shaft are between the first and second dorsal fins. Points of attachment for two spines, inferred to have been lost from the sixth and seventh pterygiophores, are marked by arrows in Figure 8B.

Other atherinoids, such as New World *Labidesthes*, have a first dorsal fin with four smaller spines supported by reduced rudimentary pterygiophores (Fig. 8C). Pterygiophores between the first and second dorsal fin are also small and platelike, lacking a median shaft characteristic of the better developed pterygiophores of *Bedotia* (Fig. 8B). In other atherinoids with reduced dorsal fins, such as *Iso*, there are no pterygiophores between the first and second dorsal fin.

First dorsal-fin rays and pterygiophores are reduced also in Old World pseudomugilids, including several species of *Pseudomugil*, but especially *Kiunga* (Saeed et al., 1989: fig. 54a). In most phallostethids, there is a small first dorsal with one or two spinous rays and reduced pterygiophores as well as a second dorsal fin (Parenti, 1989). Absence of the first dorsal fin in several phallostethid species is interpreted as convergent with Division II atherinomorphs because of the inferred close relationship of phallostethids to dentatherinids (Parenti, 1984, 1989).

Cyprinodontiforms and beloniforms have one soft-rayed, dorsal fin. All rays

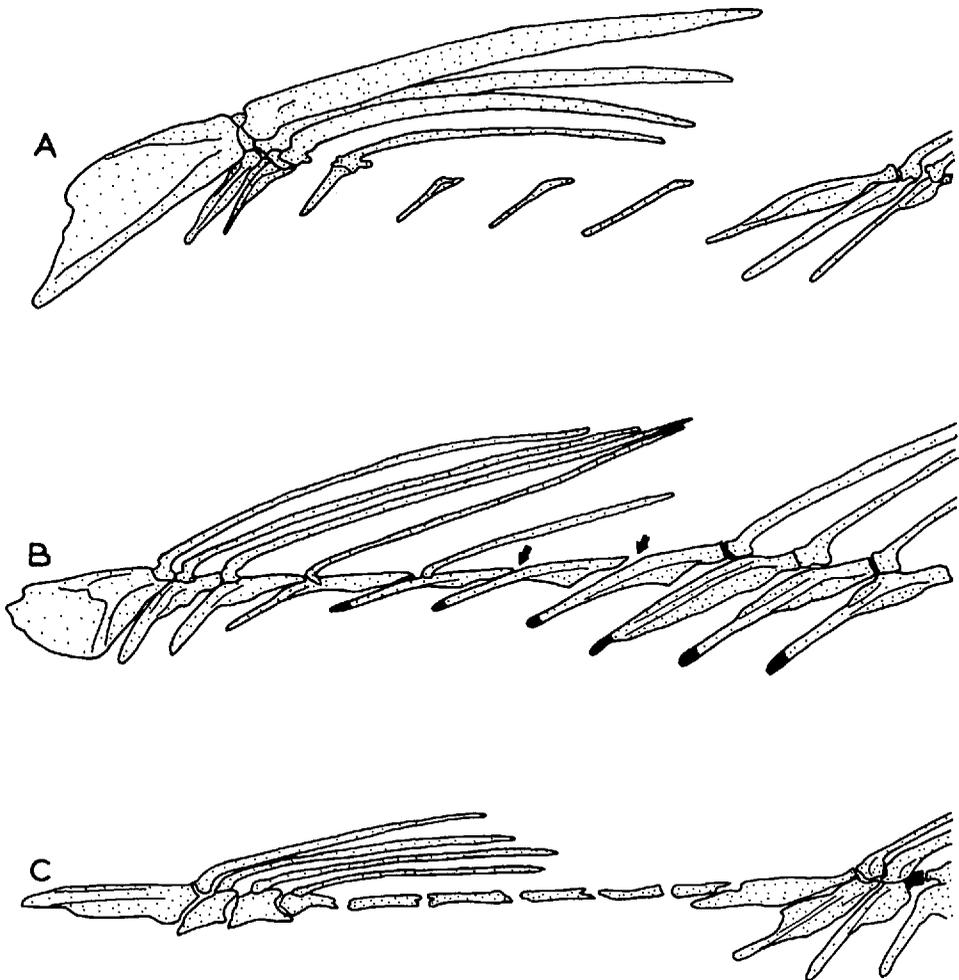


Figure 8. Diagrammatic representation of anterior dorsal fin supports in A. *Agonostomus monticola*, 31.0 mm SL (USNM 73742), B. *Bedotia* sp., 37.9 mm SL (USNM 301513), and C. *Labidesthes sicculus*, 55.0 mm SL (USNM 108573). Cartilage, blackened; bone, stippled. Not all cartilage is differentiated. Anterior to the left. Arrows point to positions where fin rays would be expected if dorsal fin were complete.

are segmented, except in some cyprinodontiforms (e.g., flagfish, *Jordanella floridae*) in which the first dorsal-fin ray is thickened and spinous (Parenti, 1981). The adrianichthyoid *Oryzias* has an anterior dorsal pterygiophore that, because of its shape, I interpret as a complex of the first pterygiophore of the second dorsal and the last in the series of pterygiophores that in plesiomorphic acanthomorphs lie between the first and second dorsal fin (Fig. 9). I propose no mechanism for formation of this complex pterygiophore. A complex anterior pterygiophore of the second dorsal fin is illustrated also for *Kiunga* (Saeed et al., 1989: fig. 54b).

Rosen (1964) discussed the possible origin of the first dorsal fin in atherinomorphs, arguing that it could have arisen independently from the condition in other acanthomorphs, or that it represented a reduction from a fully developed spinous single dorsal fin. I interpret the dorsal fins of *Bedotia* (Fig. 8B) as reduced

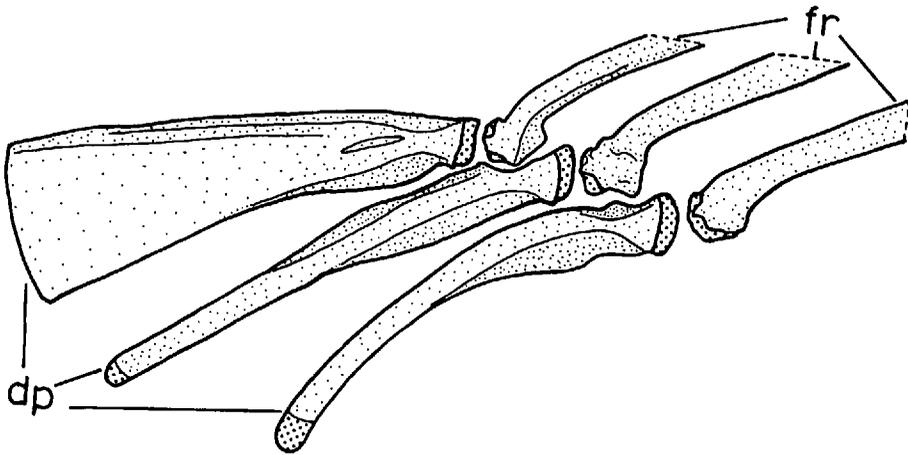


Figure 9. *Oryzias timorensis*, 25.7 mm SL (ZMA 100.571). Abbreviations: dp, anterior dorsal pterygiophores; fr, fin rays. Large stippling, cartilage; small stippling, bone. Anterior to the left.

from a single spinous dorsal fin by loss of the sixth and seventh fin rays. The first dorsal fin has been further reduced or lost during phylogeny in one group of Old World atherinoids (pseudomugilids and phallostethids) and New World atherinoids. Also, the first dorsal is lost in all Division II atherinomorphs. Hence, I interpret the single dorsal fin of Division II atherinomorphs as homologous to the second dorsal fin of atherinoids.

The two dorsal fins of mugiloids might also be derived from a single spinous dorsal fin. However, reduction of intervening pterygiophores and loss of their associated spines is interpreted to have occurred independently in mugiloids and atherinomorphs, because of the nearly complete dorsal fin in a plesiomorphic atherinomorph, *Bedotia* (Fig. 8B). This argument would be circular if the only evidence for bedotiids being plesiomorphic atherinomorphs was presence of a nearly complete dorsal fin. Other characters, discussed here and elsewhere (Rosen and Parenti, 1981; Parenti, 1984; Stiassny, 1990), that are plesiomorphic in bedotiids (and modified in some or all other atherinoids) are presence of a first pharyngobranchial bone and distinct ascending and articular processes of the premaxilla.

This description of dorsal fin evolution requires interpreting the dorsal fins of *Labidesthes* (Fig. 8C) as reduced relative to those of *Bedotia* (Fig. 8B). However, similar states in, respectively, *Dentatherina* (Ivantsoff et al., 1987: fig. 5b) and the Old World atherinid *Craterocephalus* (Ivantsoff et al., 1987: fig. 5a), led to the conclusion that "The first dorsal fin is as well developed in *Dentatherina* as it is in atherinids . . ." (Ivantsoff et al., 1987: 655).

Homology is an hypothesis that may be confirmed or rejected with additional characters or ontogenetic data, as for homology of expanded neural arches and supraneural bones in atherinomorphs and mugiloids (character 12, above). Likewise, a more detailed description of a character may resolve observers' differences. I conclude that the first dorsal fin is not "as well developed" in *Dentatherina* as in all atherinids; however, resolution of atherinoid phylogeny awaits some consensus on character description.

Larval Characters.—White et al. (1984) diagnosed atherinoids as monophyletic by presence of a derived larval pigmentation pattern: dorsal melanophores arranged in a single row, rather than in two rows or in no consistent pattern. The

derived state is also present in the plesiomorphic beloniform adrianichthyoids, considered convergent by White et al. (1984: 357). Assuming a monophyletic Atherinomorpha, characters found in atherinoids and beloniforms may be atherinomorph symplesiomorphies, atherinoid/beloniform synapomorphies, or independently derived in atherinoids and beloniforms. Division II atherinomorph synapomorphies (Rosen and Parenti, 1981; and herein) refute an atherinoid/beloniform sister group relationship. There are several symplesiomorphies of atherinoids and beloniforms, the derived states of which have been interpreted as cyprinodontiform apomorphies. For example, absence of a ligamentous attachment of A_1 to the lacrimal is a diagnostic character of cyprinodontiforms (Stiassny, 1990, and herein). For such characters, we may think of cyprinodontiforms as the most highly modified from a hypothetical atherinomorph ancestor.

A second larval character used by White et al. (1984) to diagnose atherinoids was short preanal length through flexion. With only one exception reported by White et al. (1984), preanal length of atherinoids is approximately one-third of body length, whereas preanal length exceeds that value in nearly all other acanthomorphs. Interestingly, preanal length is short also in gadids, a condition White et al. (1984: 357) considered nonhomologous because the gadid gut is always looped, unlike that of atherinoids.

Description of these larval characters is clear. However, determination of polarity is open to an alternate interpretation, that the larval characters represent atherinomorph symplesiomorphies, not atherinoid apomorphies. Short preanal length is derived in atherinoids and gadids; whether this shared derived character is a synapomorphy (=homology) may be tested with additional characters.

SISTER GROUP OF ATHERINOMORPHA

Patterson and Rosen (1989) reviewed their earlier (Rosen and Patterson, 1969) analysis of paracanthopterygian relationships, and concluded that this diverse ctenosquamate clade is possibly monophyletic. Their cladogram of relationships (Patterson and Rosen, 1989: fig. 16) depicted living percopsiform and amblyopsiform fishes as plesiomorphic to all other paracanthopterygians. Four characters were used to diagnose Paracanthopterygii: 1) a full neural spine on the second preural centrum; 2) two epural bones; 3) a single supraneural bone posterior to the first or second neural spine; and, 4) an enlarged intercalar bone that contains the glossopharyngeal foramen and forms part of the cranial wall.

Their cladogram (Patterson and Rosen, 1989: fig. 16), like most others of apomorphic teleosts since Rosen and Parenti (1981), included an Acanthopterygii, comprising the Atherinomorpha and Percomorpha. This relationship was challenged by Stiassny (1990) who proposed mugiloids as the sister group of the atherinomorphs. Here, I discuss states of Patterson and Rosen's (1989) paracanthopterygian synapomorphies in atherinomorphs and other ctenosquamates, and consider the proposal that atherinomorphs and paracanthopterygians, in whole or in part, are sister taxa.

Caudal Skeleton.—Rosen (1985: 44) considered “foolhardy” use of the derived character described simply as a full neural spine on the second preural centrum (NPU2) in acanthomorphs, unless ontogenetic data could support homology of the structure in proposed sister taxa. Cyprinodontiforms and adrianichthyoids have a full neural spine on the second preural centrum (Fujita, 1990: figs. 162–165) in all ontogenetic stages, as in *Myctophum*, *Polymixia*, and paracanthopterygians. In most adult atherinoids, other beloniforms, and numerous percomorphs, NPU2 is short (e.g., Patterson and Rosen, 1989; Saeed et al., 1989: fig. 10c).

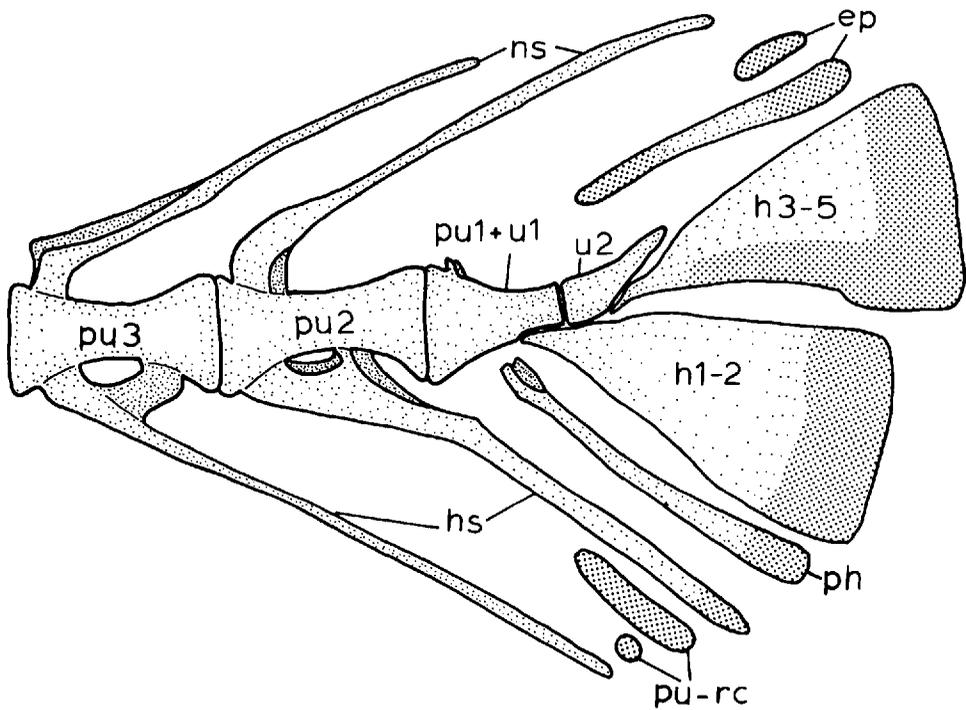


Figure 10. Diagrammatic representation of caudal fin skeleton in *Horaichthys setnai*, 8 mm SL (USNM 277482). Abbreviations: ep, epural elements; h 1–5, hypural bones 1–5; hs, haemal spines; ns, neural spines; ph, parhypural bone; pu 1–3, preural centra 1–3; pu-rc, preural radial cartilages; u 1–2, urocentra 1–2. Bone, light stippling; cartilage, dense stippling. Anterior to the left.

Early developmental stages and adults of atherinomorph species that mature at a small size, such as the atherinoids *Phenacostethus* and *Dentatherina*, and the beloniform *Horaichthys* (Fig. 10), are a source of information on polarity of caudal fin characters within atherinomorphs. The first preural and urocentra fuse into a separate centrum to which the lower hypurals articulate; upper hypurals articulate with the free second urocentrum. The parhypural is autogenous. Fujita (1992) reported the same configuration of caudal skeletal elements in early ontogenetic stages of *Oryzias latipes*. This condition is in contrast to a postflexion larval mugilid which has a urostyle, i.e., no separate preural and urocentra.

An autogenous parhypural is correlated with a nominally complex (fused?) preural and urocentrum; although, Markle (1989: 80–81) concluded that an autogenous parhypural means that the first preural centrum is never formed in gadiforms. If so, the same is true of atherinomorphs. Further, Markle (1989: 78) considered double neural and haemal spines on especially the first preural centrum to be normal, rather than teratological, for gadiforms. The same condition occurs in some specimens of *Horaichthys* and other ricefishes.

Stiassny (1990) treated absence of radial cartilages as diagnostic of atherinomorphs; however, they are variably present in atherinomorphs and paracanthopterygians (Fujita, 1989, 1990). A preural cartilage between haemal spines of the second and third preural vertebrae (called the third preural radial by Fujita, 1989, 1990: fig. 16) is present in numerous atherinomorphs. An ossified third preural radial was reported in pseudomugilids (Saeed et al., 1989: fig. 27a) and is present in adrianichthyoids. Fujita (1990) called the bone in *Oryzias* an extra caudal

ossicle; I identify it as a positional homologue of the Y-bone of gadiforms (Patterson and Rosen, 1989).

Hypothesized plesiomorphic atherinomorphs have two epural bones (e.g., *Rheocles*, *Bedotia*, *Melanotaenia*), whereas cyprinodontiforms (e.g., *Cynolebias* and *Fundulus*) have one, the more derived state based on outgroup comparison. Beloniforms may have a few as one (e.g., *Horaichthys*) or as many as three (e.g., *Hyporhamphus*, *Cypselurus*, *Strongylura*; Fujita, 1990). Thus, one could argue that atherinomorphs and paracanthopterygians share the derived condition of two or fewer epural bones only if there is a reversal to three in beloniforms.

Supraneural Bones. — Absence of supraneural bones is the last hence hypothesized most highly derived state in the transition series from three supraneural bones (plesiomorphic for acanthomorphs) to one (diagnostic of paracanthopterygians) to none (diagnostic of atherinomorphs). However, reduction in supraneural bones in paracanthopterygians and atherinomorphs is possibly not homologous; the proposal of homology is open to further test.

Skull. — The intercalar has been described as a relatively large bone in telmatherinids (sensu Kottelat, 1990) and some pseudomugilids, e.g., *Pseudomugil signifer* (Saeed et al., 1989: fig. 16a). The intercalar spans the division between the exoccipital and pterotic bones in both *Rheocles* and *Bedotia*, but I have never observed the bone with a foramen for the glossopharyngeal nerve.

List of Potential Synapomorphies of Atherinomorphs and Paracanthopterygians. — These characters previously have been unrecognized or ignored as potential synapomorphies because paracanthopterygians have been excluded as atherinomorph close relatives (Rosen and Parenti, 1981). That they are not found in all paracanthopterygians implies that the Paracanthopterygii of Patterson and Rosen (1989) may be paraphyletic, if we assume a monophyletic Atherinomorpha. Potential synapomorphies of atherinomorphs and at least some paracanthopterygians, as qualified above, are: 1) long developmental period; 2) absence of ligamentous connection between pelvic bones and ventral postcleithrum; 3) large fourth epibranchial bone; 4) full neural spine on second preural centrum; 5) ossified second preural radial bone (Y-bone) and supernumerary neural and haemal spines on one or more preural centra; 6) reduction in supraneural bones (open to interpretation of homology); 7) two epural bones (requires reversal to three in exocoetoids); and 8) short preanal length through flexion (only in atherinoids and gadids).

DISCUSSION

Paracanthopterygians, atherinomorphs, and percomorphs comprise a monophyletic group (Rosen, 1973b, 1985; Stiassny, 1986; Patterson and Rosen, 1989). Monophyly of atherinomorphs is well supported, that of paracanthopterygians less so, and that of percomorphs not at all, results of other papers in this volume notwithstanding (see also Stiassny, 1990). Whether we consider atherinomorphs more closely related to paracanthopterygians or to percomorphs may be thought of as a rooting or polarity problem. If the eight potential atherinomorph/paracanthopterygian synapomorphies discussed in the previous sections are reinterpreted as symplesiomorphies, the sister group relationship (Fig. 1B) is not supported, even in part.

Hypothesis of an atherinomorph/paracanthopterygian sister group relationship is in contrast to the proposal by Stiassny (1990) that atherinomorphs and mugiloids are sister taxa. Stiassny (1990) proposed four atherinomorph/mugiloid

synapomorphies, three of pharyngobranchial myology, and the fourth, expanded anterior neural arches. She expressed reservation about her proposal because mugiloids have the percomorph type pelvic girdle (Stiassny, 1990). Above, I question homology of expanded neural arches in atherinomorphs and mugiloids.

For now, I am satisfied to summarize relationships among ctenosquamates as in the cladogram of Figure 1C. This scheme is less resolved, hence less informative, than the two other cladograms of Figure 1, but preferable to the often cited, rarely supported atherinomorph/percomorph sister group relationship (Fig. 1A). One could tally characters in favor of an atherinomorph/mugiloid sister group relationship and those in favor of an atherinomorph/paracanthopterygian sister group relationship and choose the hypothesis supported by the most characters. However, I consider invoking the parsimony argument here premature and unsatisfactory. Numerous characters are correlated, such as the three pharyngobranchial myological modifications proposed by Stiassny (1990) or the three caudal skeleton synapomorphies I propose above, that could be treated as one character in a parsimony analysis. Character and character state definition and delineation plagues systematic methodology (Pogue and Mickevich, 1990).

Most important, data are incomplete. Testis type and arrangement of sensory olfactory epithelium in hypothesized plesiomorphic paracanthopterygians such as *Percopsis* are unknown to me. Principally for this reason, I do not summarize results of the character survey among atherinomorphs, paracanthopterygians, and percomorphs in a data matrix riddled with question marks.

Despite these shortcomings, I am optimistic about our ability to resolve further the phylogenetic relationships of ctenosquamates. Phylogenetic information in morphological systems has not been exhausted. For example, ontogeny of the caudal fin holds additional information for resolution of higher level phylogenetic relationships among ctenosquamates. Details of reproduction undoubtedly will help resolve relationships.

Atherinomorphs are diagnosed as monophyletic by 14 synapomorphies. Atherinoids are considered paraphyletic, and bedotiids the most plesiomorphic atherinomorphs (see also Stiassny, 1990). I discuss the shared derived characters of atherinomorphs and some paracanthopterygians so that additional predictions of character distribution may be made and tested. One prediction, that some paracanthopterygians have an atherinomorph type testis, will be tested in a survey of testis type in a range of paracanthopterygian taxa (Grier and Parenti, in prep.), including percopsiforms, amblyopsiforms, and gadiforms.

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