

EVOLUTIONARY RELATIONSHIPS OF THE ATHERINOPSINAE (PISCES: ATHERINIDAE)

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ABSTRACT. The Atherinopsinae, a subfamily of the silverside fish family Atherinidae, is cladistically diagnosed on the basis of five synapomorphies: 1) Baudelot's ligament ossified, 2) proximal end of fourth ceratobranchial with moderate toothplates, 3) palatine with medial bony shelf, 4) ventral projection of nasal bone contacting lachrymal, and 5) lateral ethmoid with ventral bony knob. Two tribes are recognized. The Atherinopsini is restricted to the Pacific shores of North America and includes four genera: *Atherinops*, *Atherinopsis*, *Colpichthys*, and *Leuresthes*. Its members share three derived character states: 1) supraoccipital process trifid, 2) leading edge of vomer with paired dorsal projections, and 3) expanded hypophyses formed by bifurcation of haemal spines. The Basilichthyini is distributed throughout the temperate marine and fresh waters of South America and includes two genera: *Basilichthys* and *Odontesthes*. It is characterized by three synapomorphies: 1) basioccipital fenestrated, 2) extrascapular composed of two bony elements, and 3) haemal arches expanded to form broad hypophyses. Within the northern tribe, *Leuresthes* is most closely related to *Atherinopsis* whereas *Atherinops* is considered to be most closely related to *Colpichthys*. The tropical subfamily Menidiinae is considered to be the sister group of the Atherinopsinae.

INTRODUCTION

After more than a century of effort, the evolutionary relationships of the silverside family Atherinidae have not been adequately resolved. This study attempts to answer several questions concerned with the evolutionary history of the Atherinopsinae, an American subfamily. First, is the Atherinopsinae (*sensu* Schultz, 1948) monophyletic? If so, what is its sister group? Another question involves internal relationships of the subfamily: is the Atherinopsinae composed of phylogenetically distinct North and South American lineages? The biogeographic history of the Atherinopsinae will be considered in a separate contribution.

The New World atherinids have long been considered a monophyletic group. The Atherinopsinae of Jordan and Hubbs (1919) included almost all American silversides. In a later revision, Schultz (1948:42) redefined the Atherinopsinae and restricted the subfamily "to that group of genera now known from the Americas that have the premaxillary dilated or broadened posteriorly and extending opposite or into five or more of the broadened hypophyses of the haemal arches, these specialized hypophyses mostly interconnecting

with one another by flattish, broadened, spine-like bony processes opposite the tapering part of the air bladder." This definition is based on a derived character having systematic importance at the level of the New World atherinids and excludes from the Atherinopsinae many genera included in the subfamily by Jordan and Hubbs (1919), which Schultz accommodated by the formation of a new subfamily, the Menidiinae.

Only seven of the eight genera included in the Atherinopsinae by Schultz (1948) are still recognized: *Atherinops* (Steindachner, 1876), *Atherinopsis* (Girard, 1854), *Austromenidia* (Hubbs, 1918), *Basilichthys* (Girard, 1854), *Colpichthys* (Hubbs, 1918), *Leuresthes* (Jordan and Gilbert, 1880), and *Odontesthes* (Evermann and Kendall, 1906). *Hubbsiella* (Breder, 1936) was synonymized with *Leuresthes* by Moffatt and Thomson (1975). The validity of some other atherinopsine genera, e.g. *Colpichthys* and *Atherinopsis*, have been called into question (Todd, 1976).

Schultz (1948) did not consider the Menidiinae and Atherinopsinae to be sister groups. Instead, he allied the Atherinopsinae with the Old World subfamily Atherininae because a small number of atherinine species have haemal modifications similar to those of some of the atherinopsine fishes. He did admit, however, that this similarity may be due to parallel evolution and have no bearing on the phylogenetic relationships of the two subfamilies. Jordan and Hubbs (1919) proposed that the New World silversides (the Atherinopsinae and Menidiinae of Schultz, 1948) and the Old World Atherininae formed a monophyletic group.

Patten (1978) believed the Atherinopsinae of Jordan and Hubbs (1919) to be monophyletic but did not consider this assemblage to be related closely to the Atherininae. He also questioned the division of the American atherinids into two subfamilies, charging that Schultz (1948) used primitive characters to define the Menidiinae.

The differing opinions of Patten (1978), Schultz (1948), and Jordan and Hubbs (1919) raise questions about the evo-

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lutionary relationships of the American silversides which are the basis for this study. Their resolution requires that the New World silversides be viewed in a wider phylogenetic context and that the Atherinopsinae be compared with outgroup species chosen from as many other teleostean taxa as possible.

METHODS AND MATERIALS

The methods of Willi Hennig (1966) are used herein to assess evolutionary relationships. Known commonly as cladistics, phylogenetic systematics, or cladism, this approach groups organisms solely on the basis of shared derived character states, or synapomorphies. Similarity due to the shared possession of primitive or plesiomorphic character states is discounted as uninformative and excluded from analysis.

Grouping organisms according to patterns of common ancestry demands that all taxonomic groups be monophyletic. Put another way, all members of a taxonomic group must share a common ancestor and all the descendants of that ancestor must be included in the group. Synapomorphic character states are used to diagnose taxonomic groups. The hierarchic arrangement of synapomorphic character states on a cladogram serves to define the evolutionary relationships between different groups.

Synapomorphic character states were determined by outgroup analysis (Lundberg, 1972; Watrous and Wheeler, 1981). Outgroups were chosen primarily, but not exclusively, from within the Atherinomorpha (Rosen and Parenti, 1981). In outgroup analysis, character states restricted to the ingroup are considered to be derived whereas states occurring in both the ingroup and outgroup are assessed as being primitive.

In some cases, character states that are suspected of being derived have limited occurrence among outgroup taxa and must therefore be evaluated more critically. In such instances, it is necessary to consider if it is more parsimonious to assume that the character state in question was independently derived in the ingroup and outgroup or whether it is derived for a larger group and only retained by a small number of otherwise distantly related descendants. The assumption that requires the fewest number of evolutionary steps, the sum total of all gains and losses necessary to explain the observed distribution of the character state, is accepted.

Arguments based on parsimony require a reasonable knowledge of the overall relationship of the ingroup to related lineages. For the purposes of this study, a recent phylogeny proposed for the Atherinomorpha (White et al., 1984; Collette, 1984) (Fig. 1) and the ideas of Patten (1978) concerning the relationships of the Atherinidae (Fig. 2) were used to settle questions of parsimony. In one case, the ontogeny of a character was used to polarize a transformation series between three states.

At least two male and two female specimens of every atherinopsine genus, except *Basilichthys*, were cleared and counterstained (Dingerkus and Uhler, 1977) to facilitate observation of bone and cartilage. Only a single, male specimen of *Basilichthys* was cleared and stained because of material constraints. Osteological character states judged to be phy-

logenetically informative were examined further in a number of partially dissected alcohol specimens. Material from numerous outgroups was cleared and counterstained or dissected as well.

The original description of every generic synonym is referenced in the synonymies presented in the discussion section.

The preserved materials used in this study were furnished by the following institutions: Natural History Museum of Los Angeles County (LACM), Academy of Natural Sciences of Philadelphia (ANSP), California Academy of Sciences (CAS), National Museum of Natural History (USNM), University of Arizona (UA), University of California at Los Angeles (UCLA), and University of Florida (UF). The acronym SU refers to collections of Stanford University now housed at CAS. A list of species examined is provided below. Following each catalog number, in parentheses, are the total number of specimens examined with the number of cleared and stained preparations, if any, denoted by an asterisk.

Order Atheriniformes

Family Atherinidae

Subfamily Atherinopsinae

Atherinops affinis. LACM: 346(1), 347(1), 1808(1), 1809(1), 1984(1), 1995(1), 2619(1), 6609-1(1), 6612-2(1), 6615-2(1), 6616-1(1), 6635-2(1), 6683-1(1), 7990(1), 8823-8(1), 8909-2(1), 8947-13(1), 9280-2(1), 9281-1(1), 9297-1(1), 9380-2(1), 9439-2(1), 9592-3(1), 22075(1), 20125(1*), 22304(1), 22306(1), 30706-1(1), 31699-5(1), 32068-5(1), 32084-14(1), 32085-14(1), 32086-10(2,1*), 32184-14(9,1*), 32697-1(1), 32704-2(1), 33080-1(3), 33138-1(1), 33541-1(1), 35153-10(1), 35794-1(1), 35815-1(1), 37013-1(4), 37552-5(1), 37575-7(2,1*), 38545-2(1), 38548-1(1*), 82622-5(1), W48-34(1), W49-157(1), W50-144(1), W55-20(15), W55-90(1*), W56-253(1), W63-59(1), W63-63(1), W68-43(21,2*).

Atherinopsis californiensis. LACM: 348(2,1*), 3896(1), 6735-2(1), 7936(3), 9283-1(1), 9439(3,1*), 20024(2), 20025(3,2*), 20120(1), 22300(1), 22302(1), 22795(1), 23227(1), 24066(1), 30636-6(1), 31306-2(6,3*), 31583-4(6,1*), 31807-6(3), 31864-1(1), 31940-1(1), 32043-8(1), 32044-8(1), 32056-13(3), 32059-12(1), 32704-2(1*), 32925-3(3), 32944-1(5), 33076-1(1), 34093-1(1), 37609-5(2), 42663-4(2*), W49-4(1), W49-143(2), W58-377(42,1*), W67-151(1), W67-152(1).

Basilichthys archaeus. USNM: 128536(2), 77530(1).

Basilichthys australis. LACM: 42705-1(1*); CAS: SU22735(2); USNM: 84326(4).

Basilichthys semotilus. CAS: 45193(1), 45194(2), SU23227(2).

Colpichthys regis. LACM: 7153(13,1*), 35728-1(10), 35730-1(10,4*), 39570-4(1*), W49-130(3), W50-190(2), W51-15(10), W55-12(9,3*), W55-30(4).

Leuresthes sardina. LACM: 1523(1*), 9295(1*), 35728-7(4), W49-121(1*), W50-18*(2,1*), W51-258(1).

Leuresthes tenuis. LACM: 1786(2), 1810(2), 4382(1), 4402(1), 6615(1), 6635-3(1), 6735-1(1), 8946-8(1), 9280-1(1),



Figure 1. Relationships of the Atherinomorpha (White et al., 1984; Collette, 1984).

9453-1(1), 9592-2(1*), 20123(2), 20131(3,2*), 22307(2), 22879(1), 24070(2), 31306-3(2), 31757-7(1), 31759-22(2,1*), 32056-12(1), 32597-1(4,2*), 32946-1(1), 32947-1(2), 33077-1(1), 33078-1(2), 33079-1(2), 33080-1(1*), 33139(1), 33487-1(2), 37690-1(2), 38457-1(2,1*), W51-66(28,2*), W55-115(2), W57-152(2), W66-62(3), W67-149A(1), W68-43(2), 015-SO-08MA-01(4*), 024-RB-08-MA-01(4*), 024-SO-08-MA-01(5*), 024-SO-22-MA-01(4*).

Odontesthes argentinense. USNM: 148502(4).

Odontesthes bonariensis. CAS: SU52812(4*).

Odontesthes brevipennis. USNM: 84338(1).

Odontesthes hatcheri. CAS: 12699(1), 42586(2).

Odontesthes incisus. CAS: SU31601(3); USNM: 163378(5).

Odontesthes mauleanum. CAS: 44702(2), 45201(2), SU12691(2); USNM: 77296(1), 84334(3).

Odontesthes nigricans. USNM: 77299(4), 88714(2), 103782(1).

Odontesthes perugiae. CAS: 11730(1).

Odontesthes regia. LACM: 20094(1), 42696-1(138,3*); CAS: SU6072(1), SU9285(2), 11905(2), 45171(1), 45172(2), 45173(1), 45174(3); USNM: 77633(4), 77644(1).

Odontesthes smitti. USNM: 256719(10).

Undescribed species from Gulf of California. UCLA: W78-11(4).

Subfamily Menidiinae

Archomenidia sallei. LACM: 43459-1(4).

Chirostoma grandocule. UCLA: W2-54(4).

Chirostoma labarcae. UA: 66-108-7(6).

Chirostoma sphyraena. UA: 66-128-1(2).

Coleotropis blackburni. LACM: 8335(2).

Eurystole eriarcha. LACM: 1562(1*), 9044-16(4), 31784-5(2*).

Hubbesia gilberti. LACM: 8964-2(1), 22328(7).

Labidesthes sicculus. LACM: 8965-1(2).

Melaniris chagresi. LACM: 9132-1(1*), 9148-9(1), 9167-10(7).

Melanorhinus cyanellus. LACM: 20129(1), 35486-5(1*).

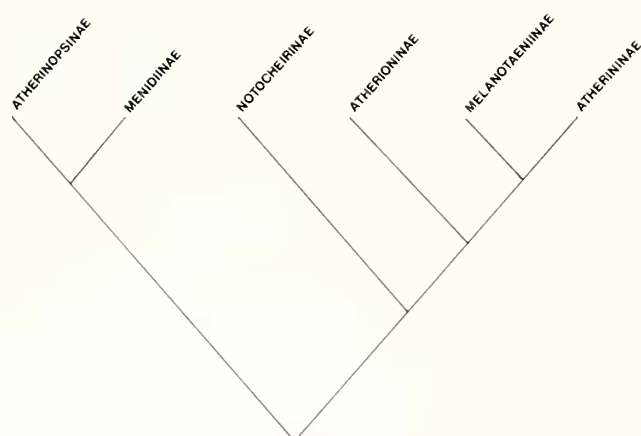


Figure 2. Relationships of the subfamilies of the Atherinidae (Patten, 1978).

Membras martinica. LACM: 8975-1(1); ANSP: 125238(5); UF: 35105(10).

Menidia beryllina. LACM: 8964-2(10).

Menidia peninsulae. LACM: 8962-2(2*).

Nectarges nepenthe. LACM: 20101(2*), 20103(1).

Poblana sp. LACM: 32616-1(4).

Xenatherina sp. LACM: 43458-1(4).

Xenomelaniris brasiliensis. ANSP: 120027(8).

Subfamily Notocheirinae

Iso rathophilus. CAS: 46621(4).

Subfamily Atherioninae

Atherion elymus. LACM: W65-31(2).

Subfamily Melanotaeniinae

Pseudomugil signifer. LACM: 34988-3(2).

Subfamily Atherininae

Atherina breviceps. LACM: 42651-1(1*), 42695-1(4,1*).

Atherinomorus ogilbyi. LACM: 37481-1(13).

Atherinomorus pinguis. LACM: 31299-20(7).

Hypoatherina harringtonensis. LACM: 5833(2*).

Hypoatherina panateia. LACM: 42472-3(6).

Order Beloniformes

Family Belonidae

Pseudotylorus angusticeps. LACM: 41470-8(2).

Family Exocoetidae

Cypselurus opisthopus. LACM: 30455-1(3).

Exocoetus monocirrhus. LACM: 30473-5(4).

Family Hemirhamphidae

Hyporhamphus unifasciatus. LACM: 6949-2(4).

Family Scomberesocidae

Cololabis saira. LACM: 34083-1(3).

Scomberesox saurus. LACM: 11223-1(4).

Strongylura timucu. LACM: 5875(8).

Order Cyprinodontiformes

Family Anablepidae

Anableps dowi. LACM: 42632-16(6*).

Oxyzygonectes dowi. LACM: 4876(3).

Family Cyprinodontidae

Belonesox belizanus. LACM: 42632-15(1).

Cyprinodon variegatus. LACM: 1309(5), 1310(4).

Floridichthys carpio. LACM: 1311(3).

Family Fundulidae

Fundulus diaphanus. LACM: 39823-1(4*).

Family Goodeidae

Goodea sp. LACM: 32615-1(2).

Xenotoca variata. LACM: 151(3).

Family Poeciliidae

Poecilia sphenops complex. LACM: 9191-21(3).

Family Profundulidae

Profundulus guatemalensis. LACM: 1969-47(4).

Family Rivulidae

Rivulus isthmensis. LACM: 2779(3).

RESULTS

In all of the atherinopsine fishes examined, Baudelot's ligament is ossified at its point of attachment to the base of the skull such that two thin, sharp spines are directed posteroventrally from the basioccipital (Fig. 3). As in most other teleost fishes, the unossified portion of this ligament has a point of attachment on the cleithrum. The placement, size, and shape of these paired ossifications are constant throughout the Atherinopsinae. Baudelot's ligament is not ossified in any of the other atheriniform species examined except *Iso rhotophilus*. Species of the marine genus *Iso* are very deep bodied and their overall appearance is quite different from that of the Atherinopsinae. This dissimilarity carries over to the ossification of Baudelot's ligament, as the orientation of the ossification on the base of the skull of *I. rhotophilus* does not resemble that characteristic of the Atherinopsinae.

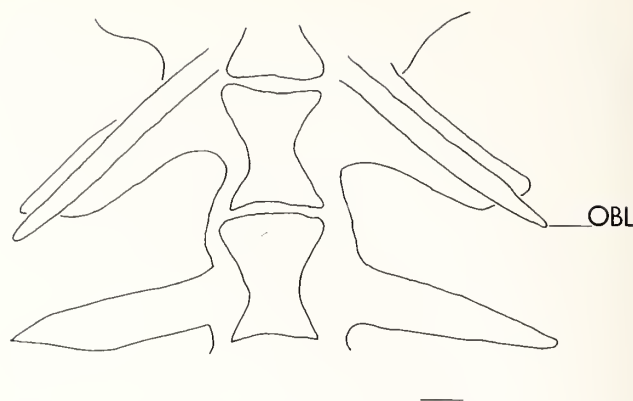
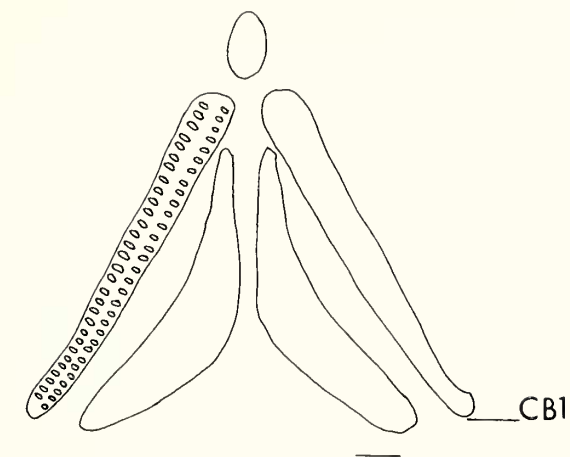


Figure 3. Ventral view of first two vertebrae and base of skull: *Colpichthys regis*. OBL = ossified Baudelot's ligament. Scale equals 1 mm.

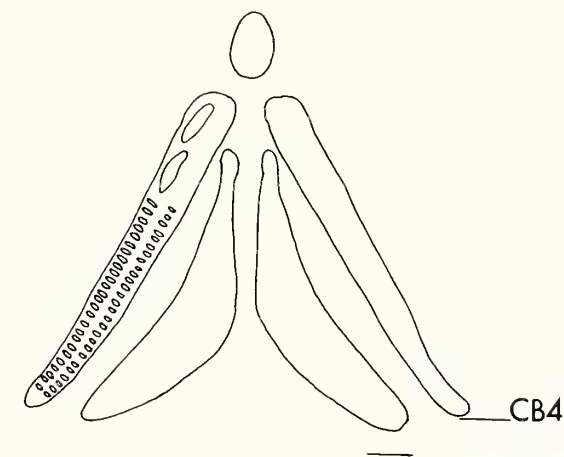
In *I. rhotophilus*, the spines are placed higher on the skull and are more laterally directed than in the atherinopsine fishes. Therefore, the condition observed in *I. rhotophilus* is considered to be independently derived and not homologous with the atherinopsine condition. Baudelot's ligament is ossified in each of the belonid, hemirhamphid, and scomberesocid species examined, but not in the exocoetids. In the halfbeaks and sauries, the ossified ligaments form flat, sword-like processes quite different from the cylindrical ossifications typical of the Atherinopsinae. In the needlefishes, the ossified portion of each ligament is much stouter than in the Atherinopsinae. For these reasons, the beloniform pattern is not considered to be homologous with the atherinopsine pattern.

A second derived character state shared by the atherinopsine fishes is found in the branchial basket: there are no enlarged toothplates on the proximal end of the fourth ceratobranchial, but instead, there is a series of paired toothplates running the length of the fourth ceratobranchial (Fig. 4a). In almost all atherinopsine species, these toothplates are relatively narrow and do not contact their partners on the dorsal midline of the fourth ceratobranchial. However, in *Colpichthys regis* and in an undescribed atherinopsine collected in the Gulf of California by Dr. Boyd Walker, these paired toothplates are expanded so that they contact their partners on the dorsal surface of the fourth ceratobranchial. The typical atheriniform condition is seen in *Menidia* (Fig. 4b) in which an enlarged toothplate occurs on the proximal end of the fourth ceratobranchial.

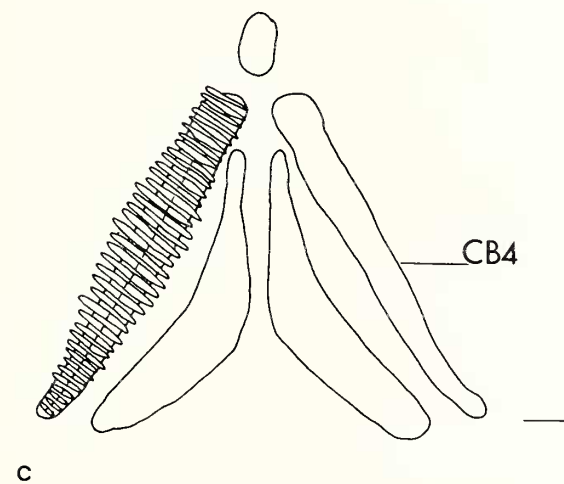
A third characteristic of the Atherinopsinae is found on the palatine bone. In every atherinopsine species examined, there is an ossified shelf on the medial side of the head of the palatine bone. This shelf serves to brace the palatine against the mesethmoid. It was not seen outside the Atherinopsinae. *Nectarges* and *Atherinomorus* (Fig. 5) were chosen to illustrate the primitive atherinomorph condition of this character. Ontogenetic stages of the palatine bone were observed in cleared and stained larval specimens of *Leuresthes tenuis*. The medial bony shelf appears after the head of the palatine has developed the hammerlike shape shared by the Atherinopsinae and Menidiinae.



a



b



c

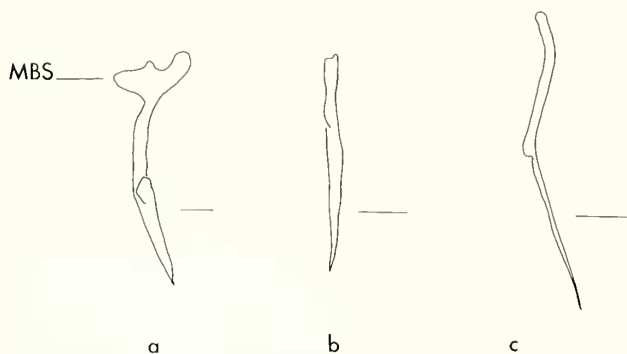


Figure 5. Posterior view of right palatine bone: a) *Leuresthes tenuis*, b) *Nectarges nepenthe*, c) *Atherinomorus pinguis*. MBS = medial bony shelf. Scale equals 1 mm.

A fourth derived feature of the Atherinopsinae concerns the state of the nasal bone. The atherinopsine nasal bone has a ventral projection (Fig. 6a) that makes contact with the anterodorsal corner of the lachrymal bone. In other atherinomorphs, this projection is lacking and connection between the nasal and lachrymal bones is accomplished via an extension of the anterior tip of the nasal sensory canal (Fig. 6b). In most atherinopsines, the ventral nasal projection is well developed but in the California and Gulf grunions, reduction of the projection seems to have accompanied enlargement of the lachrymal bone.

A fifth derived character state of the atherinopsine fishes involves the lateral ethmoid. In the Atherinopsinae, there is on the ventral surface of the lateral ethmoid a bony knob (Fig. 7a) that abuts the posterior edge of the palatine. This knob apparently provides additional support for the palatine and presumably strengthens the entire snout. There is considerable variation in this feature within the Atherinopsinae, although it was well developed in all specimens examined. It is most strongly developed in *Atherinops affinis* and least developed in some specimens of *Atherinopsis californiensis* (Fig. 7b). It was not encountered in any of the non-atherinopsine species available for comparison.

Several synapomorphic osteological features occur in the North American Atherinopsinae. The supraoccipital process of most of the North American atherinopsines is trifold (Fig. 8a). In some specimens of *Leuresthes tenuis* the supraoccipital process is bifid, but in *L. sardina* and the other North American species the supraoccipital is strongly trifold. A trifold supraoccipital process has been reported in several halfbeak species (Collette, 1966). However, this contrasts with the bifid condition of the supraoccipital process (Fig. 8b) of nearly all other atherinomorphs (Rosen, 1964). A bifid supraoccipital process is considered here to be the primitive silverside condition.

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Figure 4. Dorsal view of fourth ceratobranchial dentition in the Atherinidae: a) *Atherinops affinis*, b) *Menidia peninsulae*, c) *Colpichthys regis*. CB4 = fourth ceratobranchial. Scale equals 1 mm.

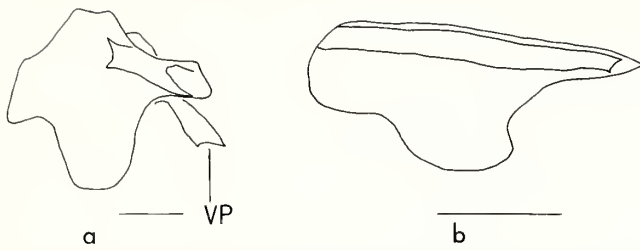


Figure 6. Medial view of right nasal bones: a) *Atherinopsis californiensis*, b) *Melanorhinus cyanellus*. VP = ventral process. Scale equals 1 mm.

Another derived character state shared by the North American genera occurs on the vomer. In the northern atherinopsines, a dorsal lip on the anterior edge of the vomer has a pair of bony projections (Fig. 9) that contact the mesethmoid. In other atherinids, there is either a single projection, as in *Menidia*, or there is none at all, as in *Iso* (Patten, 1978). Presumably, these projections help brace the mesethmoid. The mesethmoid is a point of attachment for ligaments running to the palatine and maxillary bones and it is reasonable to conclude that the additional support it receives from these paired vomerine processes serves to strengthen the snout and jaws of the atherinopsines of the northeastern Pacific.

One unique modification of the North American atherinopsines involves the development of the haemal funnel into which the swimbladder extends. The ontogeny of the broad, haemal hypophyses begins with a cartilaginous haemal arch. A groove develops on the ventral surface of the simple haemal spines that deepens as ossification proceeds. The spines finally bifurcate, with each half expanding to form a rectangular bony plate (Fig. 10a). Extending from the ventral surface of each of these plates is a long, spinelike projection that curves medially to meet its fellow from the opposite side (Fig. 11a) (Schultz, 1948; Clothier, 1951). These spines do not fuse, but form a second funnel ventral to the one formed by the rectangular plates above them. It is into this second funnel that the posterior end of the swimbladder projects. This unusual modification of the anterior haemal arches leaves them without a haemal spine and, in this way, the North American atherinopsines differ from most other teleosts. A similar condition is known to occur, however, in one other atherinid, the atherinine species *Atherinason hepsetoides* (Patten, 1978). Specimens of *A. hepsetoides* were not available for examination, but evidence presented by Patten (1978) suggests that *A. hepsetoides* is distantly related to the North American Atherinopsinae. Furthermore, none of the closest relatives of *A. hepsetoides* has developed a similar condition. I conclude that the haemal modifications of *A. hepsetoides* and of the North American atherinopsines are independently derived.

The form of the haemal arches is remarkably similar in all of the northern atherinopsines except for the undescribed species from the Gulf of California, which lacks these haemal modifications. The body cavity of this species is truncate and the swimbladder does not extend into the region of the caudal vertebrae.

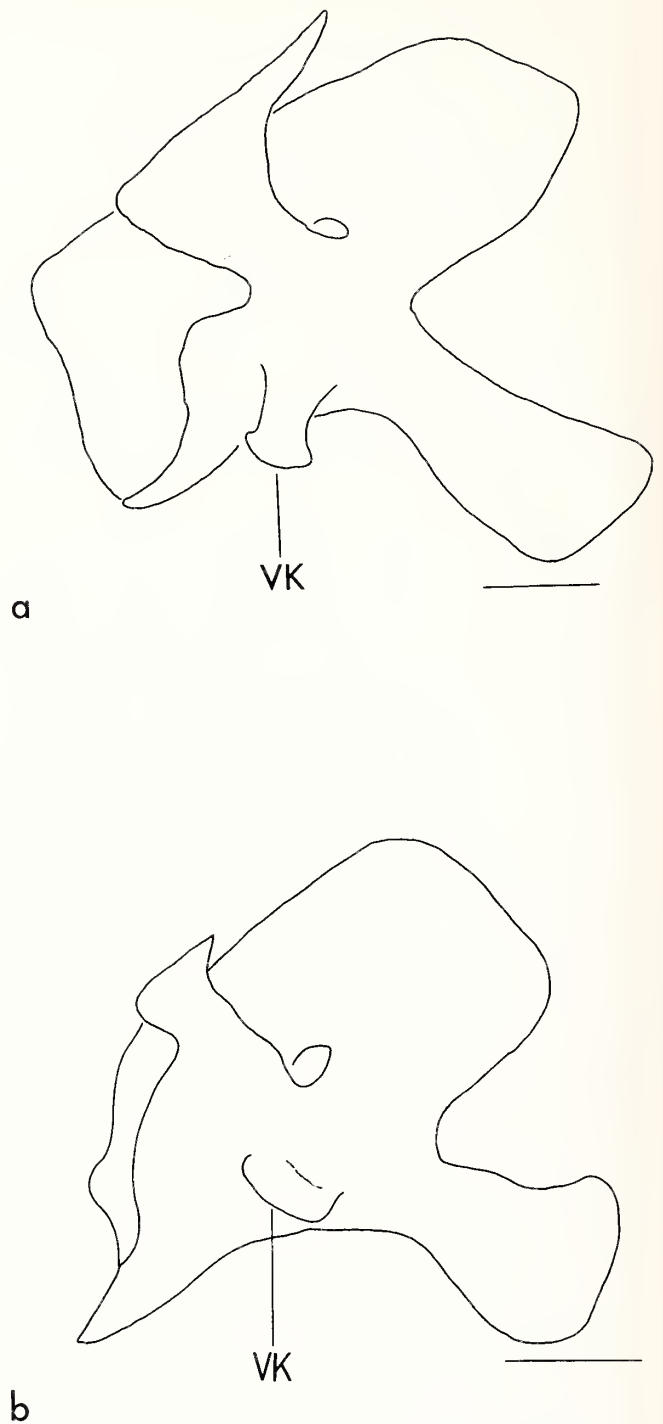


Figure 7. Ventral view of right lateral ethmoid, anterior edge to right: a) *Atherinops affinis*, b) *Atherinopsis californiensis*. VK = ventral knob. Scale equals 1 mm.

The haemal modifications of the southern species are in stark contrast with those of their northern counterparts. The development of their hypophyses could not be observed because no larval material was available but the hypophyses

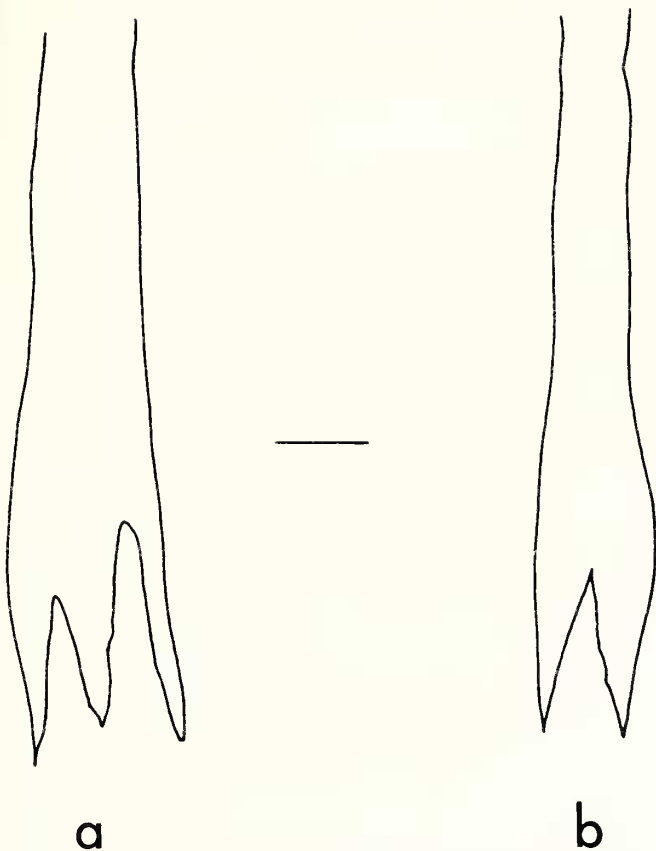


Figure 8. Dorsal view of supraoccipital process: a) *Atherinopsis californiensis*, b) *Menidia peninsulae*. Scale equals 1 mm.

of the South American atherinopsines cannot be derived from haemal spines, as they are in the North American atherinopsines, because the haemal spines of the adult fishes are intact. It appears that the haemal funnel occurring in the southern species (Fig. 10b) develops from an expansion of the haemal canals themselves instead of a bifurcation of the haemal spines. There is only a single haemal funnel in the southern atherinopsines, with the swimbladder extending into the expanded lumens of a series of haemal arches that each have a well-developed spine (Fig. 11b). The hypophyses of the South American atherinopsines are furrowed delicately and fenestrated in the same manner as the basioccipital bone (Fig. 12). In some species, the hypophyses are quite complex, as shown in Figure 10b, or they are simple. In *Basilichthys australis*, for example, the hypophyses appear to be nothing more than a simple flaring of the walls of the haemal canals. A similar condition occurs in the atherinine species *Atherina boyeri*, but it is not considered to be homologous with the South American atherinopsine condition because other evidence indicates that the Atherininae is distantly related to the Atherinopsinae (Patten, 1978). In two South American species, *Odontesthes incisus* and *O. nigricans*, the swimbladder is not posteriorly extended and the haemal arches are unmodified.

Two other derived character states are shared by the South

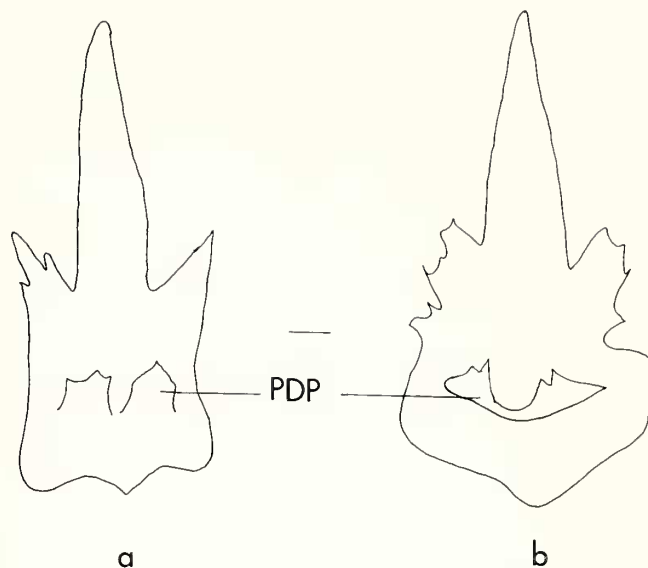
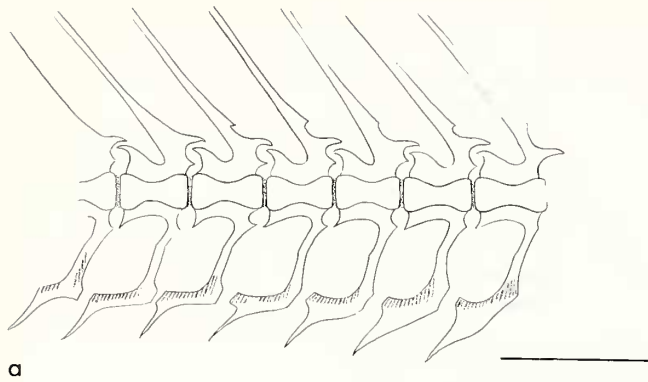


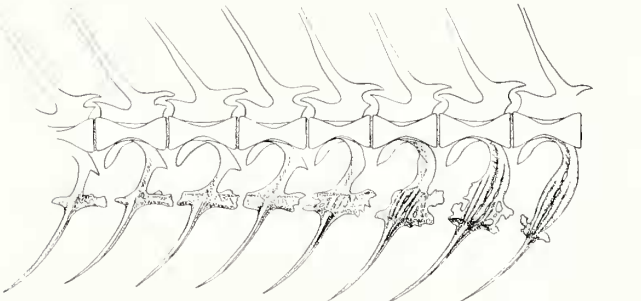
Figure 9. Dorsal view of vomer: a) *Atherinopsis californiensis*, b) *Atherinops affinis*. PDP = paired dorsal processes. Scale equals 1 mm.

American atherinopsines. First, in all of the southern species examined, the posterior portion of the basioccipital bone is sculpted by a series of irregularly spaced foramina (Fig. 12). Within the Atherinomorpha, this feature is found only in the South American atherinopsines.

Another derived feature of the South American atherinopsines involves the extrascapular bone. In most of the southern atherinopsine species, the extrascapular is composed of two bony elements (Fig. 13b, c), one oriented horizontally and the other vertically. Both elements bear sensory canals. In the North American atherinopsines, both sensory canals are accommodated by a single bone (Fig. 13a). In most atherinomorphs, the extrascapular bone is absent, but in some genera, e.g. *Menidia*, it is fused with the posttemporal (Patten, 1978). Even though these two bones are fused in *Menidia*, the direct communication between the two sensory canals suggests that the single extrascapular bone of the North American species is the ancestral condition for the subfamily. This is not surprising, because in most fishes, the extrascapular is composed of a single element (Weitzman, 1962; Mead and Bradbury, 1963; Springer, 1968; Zehren, 1979). There is some variation in the form of the extrascapular bone in the South American atherinopsines. In *Basilichthys semotilus*, for example, the extrascapular bone resembles the North American atherinopsine condition. This is not true of the other species of *Basilichthys* examined. In three specimens, two separate elements occurred. In one specimen, only one element was present; the anterior vertical element was absent on both sides. In another specimen having only one element, the posterior horizontal elements were absent. In three other specimens, both elements are present and united to form a single bone. Because the development of two extrascapular elements is widespread among the South American atherinopsine genera, it is considered to be a derived feature uniting



a



b

Figure 10. Lateral view of haemal hypophyses: a) *Atherinops affinis*, b) *Odontesthes regia*. Scale equals 1 mm.

them in a monophyletic group. The variation noted in *Basilichthys semotilus* and *Odontesthes incisus* is assumed to be secondarily derived.

The menidiine fishes share several derived character states. The parapophyses on the first vertebra are directed anteriorly, and are blunt distally (Fig. 14). The first parapophyses of most other atherinomorphs are pointed and directed posteriorly. In some cyprinodontiforms, notably *Fundulus diaphanus*, the parapophyses of the first few vertebrae project forward and in others, such as *Anableps dowi*, the parapophyses on most or all of the vertebrae are anteriorly directed. In these cases though, the parapophyses are pointed and not blunt as in the menidiines. Furthermore, only the menidiine fishes have just the parapophyses on the first vertebra modified. There is variation in this feature within the Menidiinae. In none of the menidiine genera examined, except *Chirostoma*, are the parapophyses on the first vertebra pointed and directed posteriorly, as in the atherinopsine fishes. Inspection of juvenile specimens shows this to be a modification of the typical menidiine pattern as the parapophyses on the first

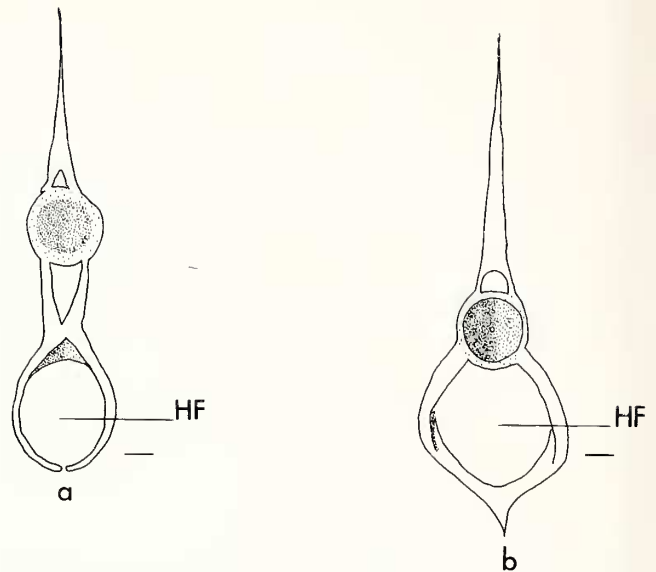


Figure 11. Anterior view of caudal vertebra: a) *Atherinops affinis*, b) *Odontesthes regia*. HF = haemal funnel. Scale equals 1 mm.

vertebra of the smaller individuals are directed anteriorly and are blunt.

In the Menidiinae and Atherinopsinae, the supraoccipital canal extends over the frontal and pterotic bones. In both subfamilies, three pores occur in the pterotic portion of the canal. However, the two American subfamilies differ in the number of pores that occur in the frontal portion of the canal. The atherinopsine fishes have five frontal pores whereas the menidiines usually have only four. When the supraorbital pores are numbered according to the system of Gosline (1949), the atherinopsine total is seven (Fig. 15a) and the menidiine total is six (Fig. 15b). There is some variation in the number of supraorbital pores in the Menidiinae. The Mexican freshwater genus *Poblana* resembles the atherinopsine fishes in having seven supraorbital pores. In *Labidesthes sicculus*, the supraorbital canal lacks a bony roof so that no pores are evident on the top of the head. This is true of the Old World atherinid subfamilies as well. Parenti (1981) concluded that it is primitive for the cyprinodontiform fishes to have seven supraorbital pores and this is assumed to be the case in the New World atherinids as well. There is great variation in the number of supraorbital pores in the Beloniformes. In some species, the cranial pores are miniscule and very numerous, numbering up to 123 in the continuous supraorbital-postorbital-temporal canal of *Scomberesox saurus* (Parin and Astakhov, 1982). In others, a pattern similar to the one seen in the Atherinopsinae occurs. No beloniform species examined during the course of this study was found to have the reduced number of supraorbital pores characteristic of the Menidiinae.

Another derived menidiine character state involves the enlarged toothplates present on the proximal end of the fourth ceratobranchial (Fig. 4b). In all menidiine species examined, these toothplates are fused to the ceratobranchial and cannot

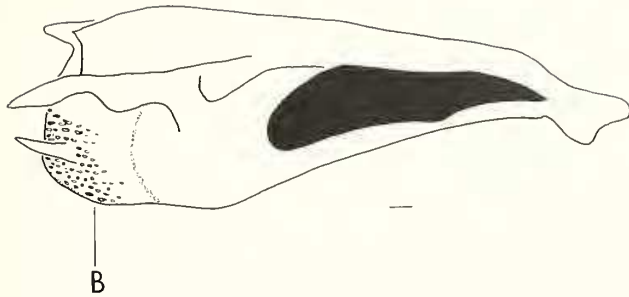


Figure 12. Lateral view of neurocranium: *Odontesthes regia*. B = basioccipital. Open space blackened. Scale equals 1 mm.

be dislodged from the branchial basket. In no other atheriniform for which information is available are the toothplates attached in this manner (Patten, 1978). In the Cyprinodontiformes, a series of teeth extends posteriorly along the dorsal surface of the fourth ceratobranchial between the paired toothplates that are arrayed along its right and left hand sides. This does not resemble the menidiine pattern. Proximal toothplates are absent in the Beloniformes.

Two unique osteological characters appear in both the Atherinopsinae and Menidiinae. First, in both these subfamilies, there is a modification of the pectoral girdle involving the scapula and cleithrum. These two bones are connected in the atherinopsine and menidiine fishes by a series of small, bony buttresses. These buttresses resemble small foramina in lateral view but are in fact bony struts passing between the cleithrum and scapula. Some specimens have many struts and others have few, but their shape, size and placement are constant in the two subfamilies. The buttresses are always elliptical in cross section and placed high along the dorso-lateral surface of the cleithrum in a horizontal or nearly horizontal arrangement. In *Atherinomor*, the only other genus in which bony struts were found to pass between the scapula and cleithrum, the struts were vertically arranged along the anterior edge of the cleithrum and are considered to be independently derived.

Another modification shared by the Atherinopsinae and Menidiinae involves the palatine bone. In the fishes belonging to these subfamilies, the head of the palatine is either straight or shaped like a hammer. In Figure 16, the range of variation exhibited by the palatine bone in New World atherinids and the atherinomorphs as a whole is illustrated. In *Leuresthes* (Fig. 16a), and all other atherinopsines, the head of the palatine is shaped like a hammer. This is true of many menidiines also, although in some, such as *Nectarges* (Fig. 16b), the palatine head is just bluntly rounded. During the course of this study, the more typical atherinomorph condition (Parenti, 1981), shown in the tapering, pointed palatine of the Old World atherinid *Atherinomor* (Fig. 16c) was not encountered in any menidiine or atherinopsine species examined.

The two grunion species share several derived character states. First, neither *Leuresthes tenuis* nor *L. sardina* have strongly developed teeth in the jaws as adults. It has been

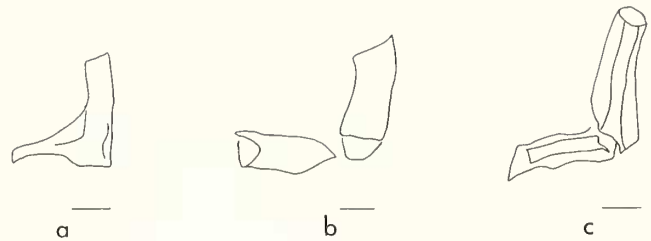


Figure 13. Lateral view of right extrascapular bone: a) *Atherinops affinis*, b) *Odontesthes regia*, c) *Basilichthys australis*. Scale equals 1 mm.

reported that minute teeth do occur in these fishes (Moffatt and Thomson, 1975) and that it is necessary to examine dried skeletal material to observe them. No teeth were seen in any of the cleared and stained or alcohol preserved specimens examined in the course of this study. There is variation in the dentition of the other atherinids. In *Atherinopsis californiensis*, the jaw teeth are arranged in several rows, whereas only a single row of teeth is found on the jaws of *Atherinops affinis*. However, no other atherinid species are known to have the weak dentition characteristic of the grunions. In fact, most atherinomorphs have well-developed teeth in the jaws.

A suite of derived traits is associated with the reproductive biology of the grunions. Both *Leuresthes tenuis* and *L. sardina* are lunar spawners that fertilize and bury their eggs at the surf line on sandy beaches during the extreme high tides of spring and early summer. The embryos develop in the sand for approximately two weeks, when high tides again reach the nests and initiate hatching (Walker, 1952). Though a few other fishes are known to spawn on a lunar cycle, e.g. *Menidia menidia*, the remarkable reproductive habits of the grunions are a well-known specialization. The eggs of both grunion species lack filaments. All other atherinopsine eggs known have filaments as do the eggs of most atherinomorphs (Rosen and Parenti, 1981; Collette, 1984).

The shape of the vomer in the California and Gulf grunions is unusual (Fig. 17a). In both *Leuresthes tenuis* and *L. sardina*, the leading edge of the vomer is emarginate and the lateral condyles are reduced greatly. This contrasts with the form of the vomer in the other atherinopsines and menidiines, where the lateral condyles are well developed and the

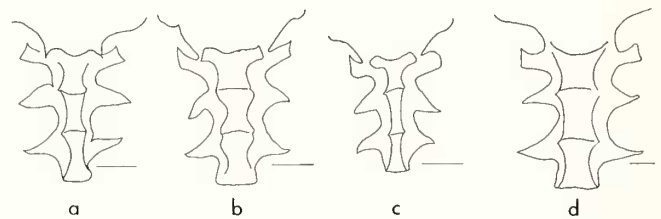
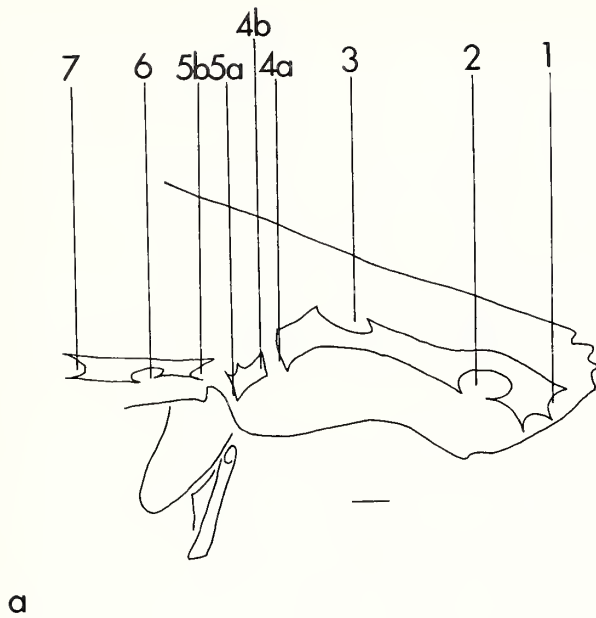


Figure 14. Ventral view of anterior vertebrae and base of skull: a) *Menidia peninsulae*, b) *Nectarges nepenthe*, c) *Melaniris chagresi*, d) *Chirostoma labarcae*. Scale equals 1 mm.



a

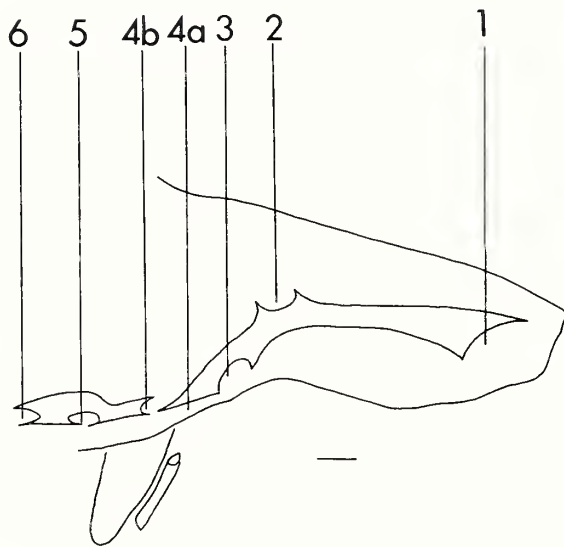


Figure 15. Supraorbital pore pattern: a) *Atherinops affinis*, b) *Melanorhinus cyanellus*. Pores numbered according to the system of Gosline (1949). Scale equals 1 mm.

leading edge has a strong median process (Fig. 17b). In overall size, the vomer of the two grunions is reduced in comparison with those of other atheriniforms.

The dorsal process on the premaxilla of *L. tenuis* and *L. sardina* is long and slender and placed near the symphysis of the upper jaw (Fig. 18a). The jaws are greatly protractile

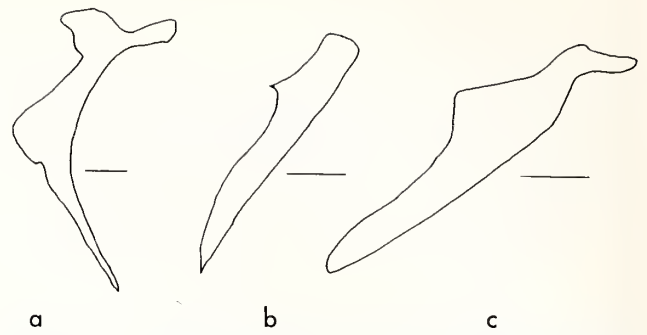


Figure 16. Lateral view of right palatine: a) *Leuresthes tenuis*, b) *Nectarges nepenthe*, c) *Atherinomorus pinguis*. Scale equals 1 mm.

in grunions and are not bound to the snout by a frenum as in *Basilichthys*, *Atherinops* or *Atherinopsis*. A similar condition is developed in *Odontesthes* (Fig. 18b), but in this South American genus, the dorsal process is placed farther back along the shaft of the premaxilla, suggesting that the dorsal processes of the northern and southern genera were independently derived.

Consideration of the other derived character states described here suggests that the evolution of jaw mobility in the Atherinopsinae involves the independent development of slender, premaxillary dorsal processes and the loss of the frenum to the upper jaw in the North American grunions and the South American genus *Odontesthes*.

Atherinopsis californiensis shares with *Leuresthes tenuis* and *L. sardina* another modification of the ethmoid region. In these three species, the lateral ethmoid has a pointed, bony strut that runs along the lateral edge of the parasphenoid (Fig. 19). This bony strut was not observed in any of the other atherinid species examined. It is lacking in the beloniform and cyprinodontiform fishes as well.

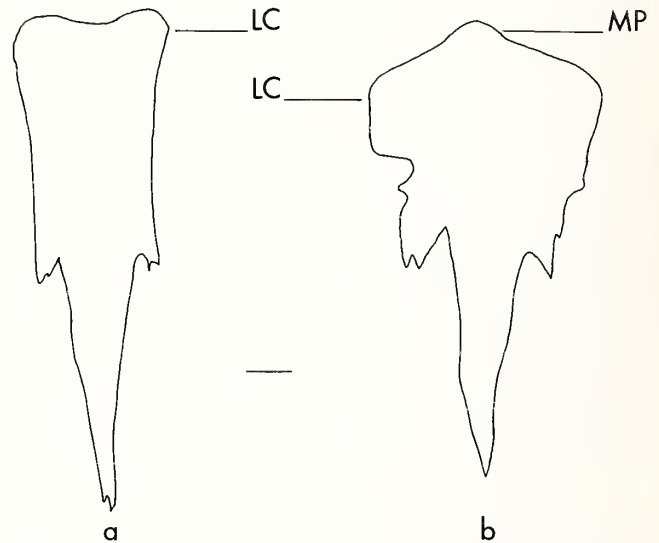
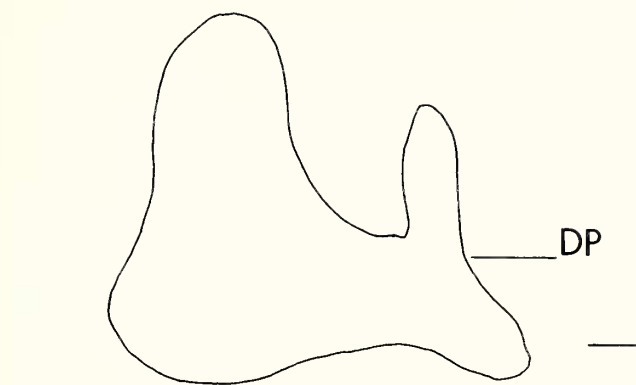
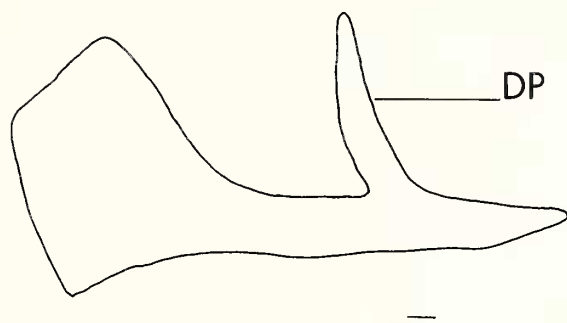


Figure 17. Ventral view of vomer: a) *Leuresthes tenuis*, b) *Atherinops affinis*. LC = lateral condyle, MP = median process. Scale equals 1 mm.



a



b

Figure 18. Lateral view of right premaxillary bone: a) *Leuresthes tenuis*, b) *Odontesthes regia*. DP = dorsal process. Scale equals 1 mm.

Another derived feature that *Atherinopsis californiensis*, *Leuresthes tenuis*, and *L. sardina* have in common involves the shape of the third epibranchial (Fig. 20a). The proximal arm of the third epibranchial of these three fishes is twisted about its long axis. Not only is the proximal arm of the third epibranchial crooked, but it is noticeably thinner in *Atherinopsis californiensis*, *Leuresthes tenuis*, and *L. sardina* than it is in the other atherinopsines and menidiines, in which the proximal arm of the third epibranchial is stout and uncurved (Fig. 20b).

A single derived character state distinguishes *Atherinopsis californiensis* from all other atherinomorphs. In *A. californiensis*, there is a small pocket on the anterior tip of the ventral process of the maxilla formed by a bony ledge projecting from its ventral surface (Fig. 23a).

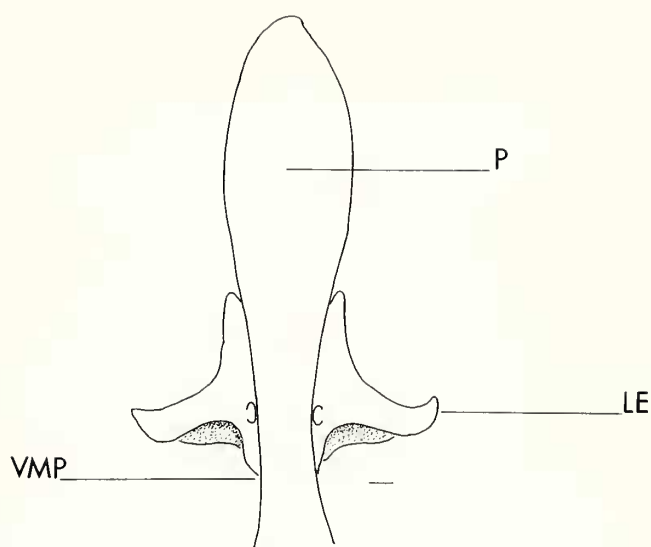


Figure 19. Ventral view of parasphenoid and lateral ethmoid: *Atherinopsis californiensis*. P = parasphenoid, MP = median process, LE = lateral ethmoid. Scale equals 1 mm.

Two unique osteological features are shared by *Atherinopsis affinis*, *Colpichthys regis*, and the undescribed atherinopsine species from the Gulf of California. In these fishes, the anterior edge of the quadrate is angled forward (Fig. 21b). This feature is most apparent in dissected specimens because the quadrate is held in position by the flesh that is digested away in cleared and stained specimens. It can, of course, be observed in cleared specimens, but mobility of the suspensorium, of which the quadrate is a part, makes interpretation of the exact orientation of the quadrate more difficult. In none of the other atherinomorph genera examined was a similar positioning of the quadrate observed. It is typical within the Atherinomorpha for the anterior edge of the quadrate to have a vertical orientation (Fig. 21a).

The bicuspid teeth shared by *Atherinopsis affinis*, *Colpichthys regis*, and the undescribed species are unlike those of any other atherinid (Schultz, 1948). In *Atherinopsis affinis*,

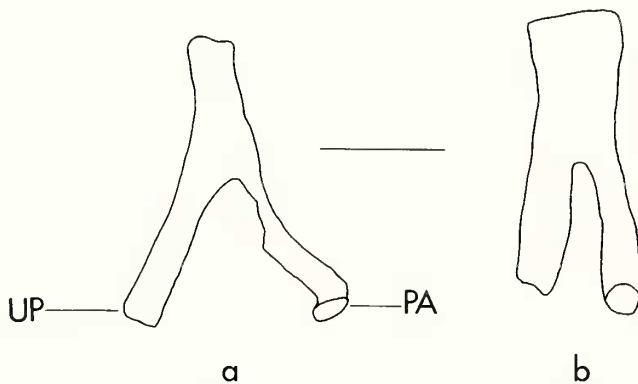


Figure 20. Left epibranchial: a) *Atherinopsis californiensis*, b) *Atherinopsis affinis*. PA = proximal arm, UP = uncinuate process. Scale equals 1 mm.

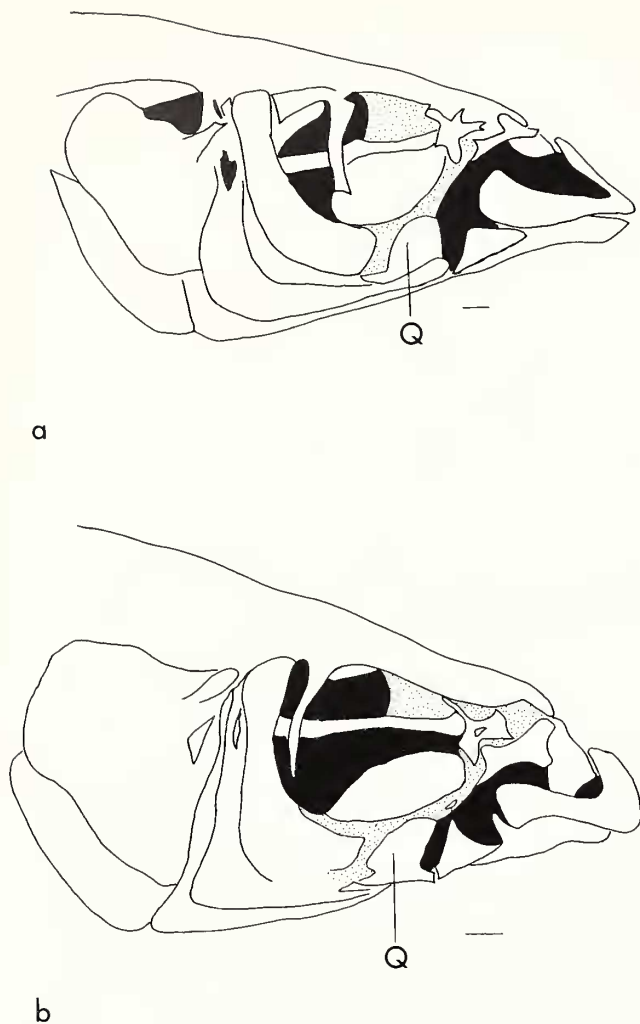


Figure 21. Orientation of the quadrate: a) *Odontesthes regia*, b) *Atherinops affinis*. Q = quadrate. Cartilage stippled, open space blackened. Scale equals 1 mm.

the cusps on each tooth are of equal size (Fig. 22b). In *Colpichthys regia* and the undescribed species, the cusps are unequal (Fig. 22a). Bicuspid and even tricuspid teeth are known to occur in some cyprinodontiform fishes (Parenti, 1981) and in the Hemirhamphidae as well.

Colpichthys regia and the undescribed atherinopsine from the Gulf of California have in common several special features involving the dorsal process of the maxilla and the dentition of the branchial basket. There is a notch in the dorsal process of the maxilla of both of these Gulf of California atherinopsines (Fig. 23b). This notch was not seen in any other atherinomorph species. Also shared by *C. regia* and the undescribed species is the modification of the fourth ceratobranchial toothplates described above. The toothplates are wide and meet on the dorsal midline of the fourth ceratobranchial (Fig. 4c). Another unique feature seen in these two species involves the teeth on the third pharyngobranchial elements. These upper pharyngeal bones are covered with

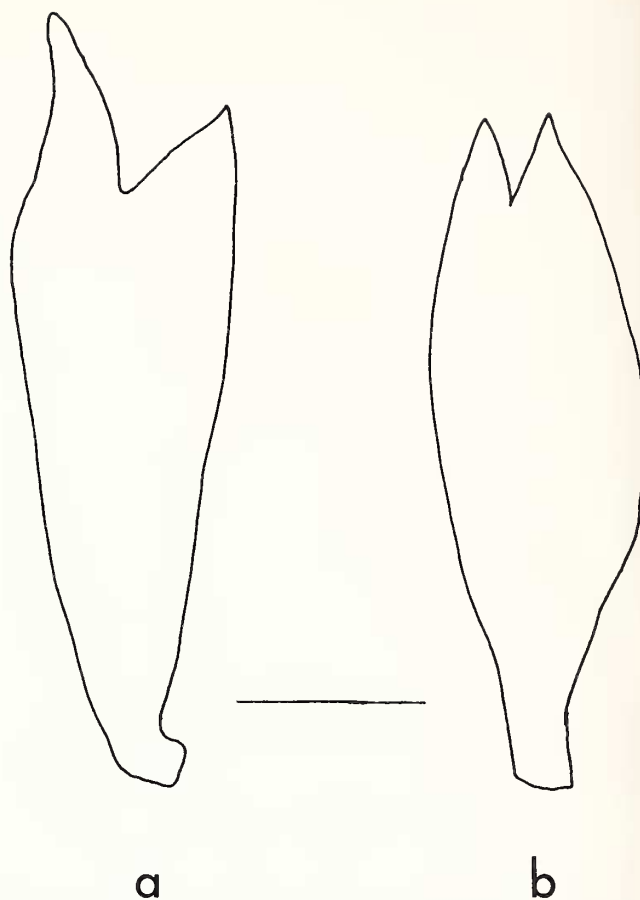


Figure 22. Jaw teeth: a) *Colpichthys regia*, b) *Atherinops affinis*. Scale equals 0.1 mm.

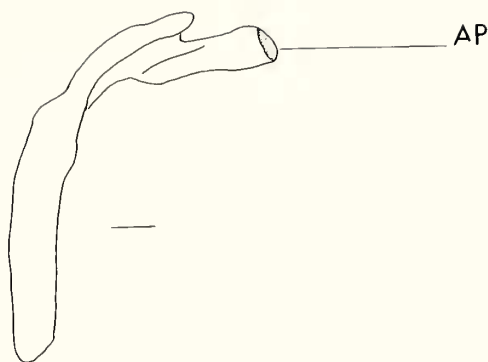
long hairlike teeth that apparently serve to strain fine sand particles.

A single derived feature distinguishes *Atherinops* from all other atherinomorph species: the fold of skin connecting the distal ends of the premaxillary and maxillary bones is frilled (Fig. 24).

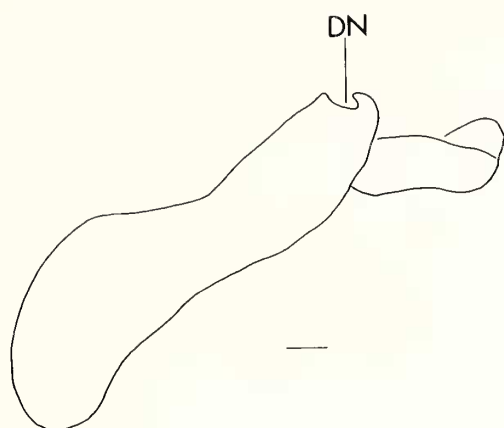
Several unique character states occur in the South American atherinopsines. In the fishes assigned to the genus *Basilichthys*, the ventral process of the maxilla has a rounded projection on its dorsal surface that was not seen in any other atherinomorph species examined (Fig. 23c).

Every species of *Odontesthes* or *Austromeniidia* examined lacks a mesethmoid. The Atherinomorpha is defined, in part, on the presence of a disclike mesethmoid. Therefore, loss of the mesethmoid is considered to be a derived character state shared by these two genera.

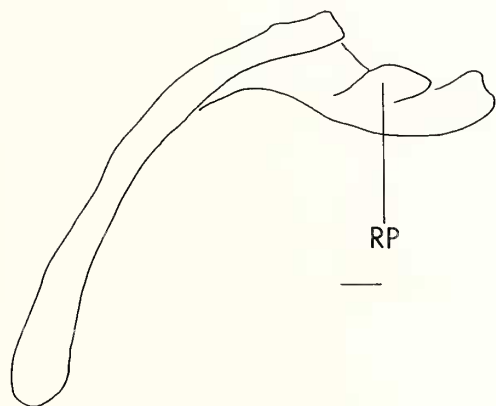
Another derived feature shared by *Odontesthes* and *Austromeniidia* involves the opercle. In every species examined, except *O. incisus*, the opercle has on its anterodorsal corner a complex array of foramina of varying sizes (Fig. 25). This condition appears to be unique within the Atherinomorpha. The absence of these foramina in *O. incisus* is judged to be a secondary loss for two reasons. First, the occurrence of



a



b



c

Figure 23. Lateral view of right maxilla: a) *Atherinopsis californiensis*, b) *Colpichthys regis*, c) *Basilichthys australis*. AP = anterior pocket, DN = dorsal notch, RP = rounded process. Scale equals 1 mm.

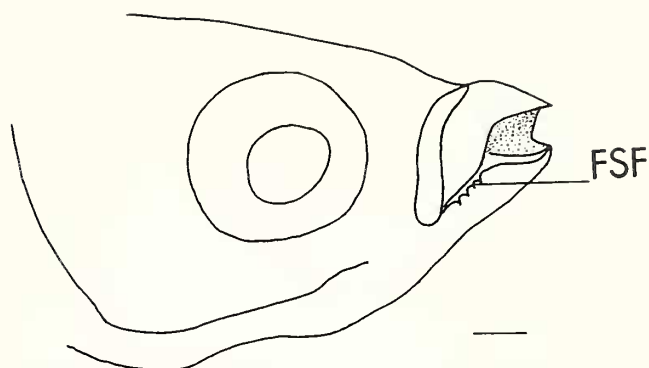


Figure 24. Lateral view of head: *Atherinops affinis*. FSF = frilled skin fold. Scale equals 1 mm.

these foramina is widespread among the other species in these genera and second, the assumption that the foramina have been lost in *O. incisus* is congruent with the other two derived character states described above.

DISCUSSION

The synapomorphic character states described in the previous section support a phylogeny of the New World atherinids (Fig. 26). Five derived character states (Node A) support the hypothesis that the Atherinopsinae (*sensu* Schultz, 1948) is monophyletic: 1) Baudelot's ligament ossified, 2) proximal end of the fourth ceratobranchial without enlarged toothplates, 3) palatine head with medial bony shelf, 4) ventral projection of nasal bone contacting lachrymal, and 5) lateral ethmoid with ventral bony knob.

The Menidiinae is proposed as the sister group of the Atherinopsinae because they share seven synapomorphies: 1) scapula and cleithrum connected by small bony struts, 2) palatine head hammer shaped, 3) premaxilla with small anterior joint and broad alveolar arm, 4) premaxilla connected to the coronoid by a short ligament 5) premaxilla free from maxilla ventrally, 6) ethmomaxillary ligament attached to palatine, and 7) posttemporal bone with flat anterior spine extending into posttemporal fossa of skull (Patten, 1978).

Three derived character states support the contention that the Menidiinae (*sensu* Schultz, 1948) is monophyletic: 1) parapophyses on the first vertebra directed anteriorly and blunt distally, 2) number of supraorbital canal pores reduced to four, and 3) toothplates fused to proximal end of fourth ceratobranchial.

The internal relationships of the Atherinopsinae are clarified by 18 derived character states. Three synapomorphies characterize a South American assemblage (Node B): 1) basioccipital fenestrated, 2) extrascapular composed of two bony elements, and 3) haemal arches expanded to form broad hypophyses. A North American lineage (Node C) is defined by three osteological modifications: 1) supraoccipital process trifold, 2) a pair of dorsal projections on leading edge of vomer, and 3) bifurcation of haemal spines forming expanded hypophyses. Within the northern line one group composed of the species of *Atherinops* and *Colpichthys* (Node D) is char-

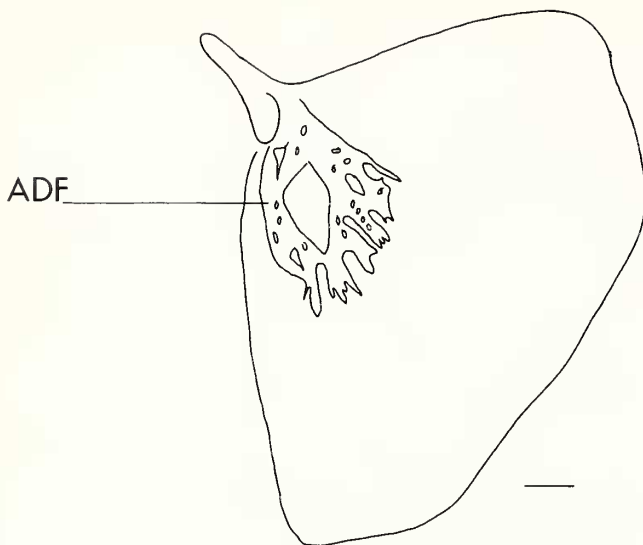


Figure 25. Medial view of right opercle: *Odontesthes regia*. ADF = anterodorsal fenestration. Scale equals 1 mm.

acterized by two derived features: 1) leading edge of quadrate angled anteriorly, not vertical, and 2) teeth bicuspid. *Atherinopsis* and *Leuresthes* comprise a second lineage (Node E) defined by two synapomorphies: 1) medial edge of lateral ethmoid produced to form a spinelike projection contacting lateral edge of parasphenoid, and 2) proximal arm of third epibranchial contorted.

Colpichthys regis and the undescribed Gulf of California species are proposed sister species sharing three derived character states: 1) dorsal process of maxilla notched, 2) teeth on third pharyngobranchial long, hairlike, and 3) paired toothplates on fourth ceratobranchial wide, gap between partners much reduced. *Atherinops* can be diagnosed by the frilled skin fold running between the distal ends of the maxilla and premaxilla.

Two South American atherinopsine groups are recognized on the basis of four synapomorphies. One assemblage, comprising the genus *Basilichthys*, is characterized by one osteological modification: ventral maxillary process with rounded projection on dorsal surface. The second assemblage, which includes all other South American atherinopsines, is defined by three derived character states: 1) mesethmoid lacking, 2) anterodorsal corner of opercle fenestrated, and 3) dorsal process of premaxilla thin and spinelike, mouth protractile.

The evolutionary relationships illustrated in Figure 26 suggest a change in the taxonomy of the Atherinopsinae. The North and South American assemblages deserve tribal status and names are proposed here for each group. The name proposed for the northern tribe, the Atherinopsini, is taken from *Atherinopsis* (Girard, 1854). The name proposed for the southern tribe, the Basilichthyini, is taken from *Basilichthys* (Girard, 1854). Both names are based on the first genus described in the tribe. None of the North American genera currently recognized need be synonymized to afford sister groups equal taxonomic rank. Four northern genera

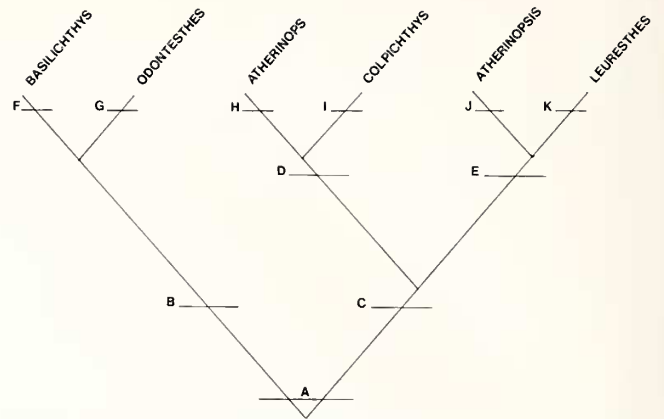


Figure 26. Generic relationships of the Atherinopsinae. Node A. Baudelot's ligament ossified, proximal end of fourth ceratobranchial with moderate toothplates, palatine head with medial bony shelf, ventral projection of nasal bone contacting lachrymal, lateral ethmoid with ventral bony knob. Node B. Basioccipital fenestrated, extrascapular composed of two bony elements, haemal arches expanded to form broad hypophyses. Node C. Supraoccipital process trifold, paired dorsal projections on leading edge of vomer, bifurcation of haemal spines forming expanded hypophyses. Node D. Anterior edge of quadrate angled forward, teeth bicuspid. Node E. Lateral ethmoid with medial process contacting parasphenoid, proximal arm of third epibranchial contorted. Node F. Maxilla ventral process with rounded projection. Node G. Anterodorsal corner of opercle fenestrated, mesethmoid lacking, mouth protractile. Node H. Skin fold running from corner of mouth to maxilla frilled. Node I. Dorsal process of maxilla notched, teeth on third pharyngobranchial hairlike, toothplates on fourth ceratobranchial expanded. Node J. Ventral process of maxilla with anterior pocket. Node K. Beach spawning habits, mouth protractile, vomer reduced, dentition reduced or lacking on jaws.

are recognized: *Atherinops*, *Atherinopsis*, *Colpichthys*, and *Leuresthes*. Included in *Colpichthys*, is the undescribed species from the Gulf of California. Two genera are recognized in the Basilichthyini: *Basilichthys* and *Odontesthes*. *Austromeniidia* is a junior synonym of *Odontesthes*.

Schultz (1948) was correct in his conclusion that the Atherinopsinae and Menidiinae are distinct evolutionary assemblages. The Atherinopsinae is diagnosed cladistically by five characters; the Menidiinae by three. However, his contention that the Atherinopsinae is most closely related to an Old World subfamily, the Atherininae, is not supported by this study.

The evidence presented here supports instead the hypothesis that the Atherinopsinae and Menidiinae "represent a lineage far removed from the ancestry of Atherininae" (Patten, 1978:99), do not form a monophyletic group, and contribute two congruent, synapomorphic character states to the definition of the New World line.

Apparently, similar osteological modifications have evolved more than once in the New World atherinids. For instance, in both the Basilichthyini and Atherinopsini, the swimbladder extends into a modified haemal funnel. Independent evolution of this character is suggested by the fact that the mor-

phology of the haemal funnel is quite different in the two atherinopsine tribes. It is problematical whether the posterior extension of the swimbladder in the northern and southern tribes evolved independently. It could be that elongation of the swimbladder occurred only once in the evolution of the Atherinopsinae and that it is a derived character state shared by all members of the subfamily. On the other hand, posterior extension of the swimbladder and the haemal funnel in the two tribes suggests that extension of the swimbladder and modification of the haemal arches are correlated because expanded haemal arches only occur in those species that have the swimbladder elongated. It seems reasonable to assume that if extension occurred only once in the Atherinopsinae, then the haemal modification in the northern and southern species would be identical. This argument is offered in support of the existence of separate North and South American tribes within the Atherinopsinae, but since its truthfulness cannot be objectively tested, posterior extension of the swimbladder is excluded from the diagnoses of the Atherinopsini and Basilichthyini.

It is interesting to note that in the atherinid subfamily most distantly related to the Atherinopsinae, the Atherininae, the swimbladder extends into modified haemal arches in several species. Some atherinine species, e.g. *Atherina boyeri*, approach the Basilichthyini in this regard. One species, *Atherinason hepsetoides*, resembles quite closely the Atherinopsini. However, the haemal arches of the Notocheirinae, Atherioninae, and Melanotaeniinae are unmodified and it has been concluded that primitively the haemal arches are unspecialized in the Atherininae (Patten, 1978). It is apparent that the similarities seen in the haemal arches of the Atherinopsinae and some atherinine species were derived independently and are nonhomologous.

The premaxilla of the two North American grunion species and the fishes of the South American genus *Odontesthes* seem to have had independent origins as well. The premaxillae of *Basilichthys*, *Atherinops*, *Atherinopsis*, and *Colpichthys* have broadly based, triangular dorsal processes and the upper jaws are not protrusile. The phylogenetic information discussed above suggests that these are the most primitive taxa in the Atherinopsinae and therefore, it is concluded that the condition of their upper jaws is the ancestral state for the subfamily. The upper jaws of *Odontesthes*, *Leuresthes tenuis*, and *L. sardina*, on the other hand, are protrusile and the premaxilla in these fishes has a long, slender dorsal process. However, as has already been mentioned, the placement of the elongate dorsal process in the northern and southern species is different and jaw protrusion is considered on the grounds of parsimony to have evolved more than once. Within the Atherinidae, there is a good deal of variation in the form of the premaxillary dorsal process. The premaxillae of the Atherinopsinae and Menidiinae are unique in that they have only a small anterior joint (Patten, 1978). Therefore, it would be unwise to compare jaw protrusion in the other subfamilies with those of the New World atherinids because the morphology of the upper jaws is different. However, it is interesting that jaw protrusion has evolved several times in the family (Patten, 1978) and that the genetic background

of these fishes allows for the development of analogous solutions to the problem of jaw mobility.

Similar situations have been documented in other taxonomic groups. In plethodontid salamanders, it has been demonstrated that morphological specializations associated with the tongue, limbs, and digits have evolved separately on several occasions (Wake and Lynch, 1976; Larson et al., 1981). The independent evolution of similar traits has also been noted in the foot structure of gekkonine and diplodactyline geckos (Russell, 1979) and in the adaptive ecology of leptodaetyline frogs (Martin, 1970).

Many systematists have studied parallel evolution and several formal definitions have been proposed. According to Simpson (1961:78), "Parallelism is the development of similar characters separately in two or more lineages of common ancestry and on the basis of, or channeled by, characteristics of that ancestry." Mayr (1969:202) defined parallelisms as "similarities resulting from joint possession of independently acquired phenotypic characteristics produced by a shared genotype inherited from a common ancestor." Hecht and Edwards (1976:654) stated that in parallel evolution "the character is present in the ancestral form but a common derived state has been independently evolved in each descendant form." Nelson (1978:123) proposed that "parallelism can be defined as the presence in two monophyletic taxa of a common character state which has been derived through identical successive character state changes from a dissimilar state present in the most recent common ancestor of both taxa."

The independent development of an association between the swimbladder and the haemal funnel in the Basilichthyini and Atherinopsini fits all of these definitions but the last. To meet the requirements of Nelson's definition, the haemal modifications of the Basilichthyini and Atherinopsini would have to develop in exactly the same manner and be identical in all respects. However, if this were true, it would be difficult to recognize that the northern and southern condition were independently derived. In fact, they would probably be viewed as a single derived character state shared by both tribes, definitive for the subfamily, but uninformative about its internal relationships.

It has been suggested that "the concept of parallelism be omitted from systematic studies" and "the term convergence be applied to all cases of nonhomologous character similarities" (Eldredge and Cracraft, 1980:74). In the case of the atherinopsine fishes, the haemal modifications of the Basilichthyini and Atherinopsini clearly are nonhomologous, but the development of a haemal funnel is a striking similarity that presumably evolved from the primitive condition held by their immediate common ancestor. I believe it misleading to call this an example of convergent evolution because the haemal morphology of the two tribes is divergent. However, the Atherinopsini and Basilichthyini evolved comparable haemal specializations that have the same function from a genotype inherited from their most recent common ancestor. This developmental potential passed on by the ancestral atherinopsine was expressed differently in its two descendant lineages, but they evolved in similar directions nonetheless,

probably because of some unknown genetic or epigenetic constraints. In this sense, parallel evolution has occurred in the Atherinopsinae and, questions of process aside, I find the definitions of Simpson (1961) and Mayr (1969) are meaningful and useful.

**KEY TO THE GENERA OF
ATHERINOPSINE FISHES**

- 1a. Supraoccipital process trifold (Fig. 8a) (sometimes bifid in *Leuresthes tenuis*); vomer with paired dorsal projections (Fig. 9); air bladder extending into haemal funnel composed of modified haemal spines (Figs. 10a, 11a); extrascapular composed of single bony element (Fig. 13a); basioccipital not fenestrated. Atherinopsini 2
- 1b. Supraoccipital process bifid (Fig. 8b); vomer without paired dorsal projections; air bladder extending into haemal funnel composed of modified haemal arches (Fig. 10b, 11b); extrascapular composed of two bony elements (Fig. 13b, c) (a single element in *Basilichthys semotilus* and some *Odontesthes incisus*); basioccipital fenestrated (Fig. 12). Basilichthyini 5
- 2a. Jaw teeth bicuspid (Fig. 22); leading edge of quadrate angled anteriorly (Fig. 21b); proximal arm of third epibranchial straight not contorted (Fig. 20b); lateral ethmoid without medial process contacting parasphenoid 3
- 2b. Jaw teeth unicuspid; leading edge of quadrate vertical (Fig. 21a); proximal arm of third epibranchial crooked, contorted (Fig. 20a); lateral ethmoid with medial process contacting parasphenoid (Fig. 19) 4
- 3a. Ventral process of premaxillary with bony pocket on anterior tip (Fig. 23a); vomer not reduced; jaws not protractile; jaw teeth not reduced *Atherinopsis*
- 3b. Ventral process of premaxillary without bony pocket on anterior tip; vomer reduced; jaws greatly protractile; jaw teeth minute or absent *Leuresthes*
- 4a. Tooth cusps equal in length (Fig. 22b); skin fold between corner of mouth and maxilla frilled (Fig. 24); dorsal process of maxilla without notch; toothplates on fourth ceratobranchial not expanded (Fig. 4a) *Atherinops*
- 4b. Tooth cusps unequal in length (Fig. 22a); skin fold between corner of mouth and maxilla not frilled; dorsal process of maxilla with notch (Fig. 23b); toothplates on fourth ceratobranchial expanded (Fig. 4c) *Colpichthys*
- 5a. Mesethmoid absent, mouth protractile; anterodorsal corner of opercle fenestrated (Fig. 25) (except in *Odontesthes incisus*); ventral process of maxilla without rounded projection on dorsal surface *Odontesthes*
- 5b. Mesethmoid present; mouth not protractile; anterodorsal corner of opercle not fenestrated; ventral process of maxilla with rounded projection on dorsal surface (Fig. 23c) *Basilichthys*

CLASSIFICATION AND SYSTEMATIC ACCOUNTS

Subfamily Atherinopsinae

Tribe Atherinopsini

Genus *Atherinops* Steindachner, 1876

Genus *Atherinopsis* Girard, 1854

Genus *Colpichthys* Hubbs, 1918

Genus *Leuresthes*

Jordan and Gilbert, 1880

Tribe Basilichthyini

Genus *Odontesthes*

Evermann and Kendall, 1906

Genus *Basilichthys* Girard, 1854

Subfamily Atherinopsinae Fowler, 1904

DIAGNOSIS. Baudelot's ligament ossified; proximal end of fourth ceratobranchial with moderate toothplates; palatine head with medial bony shelf; ventral projection of nasal bone contacting lachrymal; lateral ethmoid with ventral bony knob.

COMPOSITION. Six genera: *Atherinops* Steindachner, 1876; *Atherinopsis* Girard, 1854; *Basilichthys* Girard, 1854; *Colpichthys* Hubbs, 1918; *Leuresthes* Jordan and Gilbert, 1880; *Odontesthes* Evermann and Kendall, 1906.

DISTRIBUTION. West coast of North America from Vancouver Island to the Gulf of California in marine waters. Temperate South America in fresh and marine waters.

Tribe Atherinopsini Fowler

DIAGNOSIS. Supraoccipital process trifold; vomer with paired dorsal projections; haemal funnel developed from bifurcated haemal spines.

COMPOSITION. Four genera: *Atherinops* Steindachner, 1876; *Atherinopsis* Girard, 1854; *Colpichthys* Hubbs, 1918; *Leuresthes* Jordan and Gilbert, 1880.

DISTRIBUTION. Marine waters of western North America from Vancouver Island into the Gulf of California.

Genus *Atherinops* Steindachner

Atherinops Steindachner, 1876:89 (type species *Atherinopsis affinis* Ayres, by monotypy).

DIAGNOSIS. Atherinopsines with fold of skin running from corner of mouth to distal end of maxilla frilled.

DESCRIPTION. Baudelot's ligament ossified; proximal end of fourth ceratobranchial with moderate toothplates; palatine head with medial bony shelf; ventral projection of nasal bone contacting lachrymal; lateral ethmoid with ventral bony knob; supraoccipital process trifold; vomer with paired dorsal projections; haemal funnel comprised of modified haemal spines; jaw teeth bicuspid; anterior edge of quadrate angled forward.

COMPOSITION. One species, the type.

DISTRIBUTION. Outer coast and islands of Oregon, California, and Baja California.

Genus *Atherinopsis* Girard

Atherinopsis Girard, 1854:134 (type species *Atherinopsis californiensis* Girard, by monotypy).

DIAGNOSIS. Atherinopsines with pocket on anterior tip of ventral process of maxilla.

DESCRIPTION. Baudelot's ligament ossified; proximal end of fourth ceratobranchial with moderate toothplates; palatine head with medial bony shelf; ventral projection of nasal bone contacting lachrymal; lateral ethmoid with ventral bony knob; supraoccipital process trifid; vomer with paired dorsal projections; haemal funnel comprised of modified haemal spines; proximal arm of the third epibranchial contorted; lateral ethmoid with medial process contacting parasphenoid.

COMPOSITION. One species, the type.

DISTRIBUTION. Outer coasts and islands of North America from Vancouver Island to Baja California.

Genus *Colpichthys* Hubbs

Colpichthys Hubbs, 1918:67 (type species *Atherinops regis* Jenkins and Evermann, by original designation).

DIAGNOSIS. Atherinopsines with notch in dorsal process of maxillary bone; toothplates on fourth ceratobranchial expanded; teeth on third pharyngobranchial hairlike.

DESCRIPTION. Baudelot's ligament ossified; proximal end of fourth ceratobranchial with moderate toothplates; palatine head with medial bony shelf; ventral projection of nasal bone contacting lachrymal; lateral ethmoid with ventral bony knob; supraoccipital process trifid; vomer with paired dorsal projections; haemal funnel composed of modified haemal spines; jaw teeth bicuspid; anterior edge of quadrate angled anteriorly.

COMPOSITION. Two species: *C. regis* and a new species from Gulf of California.

DISTRIBUTION. Gulf of California.

Genus *Leuresthes* Jordan and Gilbert

Leuresthes Jordan and Gilbert, 1880:29 (type species *Atherinopsis tenuis* Ayres, by monotypy).

Hubbsiella Breder, 1936:6, figs. 2-4 (type species *Menidia clara* Evermann and Jenkins, by monotypy).

DIAGNOSIS. Atherinopsines with beach spawning habits; jaw teeth reduced or absent; mouth greatly protractile; vomer reduced.

DESCRIPTION. Baudelot's ligament ossified; proximal end of fourth ceratobranchial with moderate toothplates; palatine head with medial bony shelf; ventral projection of nasal bone contacting lachrymal; lateral ethmoid with ventral bony knob; supraoccipital process trifid; vomer with paired dorsal projections; haemal funnel composed of modified haemal

spines; proximal arm of third epibranchial contorted; lateral ethmoid with medial process contacting parasphenoid.

COMPOSITION. Two species: *L. sardina* and *L. tenuis*.

DISTRIBUTION. Outer coasts and islands of California, Baja California, and the Gulf of California.

Tribe Basilichthyini, New

DIAGNOSIS. Basioccipital ridged and fenestrated; extrascapular composed of two bony elements; haemal funnel developed from expanded haemal canals.

COMPOSITION. Two genera: *Basilichthys* Girard, 1854; *Odontesthes* Evermann and Kendall, 1906.

DISTRIBUTION. Temperate South America in marine and fresh waters including high Andean streams.

Genus *Basilichthys* Girard

Basilichthys Girard, 1854:198 (type species *Atherina microlepidota* Jenyns, by subsequent designation of Jordan, 1919).

Protistius Cope, 1874:66 (type species *Protistius semotilus* Cope, by monotypy).

Gastropterus Cope, 1878:700 (type species *Gastropterus archaeus* Cope, by monotypy).

Pisciregia Abbott, 1899:342 (type species *Pisciregia beardleei* Abbott, by monotypy).

DIAGNOSIS. Atherinopsines with rounded projection on ventral process of maxilla.

DESCRIPTION. Baudelot's ligament ossified; proximal end of fourth ceratobranchial with moderate toothplates; palatine head with medial bony shelf; ventral projection of nasal bone contacting lachrymal; lateral ethmoid with ventral bony knob; basioccipital ridged and fenestrated; extrascapular composed of two bony elements; haemal funnel developed from expanded haemal canals.

COMPOSITION. Approximately 6 species; generic revision needed.

DISTRIBUTION. Marine and fresh waters of Peru and Chile.

Genus *Odontesthes* Evermann and Kendall

Odontesthes Evermann and Kendall, 1906:94, fig. 3 (type species *Odontesthes perugiae* Evermann and Kendall, by subsequent designation of Jordan and Hubbs, 1919).

Kronia Ribeiro, 1915:9 (type species *Kronia iguapensis* Ribeiro, by monotypy).

Pseudothyryna Ribeiro, 1915:11 (type species *Pseudothyryna iheringi* Ribeiro, by monotypy).

Austromenidia Hubbs, 1918:307 (type species *Basilichthys regillus* Abbott, by original designation).

Cauque Eigenmann, 1928:56 (type species *Chirostoma mauleanus* Steindachner, by original designation).

Patagonina Eigenmann, 1928:56, 60 (type species *Patagonia hatcheri* Eigenmann, by monotypy).

Patagonia Eigenmann, 1928:56 (l.c. in footnote, *lapsus pro Patagonina*, takes same type).

? *Austroatherina* Marrero, 1950, not seen, after de Buen 1953 (type species *Atherina incisa* Jenyns).

Yaci de Buen, 1953:51, figs. 31, 32, 33 (type species *Yaci retropinnis* de Buen, by monotypy).

DIAGNOSIS. Atherinopsines with mesethmoid lacking, mouth protractile, anterodorsal corner of opercle fenestrated.

DESCRIPTION. Baudelot's ligament ossified; proximal end of fourth ceratobranchial with moderate toothplates; palatine head with medial bony shelf; ventral projection of nasal bone contacting lachrymal; lateral ethmoid with ventral bony knob; basioccipital ridged and fenestrated; extrascapular composed of two bony elements; haemal funnel developed from expanded haemal canals.

COMPOSITION. Approximately 10 species; generic revision needed.

DISTRIBUTION. Temperate South America in marine and fresh waters from Peru to southern Brazil. Also Malvinas and Juan Fernandez Islands.

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