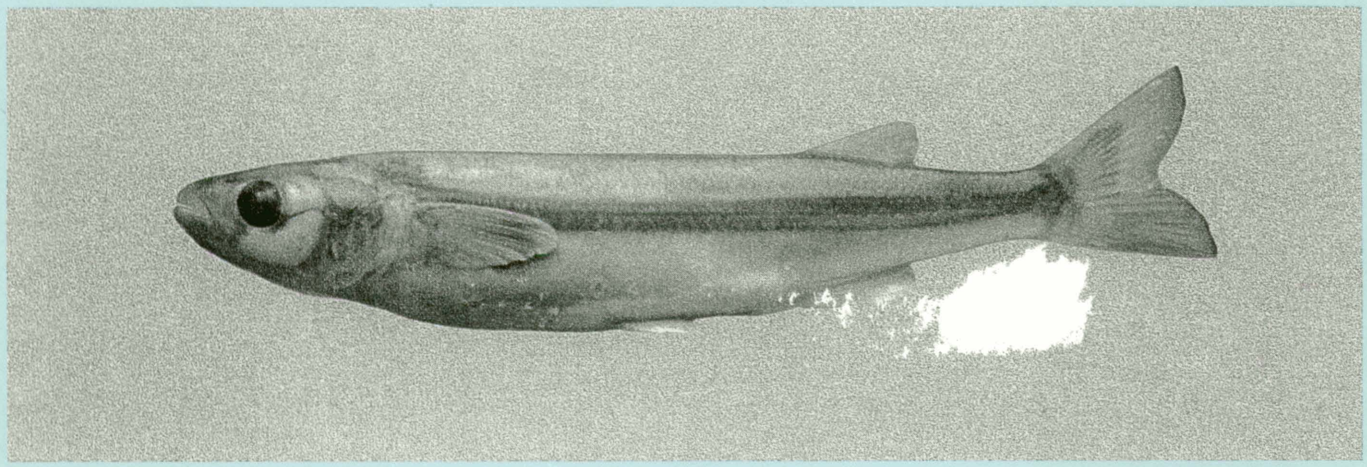
PHYLOGENETIC REVISION OF ATHERINOPSINAE (TELEOSTEI, ATHERINOPSIDAE), WITH COMMENTS ON THE SYSTEMATICS OF THE SOUTH AMERICAN FRESHWATER FISH GENUS *BASILICHTHYS* GIRARD

BY

BRIAN S. DYER



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Phylogenetic revision of Atherinopsinae (Teleostei, Atherinopsidae), with comments on the systematics of the South American freshwater fish genus *Basilichthys* Girard

by

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ABSTRACT

Dyer, B.S. 1997. Phylogenetic revision of Atherinopsinae (Teleostei, Atherinopsidae), with comments on the systematics of the South American freshwater fish genus Basilichthys *Girard. Misc. Publ. Mus. Zool. Univ. Michigan, 185:1-64, 46 figs., 3 tables.* Hypotheses of relationships among atherinopsine taxa and their monophyly are revised using mugilids, Cyprinodontea (beloniforms and cyprinodontiforms), Atherinoidei, and Menidiinae as outgroups. Anatomical evidence is compiled with published morphological and allozyme data for a phylogenetic analysis of Atherinopsinae. Diagnostic characters are provided for atherinopsine groups in addition to Menidiinae, Menidiini, and Membradini. Atherinopsidae is diagnosed by 20 characters of which six are unique within atherinomorphs.

Atherinopsinae, composed of Atherinopsini (North America: *Colpichthys*, *Atherinops*, *Atherinopsis*, *Leuresthes*) and Sorgentinini (South America: *Basilichthys*, *Odontesthes*), is diagnosed by eight characters. A phylogenetic analysis of relationships among atherinopsinin genera resulted in two most equally parsimonious hypotheses: *Colpichthys* is the sister to *Atherinops*, *Atherinopsis*, and *Leuresthes*, the latter two each others closest relatives; or *Leuresthes* is sister to *Atherinopsis*, *Atherinops*, and *Colpichthys*, the latter two as sister genera. Both sets of relationships are more parsimonious than previous hypotheses by White (morphology) and by Crabtree (allozymes) which proposed *Colpichthys* and *Atherinops*, and *Atherinopsis* and *Leuresthes* as sister taxa. A key is provided to the genera of atherinopsines and to the species of atherinopsinins.

Atherinopsini, diagnosed by seven characters (vomer with two developed dorsal laminae, dermosphenotic with three sensory-canal pores, trifid supraoccipital crest, infrapharyngobranchial 1 cartilaginous, pointed cranial process of infrapharyngobranchial 2, long uncinate process of epibranchial 3 attached proximally, haemal-hypophysis funnel), is composed of six species. *Colpichthys*, with two species (*C. regis*, *C. hubbsi*), is diagnosed by nine characters (e.g., tooth cusps asymmetrical, presence of hyomandibular nerve foramen, < 20 gill rakers on lower limb of first branchial arch, pharyngeal jaw teeth hair-like, females with ovipositors, and eggs lacking filaments). *Atherinops affinis* is diagnosed by frills of skin between maxilla and premaxilla, and two rows of subocular scales. *Atherinopsis californiensis* is diagnosed by seven characters (e.g., dermosphenotic not enclosed by bone, opercular dorsal process lacking laminar blade-like flange, small size scales). *Leuresthes*, with two species (*L. tenuis*, *L. sardina*), is diagnosed by five characters (e.g., pelvic median plate extended to anterior end, scales present on second dorsal fin, unique beach-spawning habits).

Sorgentinini, diagnosed by eight characters (e.g., ethmomaxillary ligament attached to ethmoid cartilage only, presence of basioccipital fenestration, palatorostral ligament, precaudal vertebrae 50% or more of total vertebrae, haemal-arch funnel), comprises about 25 species. *Odontesthes*, with about 20 marine and freshwater species, is diagnosed by seven characters (e.g., mesethmoid absent, enlarged trigeminofacial foramen, mandibular branch of A1 muscle tendon anterior to lacrimal branch, opercle fenestrated). *Basilichthys*, with five freshwater species, is diagnosed by 22 characters (e.g., lacrimal condyle of lateral ethmoid not extended to ventral edge, dermosphenotic medial flange reduced or absent, ventral process of maxilla with a condyle, dentary coronoid process flattened dorsally, absence of a dentary gnathic spine, ethmomaxillary ligament not attached to spoon-shaped palatine dorsal process, precaudal vertebrae over 57% of total vertebrae and first caudal vertebra over posterior half of anal fin, dorsal head scales with reversed imbrication).

Two species groups are recognized in *Basilichthys*. The *Basilichthys microlepidotus* species group comprises the nominal species *B. microlepidotus* and *B. australis* from central and southern Chile. The *Basilichthys semotilus* species group is composed of *B. semotilus* and *B. archaeus* from Peru, and an undescribed species from the Río Loa in northern Chile. The undescribed species is tentatively proposed as sister to the other species of the *semotilus* species group.

Key words: *Atheriniformes, Atherinopsini, Sorgentinini, phylogenetic systematics, morphology,* Basilichthys.

RESÚMEN

Dyer, B.S. 1997. Revisión filogenética de Atherinopsinae (Teleostei, Atherinopsidae) y comentarios sistemáticos del género dulceacuícola Sudamericano, Basilichthys *Girard. Misc. Publ. Mus. Zool., Univ. Michigan : 1-64, 46 figs., 3 tablas.*

La monofilia de la subfamilia Atherinopsinae y las hipótesis de relaciones entre sus géneros son revisadas usando como outgroups a Mugilidae, Cyprinodontea (Beloniformes y Cyprinodontiformes), Atherinoidei, y Menidiinae. Datos morfológicos y enzimáticos ya publicados son agrupados con caracteres anatómicos nuevos para un análisis filogenético del grupo. Se entregan caracteres diagnósticos tanto para los grupos atherinopsinos como para Menidiinae, Menidiini, y Membradini. Atherinopsidae es diagnosticado por 20 caracteres, de los cuales seis son únicos dentro de Atherinomorpha.

Atherinopsinae, compuesto por Atherinopsini (Norteamérica: *Colpichthys, Atherinops, Atherinopsis, Leuresthes*) y Sorgentinini (Sudamérica: *Basilichthys, Odontesthes*), es diagnosticado por ocho caracteres. El análisis filogenético de los géneros atherinopsininos dió como resultado dos hipótesis de relaciones igualmente parsimoniosas: *Colpichthys* es el grupo hermano de los demás géneros y *Atherinops* es hermano de *Atherinopsis* y *Leuresthes*; o *Leuresthes* es el grupo hermano de los demás géneros, y *Atherinopsis* es hermano de *Atherinops* y *Colpicthys*. Ambas hipótesis son más parsimoniosas que aquella presentada por White y Crabtree, basada en morfología y en aloenzimas, respectivamente, quienes propusieron a *Colpichthys* y *Atherinops*, y *Atherinopsis* y *Leuresthes* como grupos hermanos. Se provee además una clave para los géneros de Atherinopsinae y las especies de Atherinopsinini.

Atherinopsinini es diagnosticado por siete caracteres (vómer con dos procesos laminares dorsales bien desarrolladas, dermoesfenótico con tres poros del canal sensorial, cresta supraoccipital trífida, primer infrafaringobranquial cartilaginoso, segundo infrafaringobranquial con proceso cranial agudo, tercer epibranquial con proceso uncinado largo conectado proximalmente, y embudo de hipófisis hemales) y está compuesto por seis especies. *Colpichthys*, con dos especies (*C. regis, C. hubbsi*), es diagnosticado por ocho caracteres (ej., cúspides dentales asimétricos, presencia de un foramen del nervio hiomandibular, <20 branquiespinas en el ramo inferior del primer arco branquial, dientes faríngeos finos, hembras con ovipositores, y huevos sin filamentos). *Atherinops affinis* es diagnosticado por la presencia de un margen escarolado de piel entre el maxilar y premaxilar, y dos filas de escamas suboculares. *Atherinopsis californiensis* es diagnosticado por seis caracteres (ej., canal dermoesfenótico abierto, proceso opercular dorsal sin un reborde laminado, y escamas de tamaño pequeño). *Leuresthes*, con dos especies (*L. tenuis, L. sardina*), es diagnosticado por cinco caracteres (ej., placa pélvica mediana extendida hasta el extremo anterior, escamas presentes en la base anterior de la segunda aleta dorsal, y hábitos característicos de desove en playa).

Sorgentinini es diagnosticado por ocho caracteres (ej., ligamento etmomaxilar conectado solo al cartílago etmoidal, presencia de fenestraciones en el basioccipital, presencia de un ligamento palatorostral, número de vértebras precaudales 50% o más del número de vértebras totales, y embudo de arcos hemales) y está compuesto por unas 25 especies. *Odontesthes*, con unas 20 especies marinas y dulceacuícolas, es diagnosticado por siete caracteres (ej., ausencia de mesetmoides, foramen trigeminofacial agrandado, rama mandibular del tendón del músculo aductor mandibular A1 anterior a la rama lacrimal, y opérculo fenestrado). *Basilichthys*, con cinco especies dulceacuícolas, es diagnosticado por 22 caracteres (ej., cóndilo lacrimal del etmoides lateral sin extensión al borde ventral, proceso laminar medial del dermoesfenótico reducido o ausente, proceso ventral del maxilar con un cóndilo, dentario con proceso coronoides aplanado dorsalmente, ausencia de una espina mandibular del dentario, ligamento etmomaxilar sin conexión al proceso palatino dorsal, número de vértebras precaudales sobre el 57% del número total de vértebras, primera vértebra caudal sobre la mitad posterior de la aleta anal, y escamas dorsales de la cabeza con imbricación invertida).

Se reconocen dos grupos de especies en *Basilichthys*. El grupo de especies *Basilichthys microlepidotus* está compuesto por las especies nominales *B. microlepidotus* y *B. australis* del centro y sur de Chile. El grupo de especies *Basilichthys semotilus* está compuesto por *B. semotilus* y *B. archaeus* de Perú, y una especie sin describir del Río Loa en el norte de Chile. La especie no descripta está tentativamente propuesta como especie hermana de las demás especies del grupo *semotilus*.

Palabras clave: *Atheriniformes, Atherinopsini, Sorgentinini, sistemática filogenética, morfología,* Basilichthys.

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INTRODUCTION

The family of New World silversides, Atherinopsidae, is composed of the subfamilies Menidiinae and Atherinopsinae. Evidence for their monophyly and sister-group relationship was provided by White (1985) and Chernoff (1986b). White (1985) and Chernoff (1986b) both used a combination of selected taxa of Old World atherinids, melanotaeniids, notocheirids, beloniforms, and cyprinodontiforms as outgroups in their assessments of character polarity. The phylogenetic hypothesis of atheriniform interrelationships (Dyer & Chernoff, 1996) used in this study, however, dramatically changes traditional taxonomic groupings (e.g., Notocheiridae, Phallostethidae, Atherinidae) and assumptions of plesiomorphic groups (e.g., *Bedotia, Rheocles, Melanotaenia*) long held since Jordan & Hubbs (1919). In combining the hypotheses of atheriniform (Dyer & Chernoff, 1996) and atherinomorph (Rosen & Parenti, 1981; Stiassny, 1990, 1993) relationships, outgroups now have a sequential order of relationships relative to the atherinopsid ingroup. For these reasons some changes are expected in taxic relationships within the family and changes in group diagnoses.

White (1985) provided the first hypothesis of phylogenetic relationships within Atherinopsinae and recognized two tribes: Atherinopsini (North America; *Atherinopsis, Atherinops, Colpichthys, Leuresthes*) and Sorgentinini (South America; *Basilichthys* and *Odontesthes*). Crabtree (1987) presented two cladograms based on allozyme data with network relationships identical to White's cladogram, but which differed in placement of the root. Both White and Crabtree, however, did not have an adequate sample of sorgentinin species. Considering that about 80% of the approximately 30 species of atherinopsines are sorgentinins, the inclusion of missing species into the phylogenetic analysis could significantly affect the relationships proposed by White (1985) and Crabtree (1987).

Atherinopsinins are coastal marine fishes from the west coast of North America which occasionally enter estuarine environments. The group ranges from Vancouver Island, Canada, to southern Baja California and the Gulf of California. Four genera are currently recognized: *Atherinops* (topsmelt) and *Atherinopsis* (jacksmelt) with one species each, and *Colpichthys* and *Leuresthes* (grunion) with two species each.

Sorgentinin species, generally known as *pejerreyes*, inhabit temperate marine, estuarine, and freshwater environments. The coastal marine forms range from northern Peru and southeastern Brazil to the southern tip of Tierra del Fuego, including the Falkland (Malvinas) Islands and the Juan Fernandez Archipelago. Freshwater forms are found in the west-draining rivers of Peru and Chile, in Patagonia, and the Pampas region of Argentina, Uruguay, and southeastern Brazil. At present only two of the 13 described genera of sorgentinins are recognized: *Basilichthys* with 5 nominal species and *Odontesthes* with 46 nominal species.

The object of this study is to combine the data of White (1985), Chernoff (1986b), and Crabtree (1987) with the results of my own morphological studies in order to reevaluate the phylogenetic relationships among atherinopsine genera. A review of the taxonomic history of the subfamily preceeds the methods utilized in the phylogenetic analysis and character descriptions are presented prior to the phylogenetic results. Two equally-parsimonious trees are found in this study and following the systematics, a discussion section deals with alternative relationships and character evolution in the context of these phylogenetic hypotheses.

Within the South American atherinopsines the systematics of the two species groups of *Basilichthys* are discussed further, however, the relationships among species of *Odontesthes* are treated elsewhere (see Dyer, 1993: 331-501).

TAXONOMIC HISTORY

Atherinopsinae was erected by Fowler (1903) for those atheriniform fishes with "premaxillaries not freely protractile, the skin continuous mesially with forehead". In the first comprehensive revision of atheriniforms by Jordan & Hubbs (1919) the subfamily was enlarged to include almost all American silversides. Subsequently, Schultz (1948:42) redefined atherinopsines to include only those genera with distally dilated premaxillaries and a tapering gas bladder surrounded by modified, expanded haemal arches, the haemal funnel. With this diagnosis, all American silverside genera that did not share the haemal funnel characteristic were accommodated in Menidiinae. Schultz (1948) allied Atherinopsinae with Atherininae because some atherinine species also have an haemal funnel. The relationship between Menidiinae and Atherinopsinae was unclear until Patten (1978) proposed them as sister groups in his unpublished thesis, a relationship that was later corroborated by White (1985). Chernoff (1986b) revised Menidiinae phylogenetically and presented additional evidence for the sister-group relationship between the subfamilies and their monophyly. The haemal funnel was consequently hypothesized to have evolved independently in atherinines and atherinopsines (White, 1985). The sister-group relationship between the New World subfamilies is now formally recognized as Atherinopsidae, a family that is relatively distantly related to Atherinidae (Saeed *et al.*, 1994; Dyer & Chernoff, 1996), and sister group to other atheriniforms (Dyer & Chernoff, 1996). Because of significant changes in relationships and taxonomy of atheriniform fish families, a summary of the history of these changes is depicted in Table 1. Table 2 is a classification of atheriniform fishes from Dyer & Chernoff (1996) depicting the higher taxonomic categories used here.

Atherinopsinae, as recognized by Schultz (1948), was composed of seven genera: *Atherinopsis, Atherinops, Austromenidia, Basilichthys, Hubbsiella, Leuresthes*, and *Odontesthes*. These genera were grouped into the North American Atherinopsini and the South American Sorgentinini tribes (White, 1985). The monophyly of these tribes was weakly supported by Crabtree's (1987) distance-treated electrophoretic data, however, the character-coded allozyme data showed an *Atherinopsis-Leuresthes* clade to be more closely related to an *Odontesthes-Basilichthys* clade.

Atherinopsini is composed of *Atherinops, Colpichthys, Atherinopsis*, and *Leuresthes*. The two former genera and the latter two genera were proposed as sister groups by White (1985). The *Atherinops-Colpichthys* and the *Atherinopsis-Leuresthes* clades were also supported by enzymatic data (Crabtree, 1987). *Hubbsiella* was synonymized into *Leuresthes* by Moffat & Thomson (1975) and *Colpichthys* was retained as distinct from *Atherinops* by Todd (1976), White (1985), and Crabtree (1989). Although Hubbs (1918b) recognized a number of *Atherinops* species, sub-

Table 1. History of classifications of atheriniform fish families.

Jordan & Hubbs 1919	Schultz 1948, 1950	Rosen 1964	Rosen & Parenti 1981	Parenti 1984	Eschmeyer 1990	Nelson 1994	Saeed, Ivantsoff & Crowley, 1994	Dyer & Chernoff 1996
ATHERINIDAE	ATHERINIDAE	ATHERINIFORMES ATHERINOIDEA	DIVISION I	DIVISION I	ATHERINIDAE	ATHERINIFORMES	ATHERINIFORMES ATHERINOIDEA	ATHERINIFORMES
						BEDOTIOIDEI		
Bedotiinae	Bedotiinae		Bedotiidae	Bedotiidae	Bedotiinae	Bedotiidae	Bedotiidae	
						MELANOTAENIOIDEI		
Rheoclinae	Rheoclinae	Melanotaeniidae	Melanotaeniidae	Melanotaeniidae	Melanotaeniinae	Melanotaeniidae	Melanotaeniidae	Melanotaeniidae
Melanotaeniinae	Melanotaeniinae		Telmatherinidae		Pseudomugilinae (inc. Telmatherinidae)	Pseudomugilidae	Pseudomugilidae	
						ATHERINOIDEI	Telmatherinidae	
						Telmatherinidae		
	Taeniomembradinae							
	Atherininae	Atherinidae	Atherinidae	Atherinidae	Atherininae	Atherinidae	Atherinidae	Atherinidae
Antherininae	Atherioninae				Atherioninae			Atherionidae
							ATHERINOPSOIDEA	
	Notocheirinae	Isonidae	Isonidae	Isonidae	Notocheirinae	Notocheiridae	Notocheiridae Isonidae	Notocheiridae
	Atherinopsinae				Atherinopsinae			
Atherinopsinae		Atherinidae	Atherinidae	Atherinidae		Atherinidae	Atherinopsidae	Atherinopsidae
	Menidiinae				Menidiinae			
		PHALLOSTETHOIDEA		**PHALLOSTETHOIDEA**				
		Phallostethidae		Dentatherinidae	Dentatherininae	Dentatherinidae	Dentatherinidae	
PHALLOSTETHIDAE	PHALLOSTETHIDAE		Phallostethidae					Phallostethidae
		Neostethidae		Phallostethidae	PHALLOSTETHIDAE	Phallostethidae	Phallostethidae	
Nannatherininae ✶								

(✶ in Kuhliidae)

Table 2. Phylogenetic classification of Atherinopsidae.

- Series Atherinomorpha Greenwood, Rosen, Weitzman, Myers
  - Order Atheriniformes Rosen
    - Family Atherinopsidae Fowler
      - Subfamily Atherinopsinae Fowler
        - Tribe Atherinopsini Fowler
          - Genus *Atherinops* Steindachner *sedis mutabilis*
          - Genus *Atherinopsis* Girard *sedis mutabilis*
          - Genus *Colpichthys* Hubbs *sedis mutabilis*
          - Genus *Leuresthes* Jordan & Gilbert *sedis mutabilis*
        - Tribe Sorgentinini Pianta de Risso & Risso[1]
          - Genus *Odontesthes* Evermann & Kendall
          - Genus *Basilichthys* Girard
            - *microlepidotus* species group
              - *microlepidotus* Jenyns
              - *australis* Eigenmann
            - *semotilus* species group
              - *semotilus* Cope
              - *archaeus* Cope
      - Subfamily Menidiinae Schultz
        - Tribe Menidiini Schultz
          - Genus *Chirostoma* Swainson *sedis mutabilis*
          - Genus *Labidesthes* Cope *sedis mutabilis*
          - Genus *Menidia* Bonaparte *sedis mutabilis*
          - Genus *Poblana* De Buen *sedis mutabilis*
        - Tribe Membradini Chernoff
          - Genus *Atherinella* Steindachner
          - Genus *Membras* Bonaparte
          - Genus *Melanorhinus* Metzelaar
    - Suborder Atherinoidei
      - Family Notocheiridae Schultz
    - Infraorder Atherines Dyer & Chernoff
      - Family Melanotaeniidae Gill
        - Subfamily Bedotiinae Jordan & Hubbs *sedis mutabilis*
        - Subfamily Melanotaeniinae Gill *sedis mutabilis*
        - Subfamily Pseudomugilinae Kner *sedis mutabilis*
          - Tribe Pseudomugilini Kner
          - Tribe Telmatherinini Munro
      - Family Atherionidae Schultz
    - Superfamily Atherinoidea
      - Family Phallostethidae Regan
        - Subfamily Dentatherininae Patten & Ivantsoff
        - Subfamily Phallostethinae Regan
          - Tribe Phallostethini Regan
          - Tribe Gulaphallini Aurich
      - Family Atherinidae Günther
        - Subfamily Atherinomorinae Dyer & Chernoff
        - Subfamily Atherininae Günther
        - Subfamily Craterocephalinae Dyer & Chernoff
  - Superorder Cyprinodontea Dyer & Chernoff
    - Order Cypriniformes Berg
    - Order Beloniformes Berg

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[1] Pianta de Risso & Risso (1953) is the correct authorship for *Sorgentinia* and Sorgentinini, not Risso & Risso (1953) as cited by White (1989).

species, and intergrades, a single species *A. affinis* (Ayres) is recognized herein, in agreement with White (1985) and Crabtree (1987, 1989).

Sorgentinini is composed of 13 described genera and 51 nominal species. This tribe was named Basilichthyini by White (1985) who was unaware of the earlier name (see White, 1989). The number of species included in *Basilichthys* has been controversial ever since the genus was erected by Girard (1854). Girard's (1855) detailed description of the type species *B. microlepidotus* (Jenyns), included meristic and morphometric information as well as the phrase "...protrusion of upper jaw beyond the lower". The latter feature was subsequently adopted as the diagnostic trait of *Basilichthys* by many authors (Burmeister, 1861; Cope, 1874, 1878; Abbott, 1899; Fowler, 1903; Lahille, 1929a,b; Szidat & Nani, 1951; Aramburu & Ringuelet, 1967; Ringuelet *et al.*, 1967; Dazarola, 1972). Girard's (1855) description was reviewed by Thompson (1916) and again by Eigenmann (1927), both of whom concluded that *Basilichthys* is a group of fishes with a frenum between the upper jaw and the forehead. This alternative was accepted by a different suite of authors (Hubbs, 1918a; Jordan & Hubbs, 1919; Fowler, 1945a,b, 1951; Hildebrand, 1946; Schultz, 1948; De Buen, 1950, 1955; Mann, 1954; Arratia, 1981). Agreeing with Thompson (1916), Hubbs (1918a) created *Austromenidia* to distinguish the small-scale species with upper jaw protrusion from *Basilichthys* (species with a frenum) and from *Odontesthes* species with large scales. Eigenmann (1927) described *Cauque* to include four freshwater species with crenate scales that are endemic to Chile. *Patagonina* was described by Eigenmann (1927) in a footnote to accommodate *O. hatcheri* (Eigenmann, 1909), the freshwater species he described from Patagonia. Lahille (1929a) redescribed most sorgentinin species based on morphometrics and placed them in *Basilichthys.* Schultz (1948) considered *Cauque* and *Patagonina* as synonyms of *Austromenidia.* Unable to find sufficient evidence to justify the use of generic names such as *Austromenidia, Cauque,* and *Kronia,* De Buen (1950) recognized the oldest names only, *Odontesthes* and *Basilichthys.* Later, however, De Buen (1953) described *Yaci* in his revision of the silversides of Uruguay, recognized *Kronia* Miranda-Ribeiro and *Austroatherina* Marrero, and described *Tupa* as a subgenus of *Odontesthes. Austroatherina* Marrero (1950) has been used mostly for *O. incisa* (Jenyns), but is a *nomen nudum* because no type species was explicitly designated by the author. *Bachmannia* Nani (in Szidat & Nani, 1951: 336, 337) was created for all sorgentinin species with no haemal expansions (which includes *O. incisa*), but is unavailable because the name is preoccupied (Dolgopol de Sáez, 1941). *Sorgentinia* Pianta de Risso & Risso (1953) was created for the species *O. incisa* and placed in its own subfamily. Though most recent studies use either *Odontesthes* or *Basilichthys,* some authors still recognize *Austromenidia* (De la Hoz & Vial, 1988; Zama, 1988; Pequeño, 1989), *Austroatherina* (Piacentino & Torno, 1987; Piacentino, 1990), *Cauque* (Klink & Eckmann, 1985; Pequeño, 1989; De la Hoz, 1994; De la Hoz & Aldunate, 1994), *Kronia* (Piacentino & Torno, 1981; Figueiredo & Menezes, 1978), and *Patagonina* (Gobbi, 1986; Ferriz, 1987). Campos (1984) presented a comprehensive review of the taxonomic history of sorgentinin genera and revalidated the status of most genera. Campos (1984) confirmed the presence of an upper jaw frenum on the type specimens of *B. microlepidotus,* thereby resolving the issue as to whether *Basilichthys* species have a protractile upper jaw.

METHODS

Specimens dissected and examined in this study -listed in Appendix 1- were either preserved in alcohol or cleared and stained for bone and cartilage following the technique of Taylor & Van Dyke (1985). The dissection procedure of cleared-and-stained specimens is that of Weitzman (1974), modified to dissect out the branchial arches prior to the suspensorium. Figures were produced using computer graphics programs. Anatomical figures were either drawn from a stereomicroscope with an attached camera lucida or scanned directly from an acknowledged source, and Bézier-curve transformed for manipulation in the graphics software environment. Distribution maps with locality data were produced using FISHMAP, version 1.6.3 (Buckup, 1993) and modified in a graphics program for shading of distribution ranges.

Characters were polarized by multiple-outgroup comparison (Farris, 1982; Maddison *et al.*, 1984; Clark & Curran, 1986). The selected Atherinopsinae outgroups are species that represent 'basal' lineages within Menidiinae (Chernoff, 1986b), Atherinoidei (Dyer & Chernoff, 1996), Beloniformes (Collette *et al.*, 1984), Cyprinodontiformes (Parenti, 1981), and Mugilidae (Appendix 1). Features shared by two or more terminal taxa only were included in the phylogenetic analysis; autapomorphies are included in the Systematics section only.

The information was compiled into a data matrix (Table 3) of 25 taxa and 123 characters, of which 106 are morphological features and 17 are enzymatic characters extracted from Crabtree (1987). These allozyme characters (107-123) in Table 3 are coded quantitatively and qualitatively (in parenthesis) as in Crabtree (1987:table 4). Each character is sequentially numbered in Table 3 based on its position on the body. The data were analyzed cladistically using PAUP, version 3.1.1 (Swofford, 1993) and HENNIG86, version 1.5 (Farris, 1988), with outgroup rooting and the exact search procedure. All character states were coded as integers, restricting the use of '0' for the shared primitive (plesiomorphic) state, the '?' for missing data or for polymorphic taxa with three or more states, and '-' for non-applicable coding. Taxa that exhibit two states are coded with both states in Table 3. Characters (Chs) 104, 105, and 106 represent a long list of traits extracted from the literature diagnostic of Atherinomorpha, Atheriniformes, and Menidiinae, respectively. Characters 104, 105, and 106 were assigned a weight of five, three, and seven, respectively, which represent the number of character states for which they are proxies. Distribution of characters on the cladograms was analyzed with PAUP, version 3.1.1 (Swofford, 1993) and MacClade, version 3.01 (Maddison & Maddison, 1992).

The data matrix contains 31 morphological multistate characters of which six are analyzed as non-additive (Chs 3, 35, 50, 53, 60, 97). The 17 allozyme characters (Chs 107-123) are also analyzed as non-additive. The 25 multistate characters analyzed as additive were ordered considering the derived states as nested within their relatively plesiomorphic states (Lipscomb, 1992). An additive multistate character is an internested set of synapomorphies, such that the derived state is inclusive of the plesiomorphic state(s) and reflects exactly the information in additive binary coding. Hence, the criterion of inclusiveness used for ordering multistate characters is equivalent to ordering multistate characters for the ontogenetic method, i.e., the more derived states must also exhibit the less derived traits.

Characters and their character states that uniquely or unambiguously support a particular node in all equally parsimonious trees are regarded as phylogenetically diagnostic. These derived features are considered diagnostic of the clades they support, even if the characters are reversed or independently evolved in other groups. Other features that are clearly derived but optimized ambiguously at a particular node are regarded as additional support to that clade. Diagnostic and additional-support characters are listed in Appendix 2. Additional-support characters are comprised of unambiguously optimized features in only one of the cladograms, or ambiguous characters in both trees that are optimized *a posteriori* according to the procedure described in Dyer & Chernoff (1996) and summarized in Appendix 3. Characters described are only those traits that are phylogenetically informative of relationships within Atherinopsidae, but exclusive of relationships within Menidiini, Membradini, and *Odontesthes.* Also described and discussed are some characters that are important because of their historical importance in the taxonomy of the group. Eight characters present in the data matrix (Chs 8, 14, 27, 69, 87, 92, 93, 103) and six derived states of multistate characters 23, 65, 68, 79, 91, and 99, pertain only to relationships among *Odontesthes* species. These characters are only defined as coded in the data matrix, and are described and discussed elsewhere (Dyer, 1993: 331-501).

Muscle nomenclature follows Winterbottom (1974). The last rays of the anal and second dorsal fin, are double and counted as one. The dorsal-scale row that is half-shared with the lateral band, is included in the count of dorsal scale rows at the tip of the pectoral fin. The gillraker at the angle of the upper and lower limbs of the first branchial arch is included in the gillraker counts of the lower limb.

RESULTS

Two equally most parsimonious trees were found (Length=403 steps, CI=0.62, RI=0.78), both of which share the topology of relationships among tribes shown in Figure 1. The two alternative hypotheses of relationships result when the enzymatic characters are coded quantitatively and differ in the generic relationships within Atherinopsini, which are mirror images of each other (Fig. 2). When the enzymatic characters (Chs 107-123) are coded qualitatively, a single most parsimonious tree is found (Length=409 steps, CI=0.63, RI=0.78) with the topology of Figure 2A. Six genera within Atherinopsinae are recognized. The classification proposed by White (1985, 1989) is unchanged despite the ambiguity of relationships among atherinopsinin genera (Table 2).

CHARACTERS

The characters are grouped into traditional anatomical units, ordered and numbered within these groups from anterior to posterior, dorsal to ventral. This ordering provides the numerical sequence for the one given in the data matrix (Table 3). Characters that are relevant only to relationships among atherinopsid tribes, atherinopsine genera, and *Basilichthys* species groups are treated here. The citations that follow most character headings indicate the original source or pertinent discussion for that character. The relatively primitive and derived states, their distribution and variability across taxa are described for each character. At the end of each character description, in parenthesis, is the description of character states as coded in the data matrix, and the consistency and retention indices (CI,

Table 3. Data matrix of 20 atherinopsine taxa and five outgroups in upper case. Characters are ordered according to their position on the body: Neurocranium and associated sensory canal bones (1-36); Jaws and associated ligaments (37-53); Suspensorium and associated ligaments (54-68); Branchial basket (70-74); Pectoral girdle and fins (75-79); Pelvic girdle and fins (80-81); Median fins (82-85); Axial skeleton (86-95); Scales (96-103); Atherinomorpha (104); Atheriniformes (105); Menidiinae (106); Enzymatic (107-123): quantitative coding and qualitative coding, the latter in parenthesis when they differ.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24
MUGILIDAE	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0
CYPRINODONTEA	0	0	0	0	0	0	1	–	0	0	0	0	0	0	–	0	0	0	0	0	0	1	–	0
ATHERINOIDEI	0	0	0	0	2	0	0	–	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
MENIDIINI	0	0	1	1	2	0	1	–	0	0	0	0	0	0	0	0	0	1	1	1	0	1	–	0
MEMBRADINI	0	0	1	1	2	0	1	–	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0
Atherinops	1	0	3	1	2	1	1	–	0	0	2	2	0	0	1	0	1	1	1	1	1	0	1	0
Colpichthys	1	0	3	1	2	1	1	–	0	0	2	2	0	0	1	0	1	1	1	1	1	0	1	0
Atherinopsis	1	0	3	1	2	1	1	–	0	0	2	2	0	0	1	1	1	1	1	0	1	0	1	0
Leuresthes	0	0	3	1	2	1	1	–	0	0	2	1	0	0	1	1	1	1	1	1	1	0	1	0
B. semotilus	1	1	2	0	1	1	0	1	0	1	2	1	1	0	1	0	1	1	1	1	0	1	–	0
B. "loa"	1	1	2	0	1	1	0	1	0	1	1	1	1	0	1	0	1	1	1	1	0	1	–	0
B. microlepidotus	1	0	2	0	1	1	0	1	0	1	1	1	1	0	1	0	1	1	1	1	0	1	–	0
O. incisa	1	0	0	0	2	1	0	1	1	1	2	2	0	0	0	0	1	1	1	1	0	0	2	1
O. nigricans	1	0	0	0	2	1	1	–	1	1	2	2	0	0	0	0	1	1	1	1	0	0	1	1
O. regia	1	0	0	0	2	1	0	2	1	1	2	2	0	1	0	0	1	1	1	1	0	0	2	1
O. gracilis	1	0	0	0	2	1	1	–	1	1	2	2	0	1	0	0	1	1	1	1	0	0	2	1
O. smitti	1	0	0	0	2	1	0	2	1	1	2	2	0	1	0	0	1	1	1	1	0	0	2	1
O. brevianalis	1	0	0	0	2	1	1	–	1	1	2	2	0	0	0	0	1	1	1	1	0	0	1	1
O. hatcheri	1	0	0	0	2	1	1	–	1	1	2	2	0	0	0	0	1	1	1	1	0	0	1	1
O. perugiae	1	0	0	0	2	1	0	2	1	1	2	?	0	0	0	0	1	1	1	0	0	0	1	1
O. bonariensis	1	0	0	0	2	1	0	1	1	1	2	2	0	0	0	0	1	1	1	1	0	0	1	1
O. retropinnis	1	0	0	0	2	1	1	–	1	1	2	2	0	0	0	0	1	1	1	1	0	0	2	1
O. argentinensis	1	0	0	0	2	1	0	2	1	1	2	2	0	0	0	0	1	1	1	1	0	0	1	1
O. humensis	1	0	0	0	2	1	1	–	1	1	2	2	0	0	0	0	1	1	1	1	0	0	2	1
O. platensis	1	0	0	0	2	1	0	2	1	1	2	2	0	0	0	0	1	1	1	1	0	0	1	1

	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50
MUGILIDAE	0	0	0	0	1	0	–	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0&1	0
CYPRINODONTEA	0	0	0	1	0	0	–	0	0	0	–	0	0&1	0	0	1	0	0	1	0	0	0	0	0	0	0
ATHERINOIDEI	0	0	0	0	0	0	–	–	0	0	–	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?
MENIDIINI	2	0	0	0	1	1	0	0	0	0	1	1	0	1	1	0	0	0	1	1	1	1	2	1	0	1
MEMBRADINI	2	0	0	0	1	1	0	0	0	0	1	1	0	1	1	0	0	0	1	1	1	1	2	1	0	0
Atherinops	1	1	0	2	1	1	1	0	0	1	2	2	1	0	1	1	0	0	1	1	1	1	2	0	1	2
Colpichthys	1	1	0	2	1	1	1	0	0	1	2	2	1	0	1	1	0	0	1	1	1	1	1	0	1	2
Atherinopsis	0	1	0	2	1	1	1	1	0	1	2	2	1	0	1	1	0	0	1	1	1	1	2	0	0	1
Leuresthes	0	1	0	2	1	1	1	0	0	1	2	2	0	1	1	0	0	0	1	1	1	1	2	0	0	1
B. semotilus	0	1	0	1	1	1	0	1	1	1	2	2	1	0	1	1	0	1	1	1	1	0	1	3	0	0
B. "loa"	0	1	0	1	1	1	0	1	1	1	2	2	1	0	1	1	0	1	1	1	1	0	1	3	0	0
B. microlepidotus	0	1	0	1	1	1	0	1	1	1	2	2	1	0	1	1	0	1	1	1	1	0	1	2	0	1
O. incisa	1	1	0	0	1	1	1	0	1	1	2	1	0	1	1	0	1	0	1	1	1	1	2	1	0	?
O. nigricans	1	1	0	0	1	1	1	0	1	1	2	0	0	1	1	0	1	0	1	1	1	1	2	1	0	1
O. regia	1	1	1	0	1	1	1	0	1	1	2	1	0	1	1	0	1	0	1	1	1	1	2	1	0	2
O. gracilis	1	1	1	0	1	1	1	0	1	1	2	1	0	1	1	0	1	0	1	1	1	1	2	1	0	2
O. smitti	1	1	0	0	1	1	1	0	1	1	2	1	0	1	1	0	1	0	1	1	1	1	2	1	0	2
O. brevianalis	1	1	1	0	1	1	1	0	1	1	2	1	0	1	1	0	1	0	1	1	1	1	2	1	0	1
O. hatcheri	1	1	0	0	1	1	1	0	1	1	2	1	0	1	1	0	1	0	1	1	1	1	2	1	0	0
O. perugiae	1	1	0	0	1	1	1	0	1	1	2	1	0	1	1	0	1	0	1	1	1	1	2	1	0	2
O. bonariensis	1	1	0	0	1	1	1	0	1	1	2	1	0	1	1	0	1	0	1	1	1	1	2	1	0	1
O. retropinnis	1	1	0	0	1	1	1	0	1	1	2	1	0	1	1	0	1	0	1	1	1	1	2	1	0	2
O. argentinensis	1	1	0	0	1	1	1	0	1	1	2	1	0	1	1	0	1	0	1	1	1	1	2	1	0	1
O. humensis	1	1	0	0	1	1	1	0	1	1	2	0	0	1	1	0	1	0	1	1	1	1	2	1	0	1
O. platensis	1	1	0	0	1	1	1	0	1	1	2	1	0	1	1	0	1	0	1	1	1	1	2	1	0	1

Table 3. (cont.)

	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73	74
MUGILIDAE	0	0	0	1	0	1	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0
CYPRINODONTEA	0	0	0	0	?	0	?	1	1	0	0	0	?	0	0	0	0	2	0	2	0	0	0&1	0
ATHERINOIDEI	0	0	0&1	0	0	0	0	0	0	?	0	0	?	0	0	0	0	2	0	0	0	0	0&1	0
MENIDIINI	0	0	1	1	1	0	1	0	1	0	1	0	0	0	0	0	1	0&2	0	0	0	0	1	0
MEMBRADINI	0	0	1	1	1	0	1	0	0	1	1	0	0	0	0	0	1	0&2	0	2	0	0	1	0
Atherinops	0	0	0	2	1	0	0	0	0	0	1	0	0	0	0	0	1	2	0	1	1	1	0	1
Colpichthys	0	0	0	2	1	0	0	0	0	2	2	0	0	0	0	0	1	2	0	1	1	1	0	0
Atherinopsis	0	0	0	2	1	0	1	0	0	0	1	0	0	1	0	0	1	2	0	1	1	2	0	1
Leuresthes	0	0	2	2	1	0	1	0	0	1	2	0	0	0	0	0	1	2	0	1	1	2	0	0
B. semotilus	1	1	0	3	0	1	0	1	1	0	2	1	1	1	0	0	1	0	0	0	0	0	0	0
B. "loa"	1	1	0	3	0	1	0	1	1	0	2	1	1	1	0	0	1	0	0	0	0	0	0	0
B. microlepidotus	1	1	0	3	0	1	0	0&1	1	0	2	1	0	1	0	0	1	0	0	0	0	0	0	0
O. incisa	0	0	2	2	1	1	1	0	0	1	2	0	0	0	0	0	1	1	1	0	0	0	0	0
O. nigricans	0	0	2	2	1	1	1	1	0	1	2	1	0	1	2	1	1	1	1	0	0	0	0	0
O. regia	0	0	2	2	1	1	1	0	0	1	2	0	0	1	2	1	1	1	1	0	0	0	0	0
O. gracilis	0	0	2	2	1	1	1	0	0	1	2	0	0	1	2	1	1	1	1	0	0	0	0	0
O. smitti	0	0	2	2	1	1	1	0	0	1	2	0	0	1	2	1	1	1	1	0	0	0	0	0
O. brevianalis	0	0	2	2	1	1	1	0	1	1	2	0	0	0	1	1	1	1	1	0	0	0	0	0
O. hatcheri	0	0	2	2	1	1	1	0&1	1	0	2	0	0	0	1	1	0	2	0	0	0	0	0	0
O. perugiae	0	0	2	2	1	1	?	0	0	1	2	0	0	0	1	0	0	2	0	0	0	0	0	0
O. bonariensis	0	0	2	2	1	1	1	0	0	1	2	0	0	0	2	1	1	1	0	0	0	0	0	0
O. retropinnis	0	0	2	2	1	1	1	0	0	1	2	0	0	0	1	1	0	2	0	0	0	0	0	0
O. argentinensis	0	0	2	2	1	1	1	0	0	1	2	0	0	0	2	1	1	1	1	0	0	0	0	0
O. humensis	0	0	2	2	1	1	0	0	1	1	2	0	0	0	2	1	1	2	0	0	0	0	0	0
O. platensis	0	0	2	2	1	1	1	0	0	1	2	0	0	0	2	1	1	1	1	0	0	0	0	0

	75	76	77	78	79	80	81	82	83	84	85	86	87	88	89	90	91	92	93	94	95	96	97	98	99	100
MUGILIDAE	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	–	–	0	0	0	0	0	0	1
CYPRINODONTEA	0	0	0	0	0	0	1	–	–	–	–	0	0	0	0	0	0	–	–	0	0	0	?	–	0	0
ATHERINOIDEI	0	0	0	0	0	1	1	0&1	0	0	?	0	0	0	0	0	0	–	–	0	0	0	?	–	0	0
MENIDIINI	1	1	1	1	1	1	1	1	0	1	1	0	0	1	0	0	0	–	–	0	1	0	2	0	0	0
MEMBRADINI	1	1	1	1	1	1	1	1	0	1	1	0	0	1	0	0	0	–	–	0	1	0	2	0	0	0
Atherinops	0	1	1	1	1	1	2	1	0	2	0	0	0	1	1	1	0	–	–	0	0	0	2	0	0	0
Colpichthys	1	1	1	1	1	1	2	0&1	0	1	1	0	0	1	0&1	1	0	–	–	0	0	0	0	0	1	0
Atherinopsis	0	1	1	1	1	1	2	0	0	2	0	0	0	1	1	1	0	–	–	0	0	0	0	0	1	0
Leuresthes	0	1	1	1	1	0	1	1	0	2	0	0	0	1	1	1	0	–	–	0	0	0	0	0	1	1
B. semotilus	0	1	1	1	1	1	2	0	1	1	1	2	0	1	1	0	2	0	0	0	2	2	1	1	0	1
B. "loa"	0	1	1	1	1	1	2	0	1	1	1	2	0	1	1	0	2	0	0	0	2	2	1	1	0	0
B. microlepidotus	0	1	1	1	1	1	2	0	1	1	1	2	0	1	1	0	2	0	0	0	2	1	1	1	0	0
O. incisa	1	1	1	1	2	1	2	1	0	2	1	0	0	0	0	0	0	–	–	0	0	0	0	0	1	0
O. nigricans	1	1	1	1	1	1	2	0	0	2	0	0	0	0	0	0	0	–	–	0	0	0	1	1	2	0
O. regia	1	1	1	1	2	1	2	0	0	2	0	0	0	0	1	0	4	0	1	0	0	0	1	0	2	0
O. gracilis	1	1	1	1	2	1	2	0	0	2	0	0	0	0	1	0	4	1	1	0	0	0	0	0	2	0
O. smitti	1	1	1	1	2	1	2	0	0	2	0	0	0	0	1	0	4	1	1	0	0	0	1	0	2	0
O. brevianalis	0	1	1	1	?	0	2	0	0	1	?	1	0	1	1	0	3	1	1	0	?	0	1	1	2	0
O. hatcheri	0	1	1	1	1	1	2	0	0	1	1	1	0	1	1	0	1	0	0	1	1	0	0	0	1	0
O. perugiae	0	1	1	1	2	1	2	1	0	?	0	1	1	1	1	0	3	0	0	1	1	0	2	0	0	1
O. bonariensis	1	1	1	1	2	1	2	1	0	?	0	1	1	1	1	0	3	0	0	1	0	0	0	0	0	1
O. retropinnis	1	1	1	1	2	1	2	1	0	?	0	1	1	1	1	0	1	0	0	1	1	0	2	0	0	1
O. argentinensis	1	1	1	1	2	1	2	1	0	2	0	?	1	1	1	0	3	0	1	0	0	0	1	0	1	1
O. humensis	0	1	1	1	2	1	2	0	0	1	1	1	1	1	1	0	3	0	0	1	1	0	0	1	0	1
O. platensis	1	1	1	1	2	1	2	0	0	2	0	1	0	0	1	0	3	1	1	0	0	0	1	0	1	0

Table 3. (cont.)

	101	102	103	104	105	106	107	108	109	110	111	112	113	114	115	116	117	118	119	120	121	122	123
MUGILIDAE	1	0	0	0	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
CYPRINODONTEA	0	0	0	1	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
ATHERINOIDEI	0	0	0	1	1	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
MENIDIINI	0	0	0	1	1	1	1&4	1	3&4	5&6	5(7)	4&5	5&6	1&6	4(5)	8(9)	3	8&9	1	5(7)	7&8(8&9)	7&8	5&6
MEMBRADINI	0	0	0	1	1	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Atherinops	1	0	0	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Colpichthys	0	0	0	1	1	0	1&2	1	1&3	2	1(1&4)	1	2	5	1	5(5&6)	1	4&5	1	3(4&5)	4(5&6)	4&5	3
Atherinopsis	1	1	0	1	1	0	1	1	2	1	2	1	1	2	1	2	1	2	2	2	2	2	2
Leuresthes	1	0	0	1	1	0	1	1	2	1	3	1	1	3&4	2(2&3)	3&4	1	3	2&3	2(3)	1&3(3&4)	3	3
B. semotilus	1	1	0	1	1	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
B. "loa"	0	1	0	1	1	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
B. microlepidotus	0	1	0	1	1	0	3	2	4	3	4(5)	2	3	6	3(4)	6(7)	1	6	2	4(6)	5(6)	6	4
O. incisa	0	0	2	1	1	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
O. nigricans	0	1	2	1	1	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
O. regia	0	1	0	1	1	0	3	2	5	4	3(6)	3	4	7	3(4)	7(8)	2	7	4	4(6)	6(7)	6	4
O. gracilis	0	1	0	1	1	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
O. smitti	0	1	0	1	1	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
O. brevianalis	1	1	2	1	1	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
O. hatcheri	1	1	0	1	1	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
O. perugiae	1	0	0	1	1	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
O. bonariensis	1	0	0	1	1	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
O. retropinnis	1	0	0	1	1	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
O. argentinensis	1	0	1	1	1	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
O. humensis	1	0	0	1	1	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
O. platensis	0	1	0	1	1	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?

RI) for that character. When both indices have equal values only one figure is shown. Two sets of indices reflect the different values in each most-parsimonious tree. Multistate characters analyzed as non-additive are denoted with 'n-add', and those analyzed as additive are denoted with 'add'. A certain amount of morphologic variation is described that is not coded in the data matrix; this information is placed below the coding definitions that are in parenthesis.

Neurocranium and associated sensory canal bones

1 *Vomer dorsomedial ridge*.– The median process of the vomer, when present, has a rounded dorsal face in atheriniforms and outgroups. A derived condition of atherinopsines is presence of a sharp ridge on the dorsal midline of the median process of the vomer (Fig. 3B, 3C, 3D, 3E). This condition is present in all atherinopsines except *Leuresthes*. **(0=median process of vomer rounded; 1=median process with dorsal ridge; 0.50, 0.83)**

2 *Vomer dorsal spine*.– The plesiomorphic condition for atherinomorphs is absence of a posterior projection of the vomerine dorsomedial ridge. The *Basilichthys semotilus* species group has a unique condition in which the dorsomedial ridge of the vomer projects posterodorsally in the form of a spine, which does not contact the mesethmoid (Fig. 3D). **(0=no vomerine spine; 1=vomerine dorsomedial spine present; 1.00)**

3 *Vomerine posterodorsal lamina* (White, 1985).– A relatively low anterior face of the vomer -between the lateral condyles- is the plesiomorphic condition for atherinomorphs. A derived condition of menidiines is a broad, median lamina that projects posterodorsally and articulates with the mesethmoid (Fig. 3A; Chernoff, 1986b). In Atherinopsini the anterior face of the vomer has a pair of parasagittal laminae that project posterodorsally over the ethmoid cartilage and contact the mesethmoid (Fig. 3B; White, 1985). In *Basilichthys*, the anterior face of the vomer is projected posterodorsally between the dorsomedial ridge and lateral condyles, and houses an anteroventral portion of the ethmoid cartilage. The dorsal laminae are far more developed in atherinopsinins than in *Basilichthys* (Fig. 3C, 3D). The vomer in *Odontesthes* has a very narrow anterior face, hardly overlapping the anteroventral margin of the ethmoid cartilage, and has no posterodorsal laminar projections (Fig. 3E). **(0=no posterodorsal lamina on the anterior face of the vomer; 1=presence of a single, median, and wide posterodorsal laminar process; 2=presence of two parasagittal posterodorsal laminae; 3=presence of two well-developed parasagittal posterodorsal laminae; 1.00; n-add)**

4 *Vomerine anterior shelf*.– The anterior face of the vomer is narrow in atherinopsid outgroups (Dyer & Chernoff, 1996; Parenti, 1981). A derived condition present in Menidiinae and Atherinopsini is a dorsoventrally flattened extension of the anterior face of the vomer into a shelf-like elongation of the rostral region (Fig. 3A, 3B). This condition is not present in Sorgentinini (Fig. 3C, 3D, 3E). **(0=vomer anterior face narrow; 1=vomer with anterior shelf; 0.50, 0.80)**

5 *Vomer ventral face curvature* (Dyer & Chernoff, 1996).– The lateral condyles of the vomer are level with the median ventral line in atheriniform outgroups and the ventral face of the vomer is flat. In all atheriniforms examined the vomer is arched ventrally such that the lateral condyles are ventral relative to the median ventral line (Dyer & Chernoff, 1996). This ventral arch of the vomer results in a concave ventral face in transverse section (Fig. 3, frontal views). In *Basilichthys* the vomer is arched

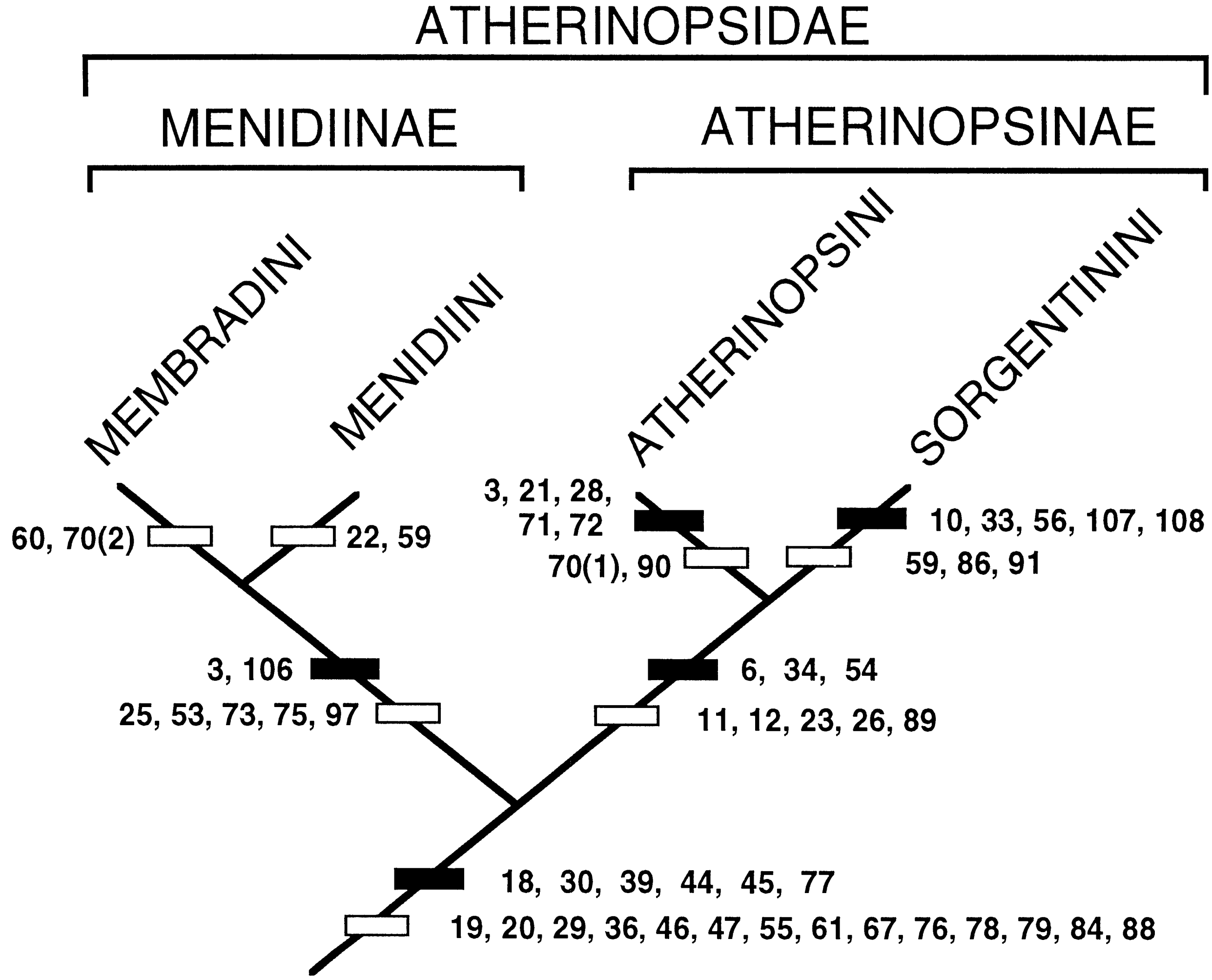

Fig. 1. Relationships among atherinopsid tribes (L=403, CI=0.62, RI=0.78). Diagnostic characters, unambiguously derived traits at that node in both equally parsimonious trees, are in bold. Unique characters within atheriniforms are opposite black bars; and homoplasious characters independently derived elsewhere in atheriniforms are opposite white bars. Diagnostic characters and additional support is listed in Appendix 2.

to a lesser extent and, consequently, the anteroventral face of the vomer is relatively flattened frontally (Fig. 3C, 3D). **(0=vomer ventral face flat; 1=vomer ventral face slightly concave; 2=vomer ventral face strongly concave; 0.67, 0.86; add)**

6 *Ethmoid cartilage folded ventral of vomer midline.*– The ethmoid cartilage block is dorsal to all portions of the vomer in atheriniforms and outgroups. A derived condition found in atherinopsines is for the lateral face of the ethmoid cartilage, that which articulates with the palatine, to be folded with the ventral arch of the vomer (Ch. 5) to a position below the vomerine midline (Fig. 3). **(0=ethmoid cartilage dorsal of vomer midline; 1=ethmoid cartilage folded ventral of vomer midline; 1.00)**

7 *Vomerine teeth.*– Vomerine teeth in atherinomorph outgroups are in a U or V-shaped band along the anteroventral border of the bone. In atherinoids, the plesiomorphic condition is found in bedotiines, melanotaeniines, and some atherinids, but vomerine teeth are also found in two separate patches under the lateral condyles (e.g., *Iso*, *Atherion*), or absent (e.g., Pseudomugilinae, Phallostethidae). Vomerine teeth are absent in Cyprinodontea except aplocheiloids (Parenti, 1981: 401), Atherinopsini (Fig. 3B), and in Menidiinae except for *Atherinella serrivomer* (Chernoff, 1986a), *Chirostoma humboldtianum*, *Ch. estor estor*, and *Ch. bartoni* (Barbour, 1973). In sorgentinins, presence of teeth is variable within and among species, except in *Odontesthes hatcheri*, *O. humensis*, *O. retropinnis*, *O. nigricans*, *O. gracilis*, and the subgenus *Cauque* (Fig. 3D) which consistently lack teeth. *Basilichthys* usually has a single, medial patch (Fig. 3D). **(0=vomerine teeth present; 1=vomerine teeth absent; 0.13, 0.42)**

8 *Number of vomerine tooth patches.*– **(0=vomerine teeth in a band; 1=single median vomerine tooth patch; 2=three vomerine tooth patches; 0.50, 0.60; add)**

9 *Mesethmoid* (White, 1985; Chernoff, 1986b).– The plesiomorphic form of the atherinomorph dorsal mesethmoid (Tigano & Parenti, 1988) is a flat or slightly convex disk-like bone (Chernoff, 1986b). The size of the mesethmoid, its shape,

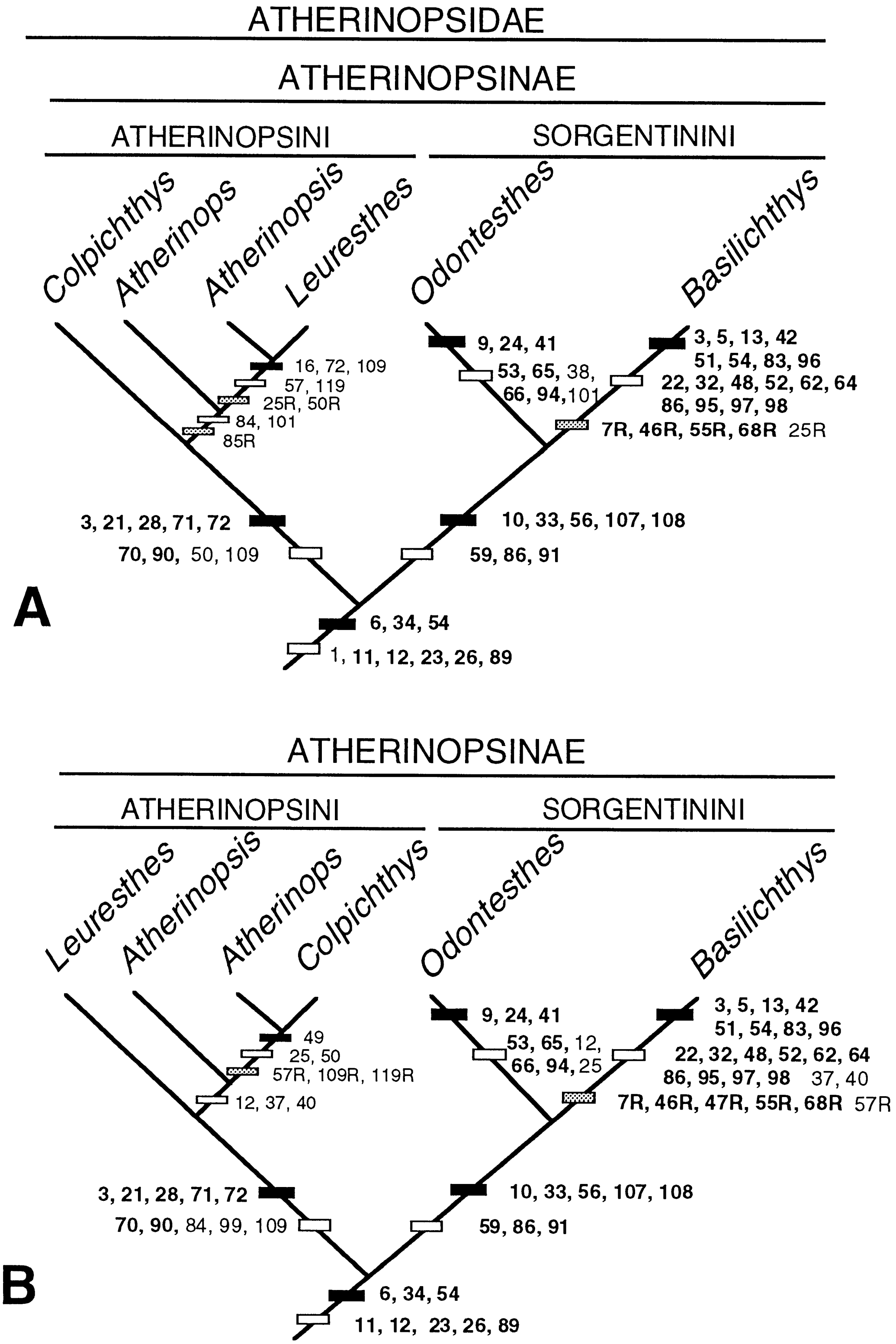

Fig. 2. Relationships among atherinopsine genera (L=403, CI=0.62, RI=0.78). Diagnostic characters, unambiguously derived traits at that node in both equally parsimonious trees, are in bold. Unique characters within atheriniforms are opposite black bars; reversed characters (with an "R") are opposite grey bars; and homoplasious characters independently derived elsewhere in atheriniforms are opposite white bars. Diagnostic characters and additional support is listed in Appendix 2; A, *Colpichthys* is sister to *Atherinops*, *Atherinopsis*, and *Leuresthes*; B, *Leuresthes* is sister to *Atherinopsis*, *Atherinops*, and *Colpichthys*.

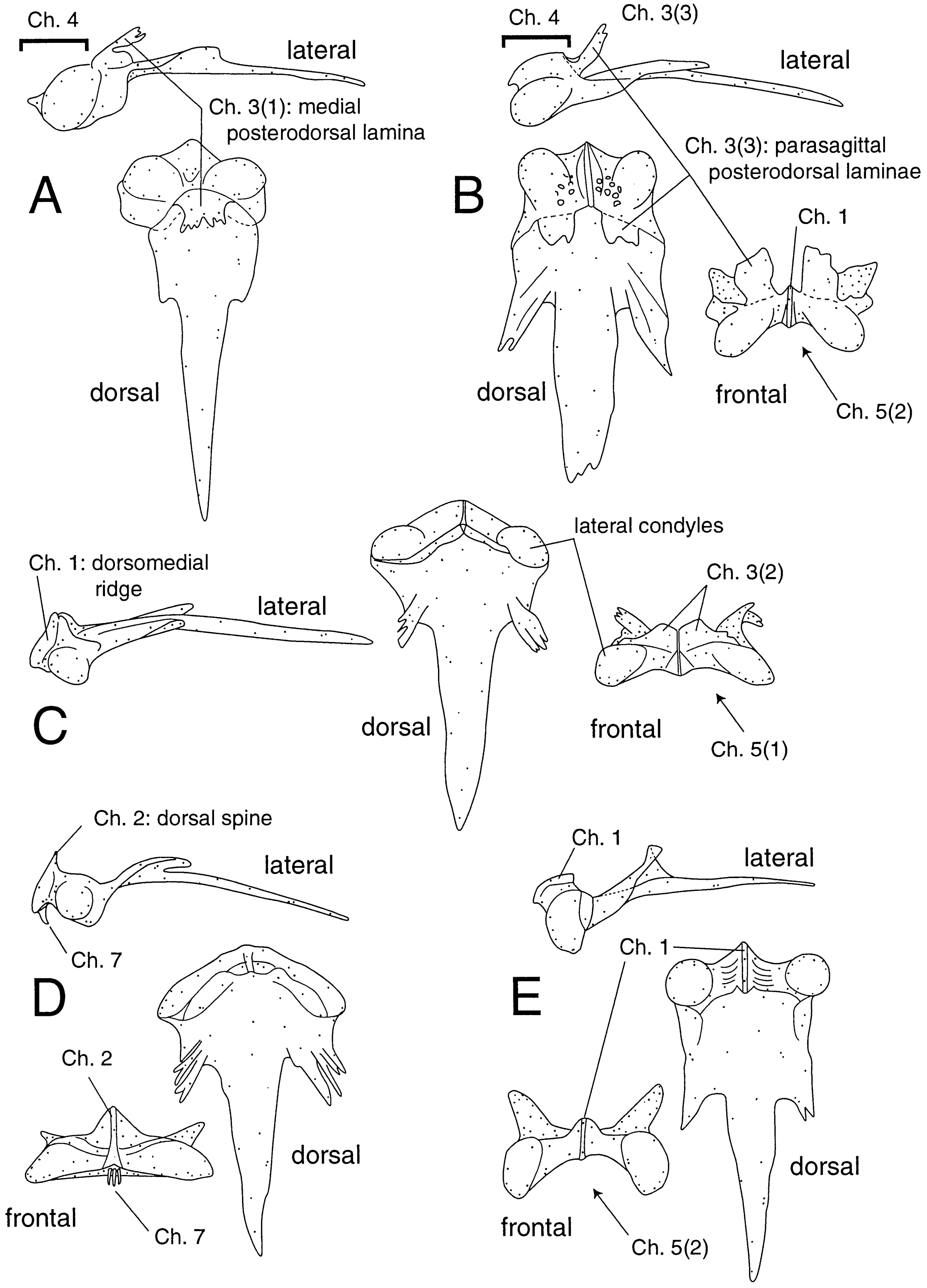

Fig. 3. Dorsal, lateral, and frontal views of the vomer; A, *Menidia beryllina* (UMMZ 107098); B, *Atherinops affinis* (UMMZ 232001); C, *Basilichthys australis* (UMMZ 215508); D, *Basilichthys semotilus* (UMMZ 218050, 215520); E, *Odontesthes brevianalis* (UMMZ 215459).

and which bones it contacts is quite variable within atherinomorphs (Dyer & Chernoff, 1996). Absence of a mesethmoid is a derived condition of *Odontesthes* (Fig. 4; White, 1985; De la Hoz & Vial, 1988). A mesethmoid is also lacking in the atherinoids *Notocheirus*, *Craterocephalus*, and *Pseudomugil* (Dyer & Chernoff, 1996). **(0=mesethmoid present; 1=mesethmoid absent; 1.00)**

The mesethmoid is morphologically diverse in the membradins; either convex, concave, or step-shaped, with or without ridges, and contacting the dorsal lamina of the vomer (Chernoff, 1986b). In atherinopsines the mesethmoid is convex, oval to squarish, with anterolateral and posterolateral (endochondral) processes in larger specimens. In atherinopsinins the anterolateral processes contact the paired dorsal laminae of the vomer (Ch. 3) and the posterolateral processes are overlapped by the frontal. The mesethmoid is isolated in *Basilichthys* (Fig. 5; De la Hoz & Tosti-Croce, 1981: fig. 2) as in the menidiines *Atherinella balsana* and *A. callida* (Chernoff, 1986b), and the posterolateral processes are slighlty overlapped by the frontal in larger specimens.

10 Ethmomaxillary ligament - ethmoid attachment.– The posterior end of the ethmomaxillary ligament is primitively attached to the mesethmoid in atheriniforms. A derived condition of sorgentinins is the posterior attachment to the ethmoid cartilage (Figs 4, 5). A very short ligament between the maxilla and the ethmoid cartilage is also present in *Notocheirus*. **(0=ethmomaxillary ligament attached to mesethmoid; 1=ethmomaxillary ligament attached to ethmoid cartilage; 1.00)**

11 Nasal ventral process (White, 1985).– The anterior end of the nasal bone is curved ventrally and attached by a short ligament to the anterior end of the lacrimal, with both nasal and lacrimal tips attached by a wide ligament to the head of the maxilla (Dyer & Chernoff, 1996). In atherinopsines, *Menidia*, and *Chirostoma*, the anterior end of the nasal is a laminar process that projects ventrally to the anterior end of the subnasal shelf of the lacrimal and forms an anterior bony wall to the olfactory sac (Fig. 6). In atherinopsines except for the *Basilichthys microlepidotus* species group and an undescribed species of *Basilichthys* from the Río Loa, the ventral end of the nasal is pointed and overlaps the subnasal shelf of the lacrimal (Fig. 6A). **(0=no nasal ventral process; 1=nasal ventral process present; 2=nasal ventral process present and pointed, overlapping the lacrimal subnasal shelf; 0.60, 0.82; add)**

12 Nasal sensory canal.– The plesiomorphic condition of the nasal sensory canal is for it to be attached to the nasal bone along its entire length. In *Leuresthes* and *Basilichthys* the anterior portion of the sensory canal is slightly detached (Fig. 6B, 6C). In atherinopsines other than *Basilichthys* and *Leuresthes*, a greater portion of the anterior sensory canal is detached from the nasal bone and directed anteriorly (Fig. 6A). **(0=nasal sensory canal fully attached to nasal bone; 1=nasal sensory canal detached anteriorly; 2=nasal sensory canal greatly detached anteriorly; ?=polymorphic; 0.50, 0.86 / 0.67, 0.93; add)**

13 Lacrimal condyle position.– The preorbital wing of the lateral ethmoid articulates along its lateral ridge and cartilaginous condyle with the lacrimal bone (Figs 4, 5). The plesiomorphic condition is for the lacrimal condyle of the lateral ethmoid to extend to the ventral edge of the preorbital wing's lateral ridge (Figs 7, 8). A derived condition found in *Basilichthys* is for the lacrimal condyle not to reach the ventral edge of the lateral ridge (Fig. 9). **(0=lacrimal condyle of lateral ethmoid extended to ventral edge of lateral ridge; 1=lacrimal condyle of lateral ethmoid does not reach the ventral edge of the lateral ridge; 1.00)**

14 Lacrimal condyle shape.– **(0=lacrimal condyle of lateral ethmoid oval in shape; 1=lacrimal condyle of lateral ethmoid enlarged and rounded in shape; 1.00)**

15 Lateral ethmoid ventral condyle (White, 1985).– In atheriniforms and mugilids the ventral ridge of the lateral ethmoid's preorbital wing has a medial cartilaginous condyle (Figs 7, 8) that articulates with the palatoquadrate cartilage posterior to the palatine. Atherinopsini and *Basilichthys* have a derived condition in that the cartilaginous condyle is ossified and displaced anteriorly from the ventral ridge and directed anteroventrally to the palatoquadrate cartilage (Fig. 9; bony knob of White, 1985: figs 7, 19). The bony knob is larger in atherinopsinins than in *Basilichthys.* **(0=lateral ethmoid ventral condyle cartilaginous; 1=lateral ethmoid ventral condyle ossified; 0.50, 0.83)**

16 Lateral ethmoid - parasphenoid contact (White, 1985).– The lateral ethmoid does not contact the parasphenoid bone in mugilids and atherinomorphs (Figs 7, 8, 9). In *Leuresthes* and *Atherinopsis* the lateral ethmoid extends to the parasphenoid as a posteromedial process (White, 1985a: fig. 19). **(0=lateral ethmoid separated from parasphenoid; 1=lateral ethmoid widely in contact with parasphenoid; 1.00 / 0.50, 0.00)**

17 Supraorbital sensory canal pores (White, 1985).– The pattern of sensory canals of the head in atherinomorphs was first studied by Gosline (1949) in cyprinodontiforms. Parenti (1981) agreed with Gosline (1949) in that seven supraorbital pores is the most generalized pattern for cyprinodontiforms. White (1985) assumed the generalized cyprinodontiform pattern to be primitive and proposed five frontal pores to be the plesiomorphic condition for atherinopsids. The seven supraorbital pores in cyprinodontiforms are restricted to the nasal and frontal bones, whereas in atherinopsids three canal pores are present on the pterotic. White's numbering system for the supraorbital pores, though acknowledged so, is not exactly that of Gosline's in that pore one of White is equivalent to pore two of Gosline. Because of this mismatch of pores and numbers, White counted a total of seven supraorbital plus pterotic pores when in fact atherinopsids have eight pores on the head (six supraorbital plus two pterotic), not including the extrascapular and postemporal pores (Fig. 10). White (1985) counted the number of pores on the frontal bone rather than the sensory canal pores in the skin and concluded that menidiines had a derived condition of only four frontal pores. Menidiines, however, have five skin pores over the frontal, but the anterior two are not separated by a bony bridge (Fig. 10C). The dorsal pores of the head have been numbered according to Gosline's (1949) original scheme. The orientation of the pores and their bony association has been included as a way to ascertain homologous

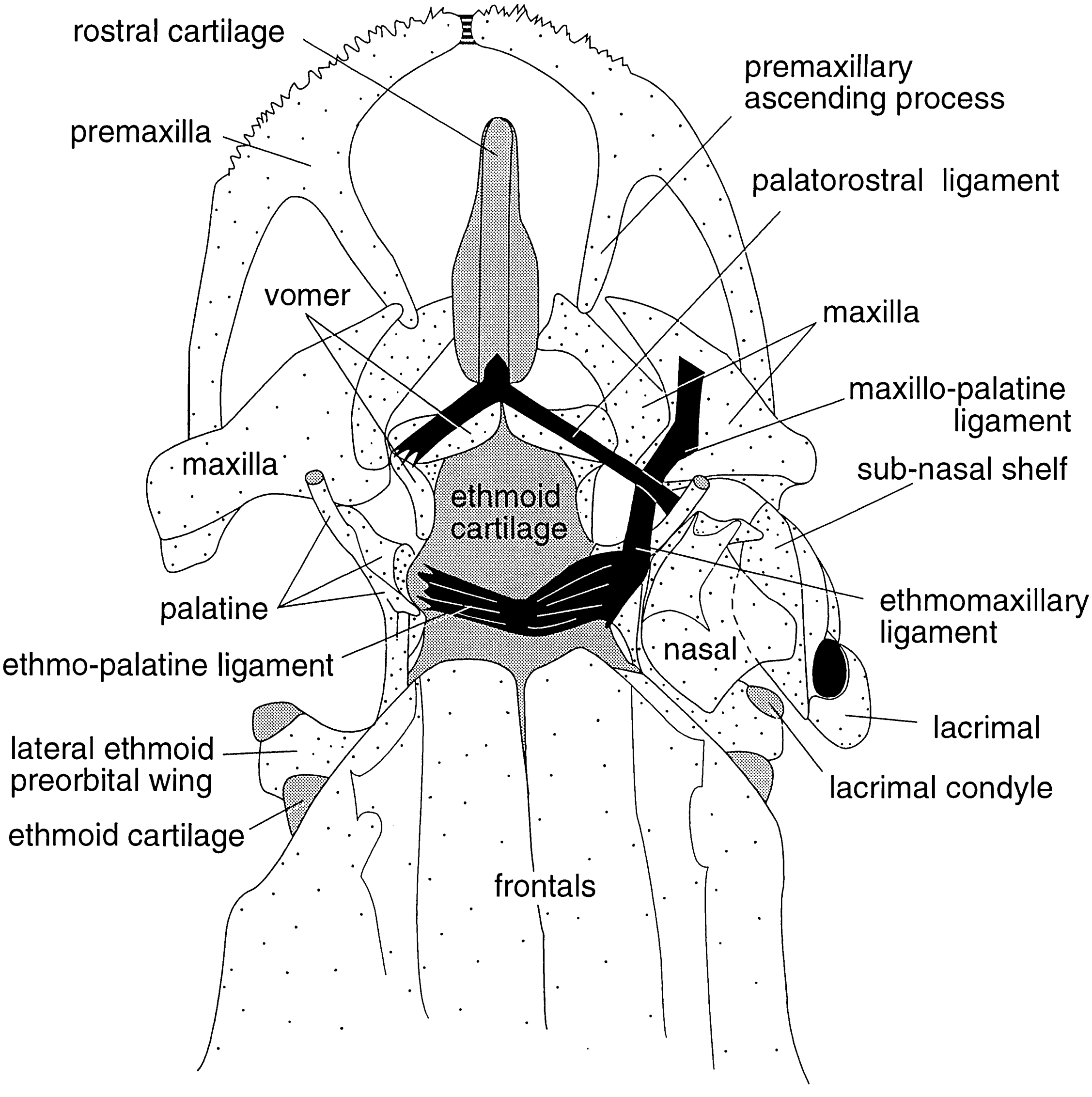

Fig. 4. Dorsal view of the ethmoid region of *Odontesthes retropinnis* (UMMZ 218796). Left lacrimal and nasal bones removed.

pores across taxa. The plesiomorphic condition for atheriniforms as inferred from the pattern present in mugilids (Fig. 10A) and cyprinodontiforms is as follows: pore two is connected to the nasal canal, pore six is connected to the dermosphenotic and pterotic canals, and pore eight is connected to the temporal-bone canals. Frontal pores three, five, and six are directed laterally, and pore four is directed medially. The above pattern of frontal pores is present also in menidiines (Fig. 10C). A relatively derived pattern present in Atherinopsinae (Fig. 10D), notocheirids, and melanotaeniids, is pore five directed posteromedially rather than anterolaterally (Fig. 10A, 10B, 10C). **(0=pore 5 directed anterolaterally; 1=pore 5 directed posteromedially; 0.50, 0.75)**

In mugilids (Fig. 10A), pore five is displaced anteriorly relative to atherinomorphs and the preopercular canal is connected to pore eight rather than to pore seven as in atheriniforms (Fig. 10B, 10C, 10D).

18 Sphenotic postorbital process (Chernoff, 1986b).– A small and narrow postorbital process with only the levator arcus palatini (LAP) muscle attached, is the plesiomorphic condition found in atherinoids, Cyprinodontea, and mugilids. The derived condition of atherinopsids is a wide based postorbital process (Figs 7, 8, 9) with an enlarged posterodorsal face to which the dilator operculi (DO) muscle is attached. In atherinopsids, the LAP muscle is attached to the anteroventral face only of the postorbital process. **(0=postorbital process small and narrow; 1=postorbital process wide; 1.00)**

19 Dermosphenotic articulation.– The plesiomorphic condition of atheriniforms is for the dermosphenotic to be articulated dorsally to the frontal and along its entire posterior length with the anterior face of the postorbital process. The derived condition found in atherinopsids is for the dermosphenotic to be connected dorsally to the frontal or frontal-sphenotic junction

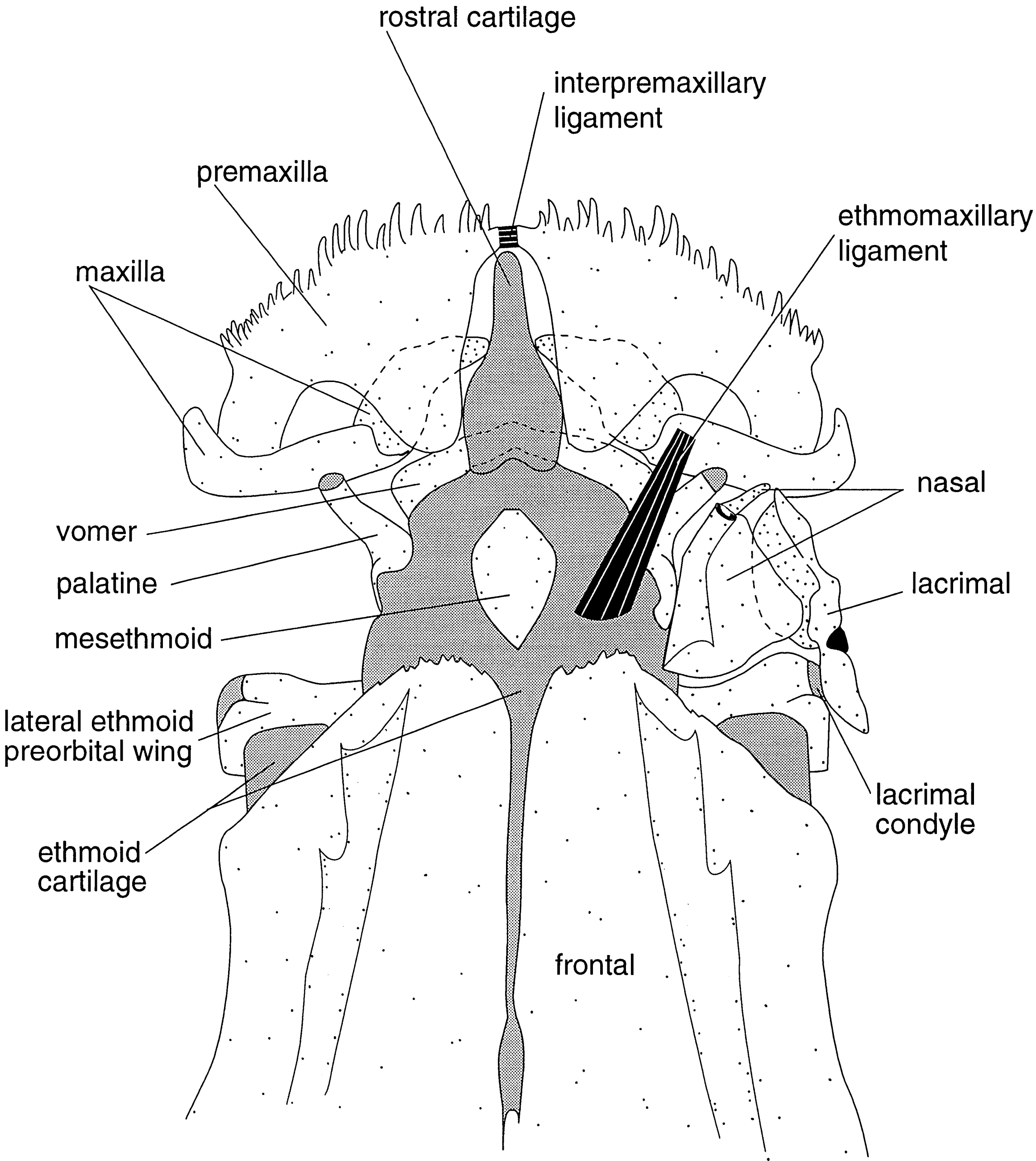

Fig. 5. Dorsal view of the ethmoid region of *Basilichthys* sp. (UMMZ 215520). Left lacrimal and nasal bones removed.

by fibrous skin only, detached from the postorbital process (Figs 8, 11; De la Hoz & Tosti-Croce, 1981). In mugilids the dermosphenotic is also detached from the postorbital process and connected dorsally to the frontal only by thickened skin. **(0=dermosphenotic articulated to postorbital process and frontal; 1=dermosphenotic not articulated to postorbital process, connected dorsally to frontal or sphenotic-frontal articulation; 0.50)**

The menidiine *Melanorhinus* has another derived condition in which the dermosphenotic is entirely articulated to the anterior face of the postorbital process, not to the frontal.

20 Dermosphenotic sensory canal.– The plesiomorphic condition present in Cyprinodontea and atherinoids is an open dermosphenotic sensory canal which is not fully enclosed by bone. An enclosed bony tube is present in mugilids, in menidiines except for *Atherinella*, and in atherinopsines (Fig. 12) except for *Atherinopsis* and *Odontesthes perugiae*. **(0=dermosphenotic sensory canal open; 1=dermosphenotic sensory canal enclosed; 0.25)**

21 Dermosphenotic pores.– The dermosphenotic sensory canal is plesiomorphically connected to the supraorbital canal dor-

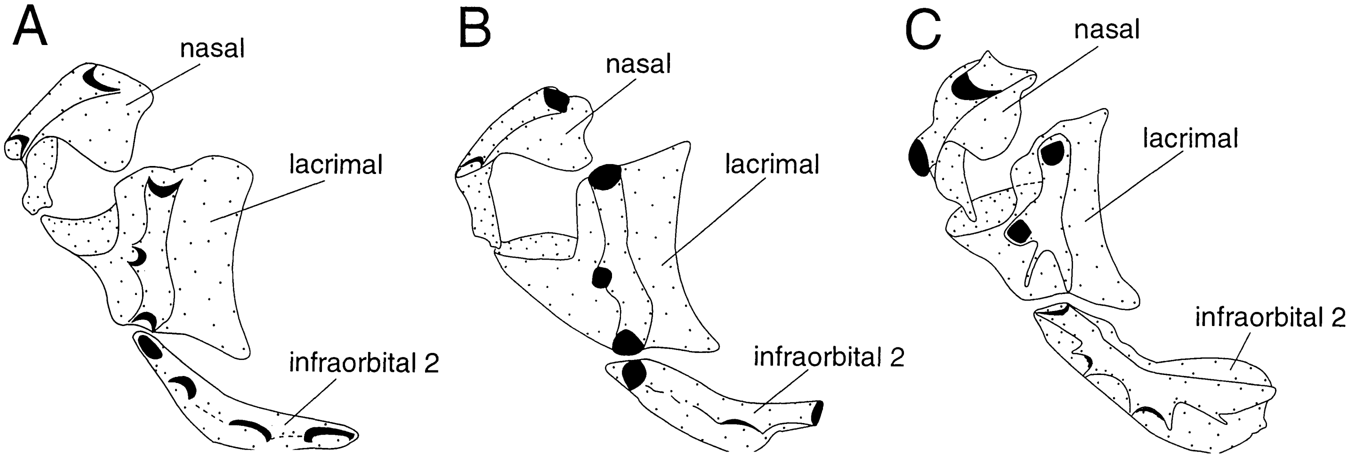

Fig. 6. Anterior infraorbitals and nasal bones; A, *Odontesthes retropinnis* (UMMZ 231950); B, *Basilichthys semotilus* (UMMZ 217989); C, *Basilichthys australis* (UMMZ 215507).

sally (Ch. 17: pore 5) and has a single pore ventrally (Figs 11, 12B, 12C). A derived condition unique to Atherinopsini is presence of an additional pore (Fig. 12A). **(0=dermosphenotic with two pores; 1=dermosphenotic with three pores; 1.00)**

22 *Dermosphenotic medial flange.*– Presence of a medial flange along the internal face of the dermosphenotic bone is a plesiomorphic condition for atheriniforms (Fig. 12A). *Basilichthys*, Menidiini, and Cyprinodontea have the derived condition of lacking a medial flange, except that in *Basilichthys* the flange is reduced to the extent of the tubular sensory nerve canal (Fig. 12B). **(0=medial flange present; 1=medial flange absent; 0.33, 0.50)**

23 *Dermosphenotic postocular shelf.*– Presence of a narrow medial flange along the internal face of the dermosphenotic is the plesiomorphic condition for atheriniforms. A well developed medial flange, or postocular shelf, at the dorsal half of the bone is a derived condition of atherinopsines except for *Basilichthys* (Fig. 12A, 12C). **(0=medial flange narrow; 1=postocular shelf on dorsal half of dermosphenotic; 2=postocular shelf along entire length of dermosphenotic [Dyer, 1993: 343]; 0.40, 0.63; add)**

24 *Trigeminal foramina.*– Full enclosure of the trigeminal foramina by the prootic is the plesiomorphic pattern for atheriniforms (Figs 9, 13). The foramen for the trigeminal nerve

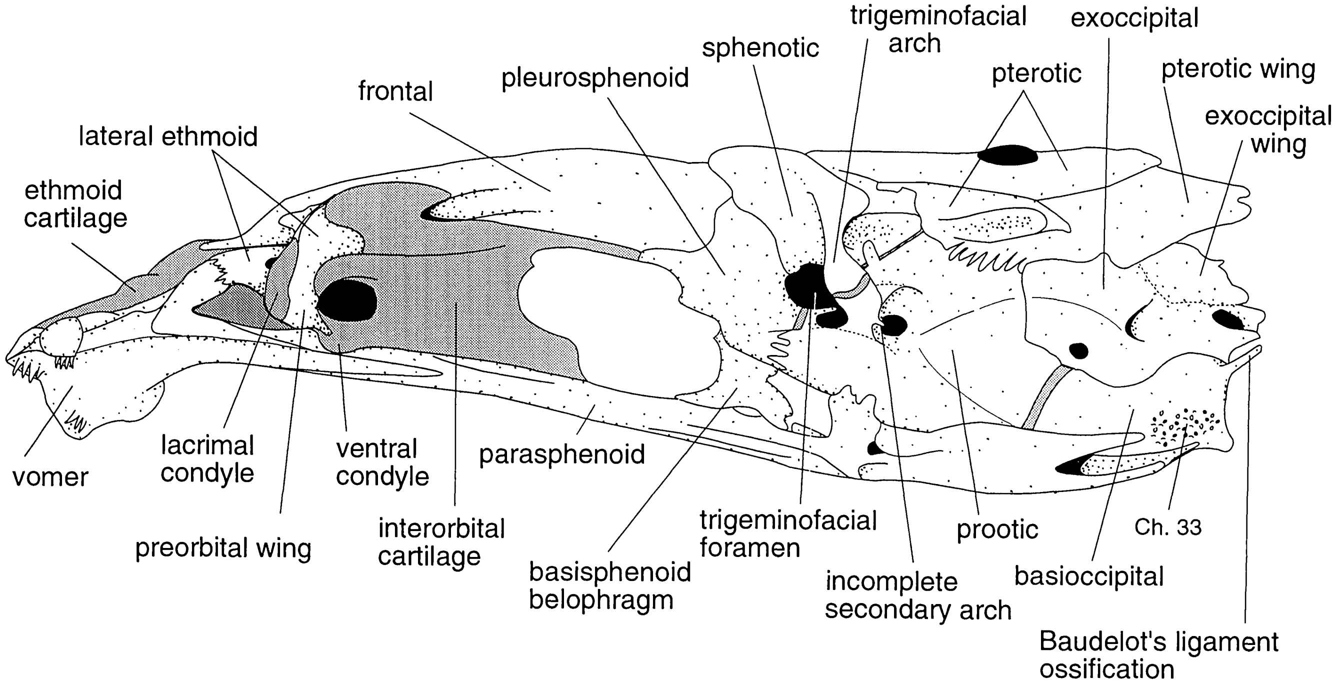

Fig. 7. Ventrolateral view of the neurocranium of *Odontesthes orientalis* (MNHN-M 2670).

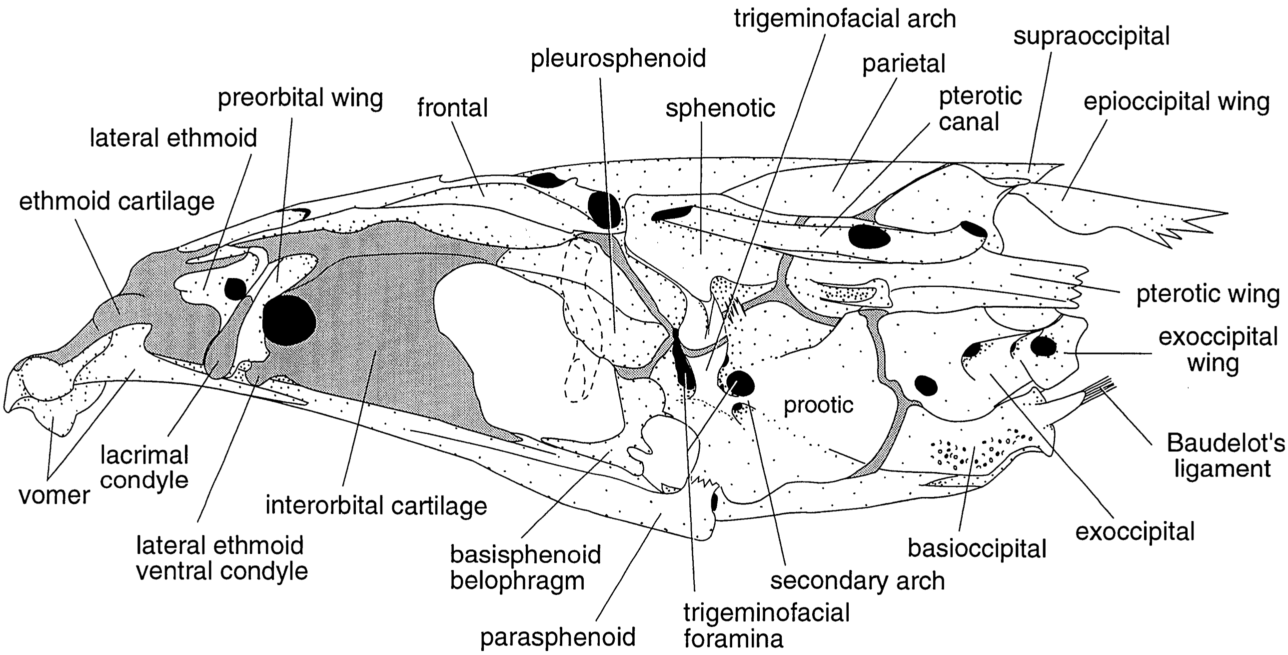

Fig. 8. Ventrolateral view of the neurocranium of *Odontesthes hatcheri* (UMMZ 218450). Dermosphenotic in dashed line.

(V) is derived in *Odontesthes*, with an enlarged anterodorsal opening enclosed by the prootic, pterosphenoid, and sphenotic (Figs 7, 8). **(0=trigeminal foramen fully enclosed by the prootic; 1=trigeminal foramen enclosed by the prootic, sphenotic, and pterosphenoid; 1.00)**

The trigeminal foramen is usually a single large foramen, though sometimes it is subdivided by thin ossification of the membrane that separates the jugular vein from the trigeminofacial chamber (De Beer, 1937: 121,128). The foramen of the palatine or occulomotor nerve is also derived in *Odontesthes* in that it is not fully enclosed by the prootic as in other atherinopsids (Fig. 9), but rather shared with the basisphenoid, or absent altogether (Figs 7, 8).

25 *Trigeminofacial arch or lateral commissure.*– The bony arch of the prootic, lateral to the trigeminofacial foramina or lateral commissure, is traversed by the jugular vein and orbital artery (Goodrich, 1930: 273-278). Atheriniform outgroups have a

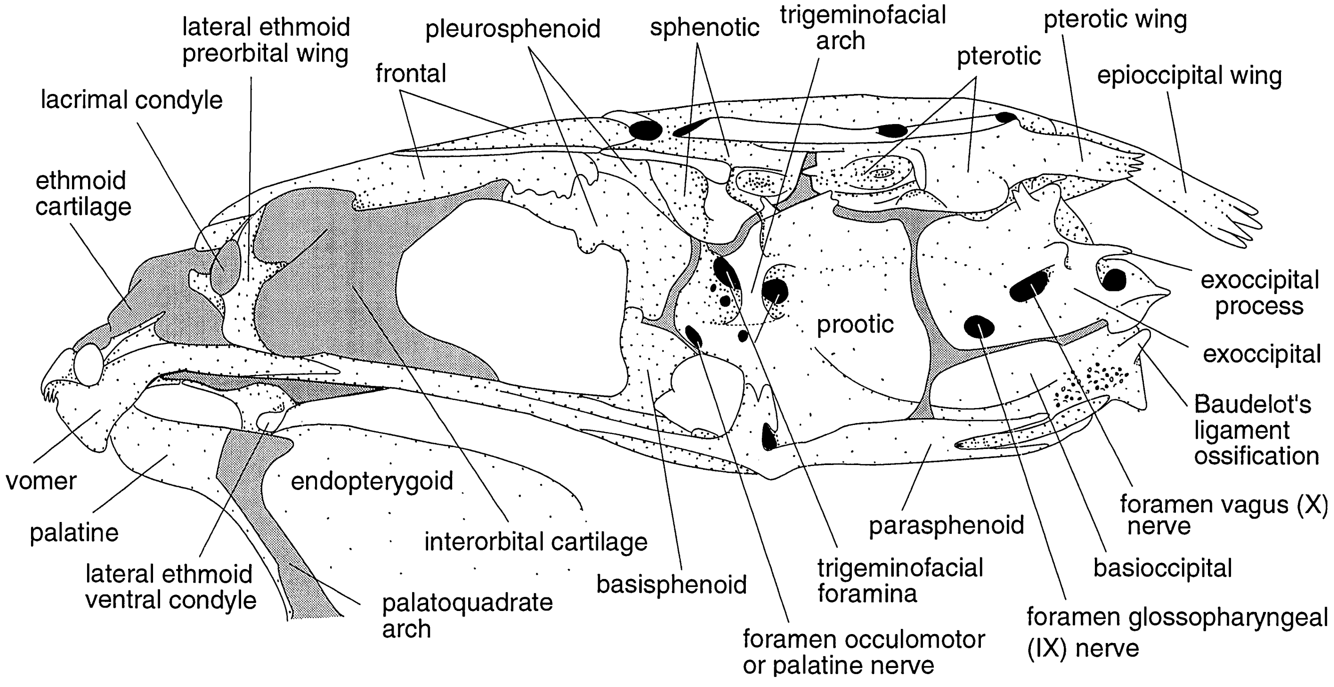

Fig. 9. Ventrolateral view of the neurocranium of *Basilichthys microlepidotus* (UMMZ 215499) and a medial view of anterior portion of the right suspensorium.

single arch lateral to the trigeminofacial foramina. A derived condition is found in atherinopsids in which a secondary arch separates the orbital artery posteroventrally from the larger posterior opening of the jugular vein and facial (VII) nerve (Fig. 8). The secondary arch is absent in *Basilichthys* (Fig. 9), *Atherinopsis*, and *Leuresthes*; this arch is incomplete or weakly developed in some specimens of *Odontesthes* (Fig. 7). A uniquely derived condition is found in all menidiines except *Labidesthes* in which a wide bony tube encloses the jugular vein posterior to the trigeminofacial arch (Fig. 13). This forms a posteromedial foramen for the hyomandibular nerve and a posterodorsal foramen presumably for the opercularis nerve that innervates the adductor and levator operculi muscles (Harrison, 1981). **(0=single trigeminofacial arch; 1=secondary trigeminofacial arch present; 2=bony enclosure of jugular vein posterior to trigeminofacial arch; 0.50, 0.78; add)**

26 *Basisphenoid belophragm.*– The ventral, laminar projection of the basisphenoid (belophragm of Chabanaud, 1936) in atheriniform outgroups divides the anterior opening of the posterior myodome and is relatively long and slender (Dyer & Chernoff, 1996). The dorsal rami of the basisphenoid (meningosts of Chabanaud, 1936) are in the horizontal plane, forming the anterior roof of the posterior myodome. The basisphenoid in mugilids is greatly reduced either to presence of a long and slender belophragm only or absence of both belophragm and meningosts. The basisphenoid is absent in cyprinodontiforms and adrianichthyoids, but present and well developed in exocoetoids. Atherinopsines and species of *Chirostoma*, have a derived condition in which the belophragm is very short ventrally and is mostly projected anteriorly along the dorsal midline of the parasphenoid towards the interorbital cartilage (Figs 7, 8, 9). The meningosts are oriented diagonally in cross section, converging at the midline close to the parasphenoid and separating the posterior myodome eye muscles. **(0=basisphenoid belophragm long and slender; 1=belophragm short projected anteriorly; 1.00)**

A derived but variable trait is found in *Basilichthys semotilus* species group and in the Río Quilimarí population of *B. microlepidotus*: the anteroventral tip of the belophragm is extended anteriorly and is in contact with the posterior end of the interorbital cartilage (Fig. 11). Presence or absence of this feature is independent of size or sex, found consistently only in the Río Loa population of *B. semotilus* species group.

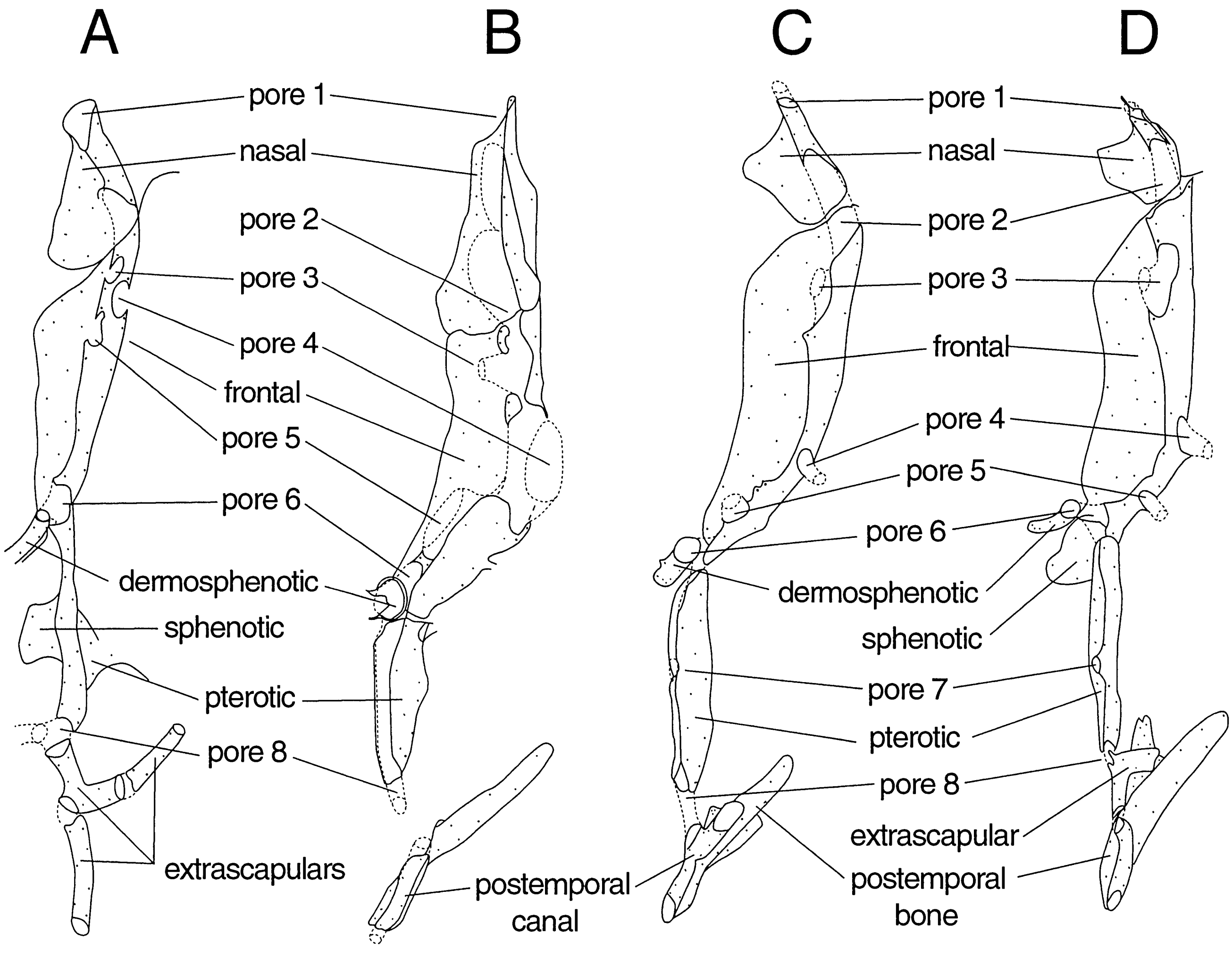

Fig. 10. Dorsal view of the left supraorbital and temporal sensory canals and pores; A, *Agonostomus monticola* (UMMZ 199463); B, *Hypoatherina bleekeri* (FMNH 57459); C, *Menidia beryllina* (UMMZ 203149); D, *Atherinops affinis* (UMMZ 72212).

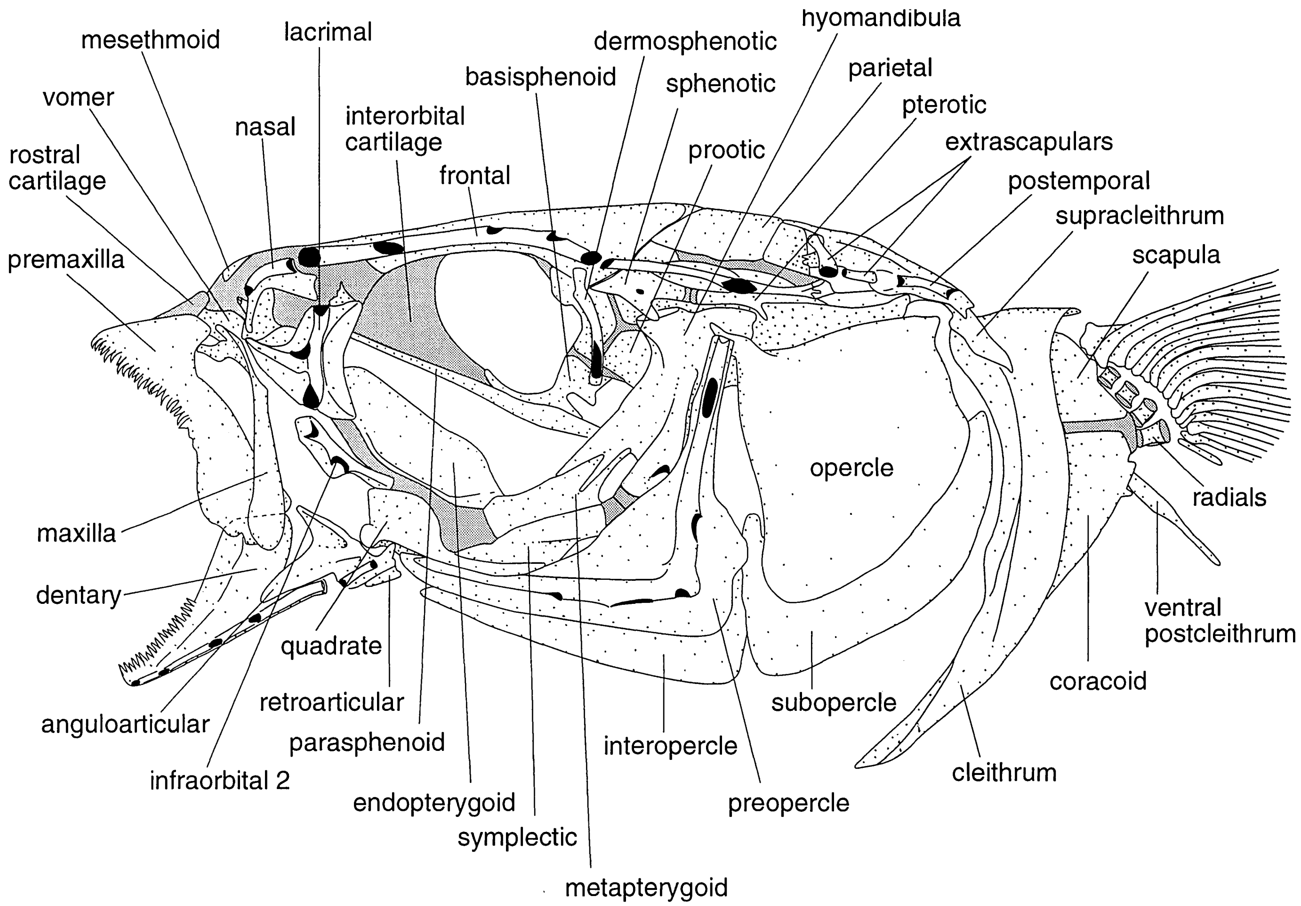

Fig. 11. Lateral view of the head and pectoral girdle of *Basilichthys* sp. (UMMZ 215519).

27 Parasphenoid ventral ridge.– **(0=anterior end of parasphenoid ventral ridge, smoothly tapered; 1=anterior end of parasphenoid ventral ridge, rounded; 0.50)**

28 Supraoccipital crest (White, 1985).– The plesiomorphic condition found in mugilids, atherinoids, and menidiines is a single vertical laminar crest projecting posteriorly from the supraoccipital bone into the vertical septum (Fig. 14A). In Cyprinodontea, two posterodorsal laminar projections form a V-shaped supraoccipital crest that reach the base of the supraoccipital bone. Atherinopsini and *Basilichthys* also have bifid supraoccipital crests, but are projected instead from a single, basal laminar crest (Fig. 14B, 14C). In atherinopsinins, the supraoccipital crest appears trifid in dorsal view (White, 1985) because the posterior border of the single basal lamina projects posteriorly from the point of bifurcation (Fig. 14C). **(0=single supraoccipital crest; 1=bifid supraoccipital crest; 2=trifid-like supraoccipital crest; 0.50, 0.80; add)**

29 Pterotic wing.– The posterolateral border of the pterotic is a diagonal ridge that is continued ventrally by the exoccipital, with or without an intercalar bone. Presence of a wide laminar flange from the posterior ridge of the pterotic is a derived feature of mugilids and atherinopsids (Figs 7, 8, 9; Starks, 1899). The pterotic wing receives muscle attachments from the cleithrum and opercle and forms the lateral enclosure of the epaxial muscles that extend into the temporal fossa. **(0=no pterotic wing; 1=pterotic wing present; 0.50)**

30 Exoccipital wing (Chernoff, 1986b).– The plesiomorphic atheriniform condition is for a smooth dorsal face of the exoccipital condyle. Atherinopsids, except for *Labidesthes* and *Melanorhinus*, have the derived condition of a laterodorsal lamina projecting from the exoccipital process in the form of hooks or a perforated flange. In *Basilichthys* a hook or spine is present (Fig. 9), whereas in all other atherinopsines examined the exoccipital presents a flange of varying degrees of development, posterior to the attachment of the postemporal ventral process (Figs 7, 8). Chernoff (1986b) proposed this feature as characteristic of Menidiinae, but its presence in all atherinopsines suggests it is characteristic at the more general level of Atherinopsidae. Wings or hooks are present in atherinopsines larger than 100 mm SL. **(0=exoccipital without a wing or processes; 1=exoccipital with a wing or processes; 1.00)**

31 Pterotic and exoccipital wings contiguous.– The pterotic wing of mugilids, menidiines, and *Basilichthys* (Ch. 29) tapers ventrally without reaching the exoccipital wing (Ch. 30). In atherinopsinins and *Odontesthes* the pterotic wing is contiguous with the exoccipital wing (Figs 7, 8). **(0=pterotic wing not contiguous with exoccipital wing; 1=pterotic wing contiguous with exoccipital wing; 0.50, 0.80)**

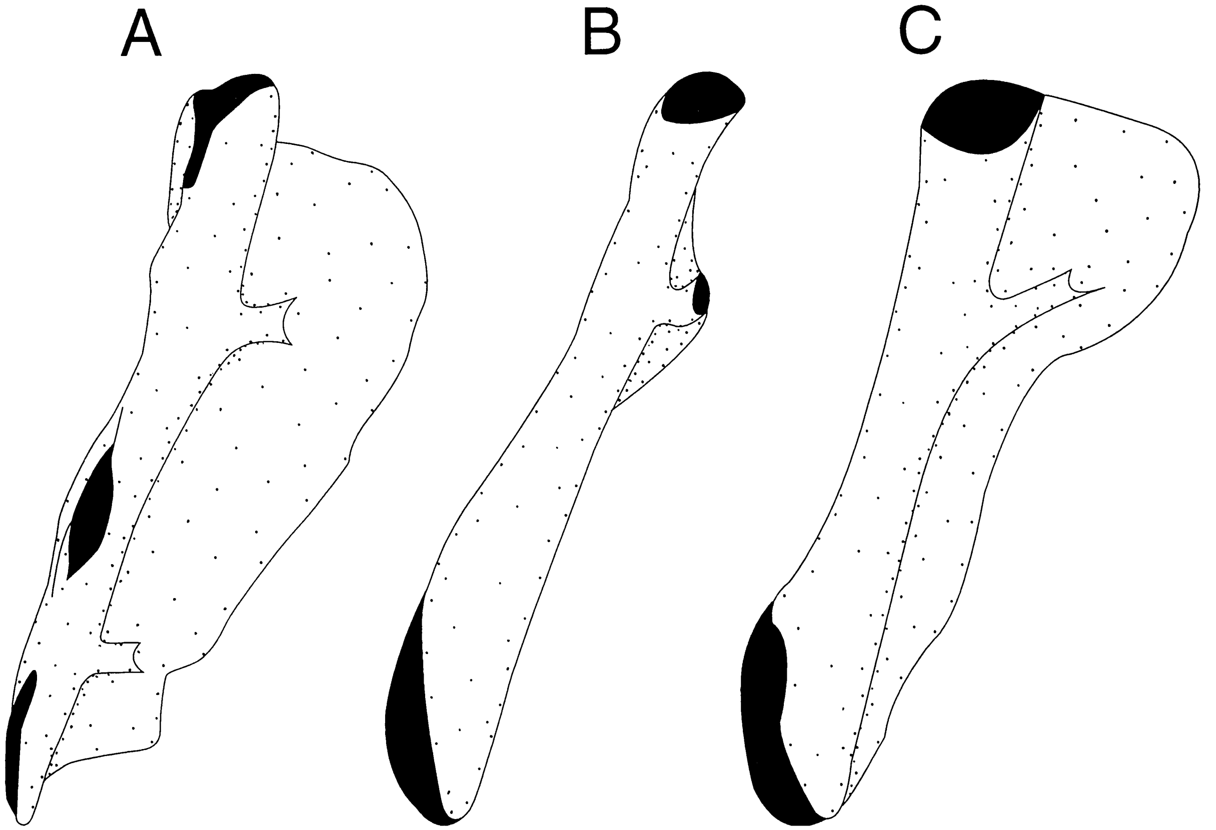

Fig. 12. Posterior view of the left dermosphenotic; A, *Atherinops affinis* (UMMZ 72212); B, *Basilichthys microlepidotus* (UMMZ 215502); C, *Odontesthes brevianalis* (UMMZ 215459).

32 Pterotic and epioccipital wings contiguous.– The pterotic wing in atherinopsid outgroups tapers ventrally only towards the exoccipital. *Basilichthys* and *Atherinopsis* have an additional horizontal flange, ventral to the epaxial musculature of the temporal fossa, that is contiguous with a basal widening of the epioccipital wing. **(0=pterotic wing not contiguous with epioccipital; 1=pterotic wing contiguous with epioccipital wing; 0.50, 0.67)**

33 Basioccipital fenestration (White, 1985).– The posterior region of the basioccipital is smooth in atherinopsid outgroups. A derived condition found in sorgentinins is the fenestration of the basioccipital bone (Figs 7, 8, 9; White, 1985: fig. 12). **(0=basioccipital bone smooth; 1=basioccipital fenestrated; 1.00)**

34 Baudelot's ligament ossification (White, 1985).– An unossified Baudelot's ligament is the plesiomorphic condition for atheriniforms. A derived condition found in beloniforms (except for exocoetids) and atherinopsines is ossification of the ligament at its attachment to the basioccipital (Figs 7, 8, 9; Starks, 1899: fig. II,2). **(0=Baudelot's ligament not ossified; 1=Baudelot's ligament ossified proximally; 1.00)**

Baudelot's ligament is attached to the exoccipital in *Melanorhinus* and is absent in notocheirids.

35 Extrascapular and postemporal canal bones (White, 1985).– An *a priori* assessment of similarity of the extrascapular and postemporal canal bones in atherinopsids is problematic (Dyer & Chernoff, 1996). The postemporal in Menidiinae has a bony sensory canal with three pores (Figs 10C, 15A), and Atherinopsinae has a postemporal canal with two pores (Figs 10D, 11, 15B, 15C). Menidiines have no extrascapular bones (Fig. 10C) whereas atherinopsines have an extrascapular bone with three pores (Fig. 10D, 11) that is sometimes divided in two separate elements (Fig. 11) (see Discussion). Based on morphological similarity of the canal bones proper, regardless of the underlying bone to which they may attach, the postemporal canal bone of menidiines and the extrascapular of atherinopsines meet all *a priori* tests of similarity (Patterson, 1982) and are considered to be potential homologues. **(0=three- and two-pore canal bones present, not fused to underlying bone; 1=two-pore canal bone absent, three-pore canal bone fused to postemporal; 2=two-pore canal bone fused to postemporal, three-pore canal bone(s) not fused to underlying bone; 1.00; n-add)**

36 Postemporal anterior process (Chernoff, 1986b).– The plesiomorphic condition of atheriniforms is for the postemporal to have two processes; a dorsal process that articulates with the epioccipital and a ventral process that articulates with the intercalar or exoccipital. The derived condition of atherinopsids is presence of an anterior spine-like process of variable length projected into the temporal fossa (Fig. 15). A further derived condition is found in Atherinopsini and *Basilichthys*, in which the anterior process of the postemporal is widened and lami-

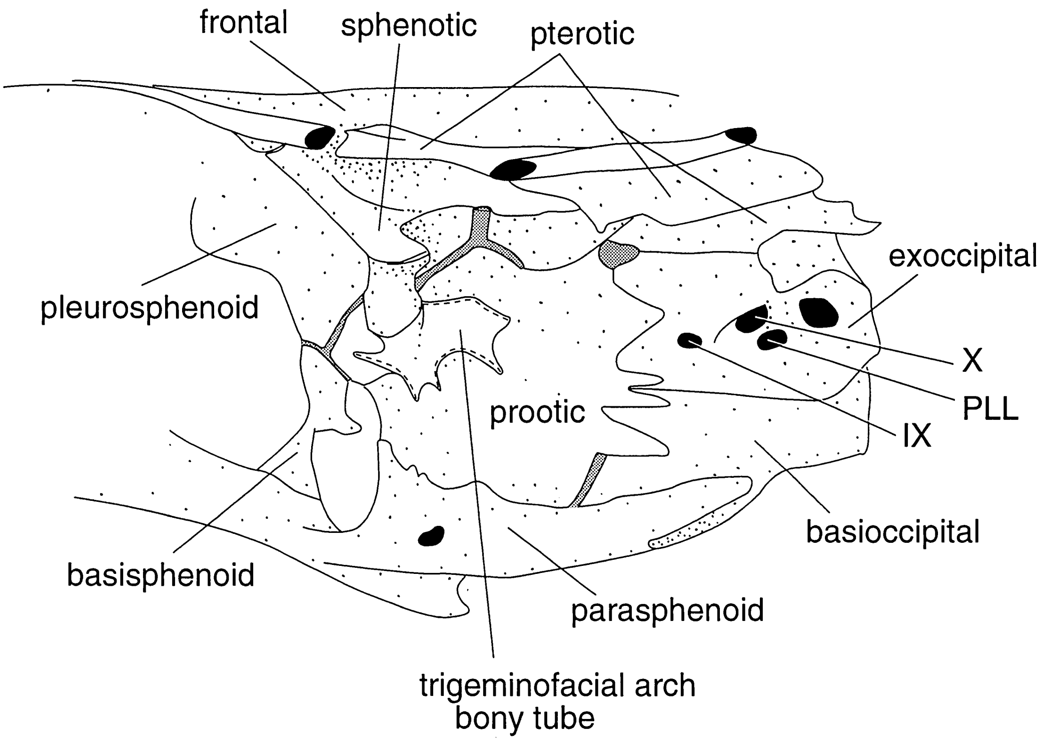

Fig. 13. Left ventrolateral view of the otic and occipital regions of the neurocranium of *Membras gilberti* (UMMZ 202405). IX: glossopharyngeal nerve; X: vagus nerve; PLL: posterior lateral line nerve.

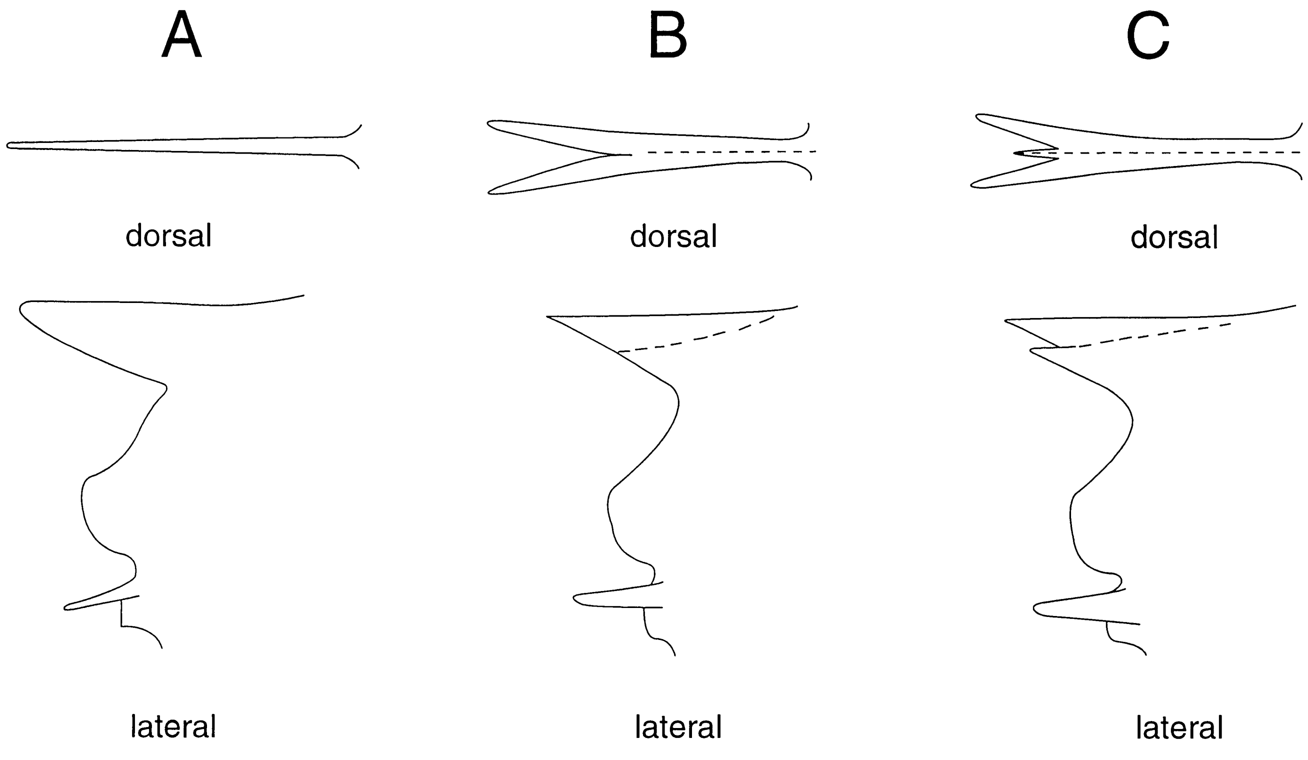

Fig. 14. Schematic dorsal and lateral views of the supraoccipital crest; A, *Odontesthes*; B, *Basilichthys*; C, *Atherinops*.

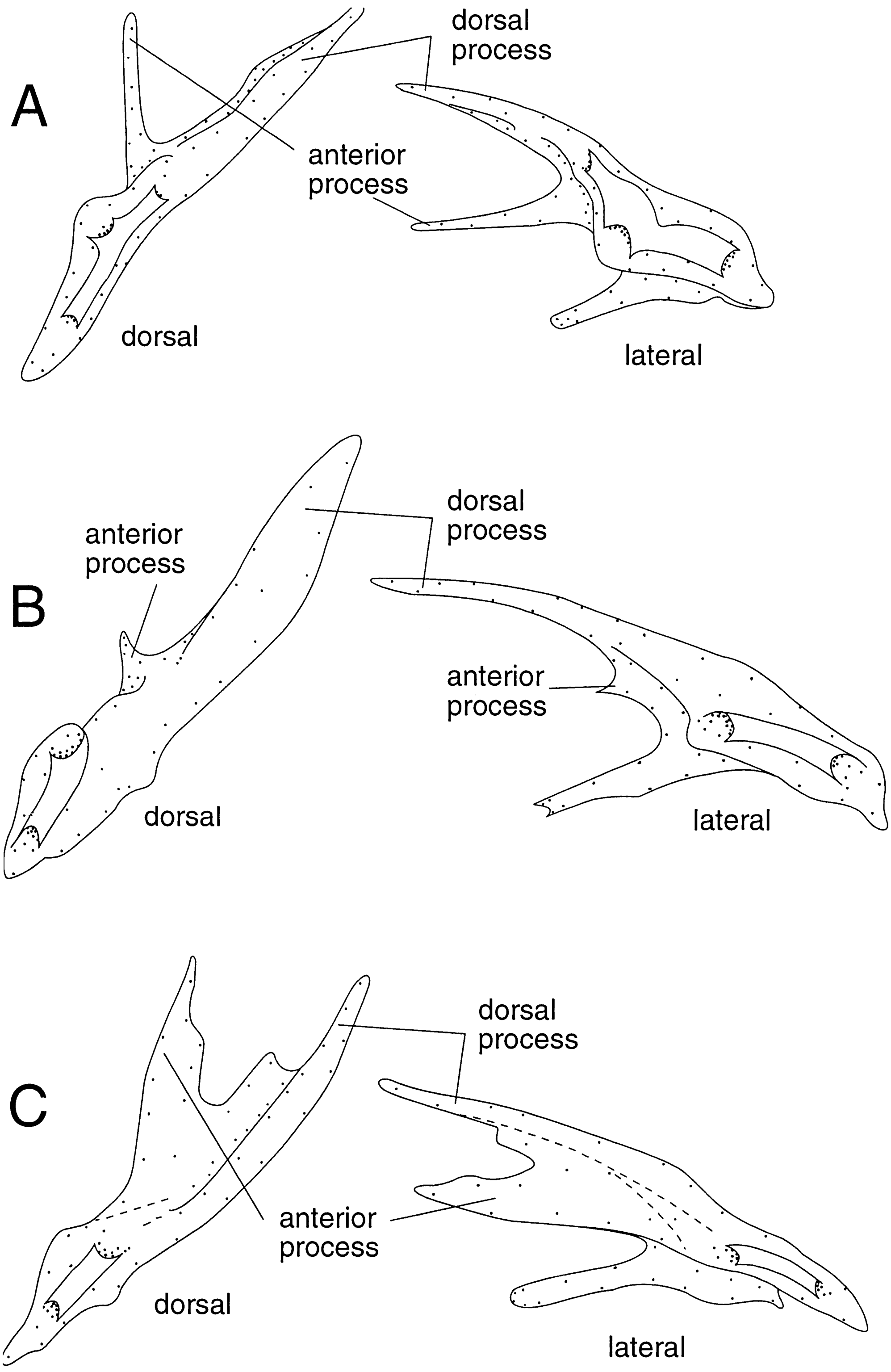

Fig. 15. Dorsal and lateral views of the left postemporal bone; A, *Menidia*; B, *Odontesthes brevianalis* (UMMZ 215459); C, *Basilichthys australis* (UMMZ 215508).

nar (Figs 10D, 15C). **(0=no postemporal anterior process; 1=postemporal anterior process present, spine-like; 2=postemporal anterior process wide; 0.40, 0.73; add)**

Jaws and associated ligaments

37 Upper jaw frenum.– Presence of a fold of skin between the dorsal processes of the maxillae and the premaxillary ascending processes is a plesiomorphic condition for atheriniforms. Presence of a continuous, unfolded sheath of skin between the upper jaws and forehead, or frenum, is a derived feature shared by the atherinopsine genera *Atherinopsis*, *Atherinops*, *Colpichthys*, and *Basilichthys* (Fig. 16). **(0=no upper jaw frenum; 1=upper jaw frenum present; 0.50, 0.60 / 0.67, 0.80)**

38 Premaxillary ascending process (dorsal process of White, 1985).– The premaxillary ascending process with a wide base close to the symphysis is the plesiomorphic condition for atheriniforms (Fig. 5; Schultz, 1948: plates 1, 2). A derived condition of atherinopsids is for the ascending process of the premaxilla to have a relatively narrow base, displaced laterally from the midline (Fig. 4). This condition is found in menidiines (except for *Labidesthes* and a species group of the subgenus *Eurystole*; Chernoff, 1986b), *Leuresthes*, and *Odontesthes* (Figs 17, 18; Schultz, 1948; White, 1985; De la Hoz *et al.*, 1994). **(0=base of premaxillary ascending process wide and close to symphysis; 1=base of premaxillary ascending process narrow and displaced from the symphysis; 0.33, 0.78)**

In atherinoids, the ascending process has a wide base and is elongated posterodorsally in several groups (Saeed *et al.*, 1994; e.g., phallostethids, *Stenatherina*, *Craterocephalus*, and *Kestratherina*).

39 Premaxillary anterior joint (Patten, 1978).– A relatively wide ligamentous articulation between the anterior ends of both premaxillae is the plesiomorphic condition for atheriniforms. The derived condition found in all atherinopsids is a narrow ligamentous articulation between both premaxillae (Figs 4, 5; De la Hoz & Vial, 1988). This condition is most noticeable in species with narrow-based ascending processes (Ch. 38). **(0=pre-**

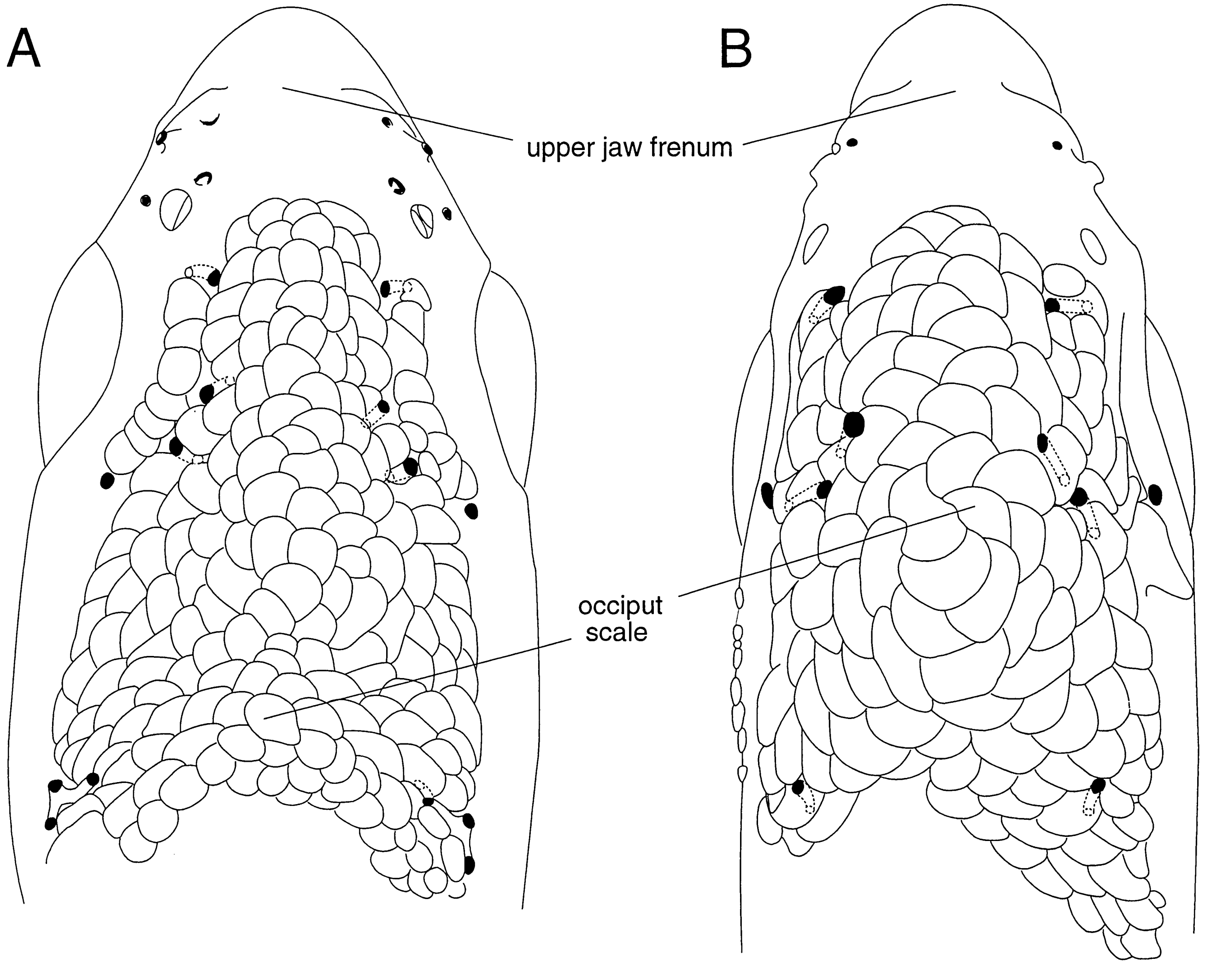

Fig. 16. Dorsal view of the head of *Basilichthys*; A, *B. microlepidotus* (UMMZ 215517); B, *B. semotilus* (UMMZ 218050).

maxillary anterior joint wide; 1=premaxillary anterior joint narrow; 1.00)

40 Dorsal process of maxillary head.– A well developed dorsal process of the maxillary head is the plesiomorphic condition for atherinomorphs (Figs 17, 18). A reduced dorsal process is considered a derived condition present in Cyprinodontea, *Basilichthys*, *Atherinops*, *Atherinopsis*, and *Colpichthys* (Figs 19, 20, 21). **(0=dorsal process of maxilla developed; 1=dorsal process of maxilla reduced; 0.25, 0.50 / 0.33, 0.67)**

41 Ventral process of maxillary head.– The plesiomorphic condition for atheriniforms is for the ventral process of the maxilla to be longer than the dorsal process, projecting anteriorly and medially. A derived condition found in *Odontesthes* is for the dorsal and ventral processes to be of roughly the same length (Figs 17, 18). A similar condition is found in some membradins (Chernoff, 1986a,b). **(0=ventral process of maxilla longer than dorsal process; 1=dorsal and ventral processes of maxilla about equal in length; 1.00)**

42 Condyle on the ventral process of the maxilla ("rounded process", White 1985).– The ventral process of the maxilla is usually flat or thickened in its entire length and articulates dorsally with the ascending process of the premaxilla. Presence of a rounded thickening that functions as a condyle on the dorsal surface of the maxillary ventral process is unique to *Basilichthys* (Fig. 21). This feature is absent in all other atheriniforms examined. **(0=no condyle on maxillary ventral process; 1=condyle present on maxillary ventral process; 1.00)**

43 Postmaxillary process of the premaxilla (Patten, 1978; Chernoff, 1986b).– A postmaxillary process on the alveolar arm of the premaxilla, projected medial to the maxilla is plesiomorphic for atheriniforms, present in mugilids except *Mugil*, and atherinoids except *Notocheirus*. Absence of this feature (Figs 17-20) is considered derived and was regarded as diagnostic of atherinopsids by Chernoff (1986b). This feature is ambiguously optimized however, because it is also absent in *Notocheirus* (Rosen, 1964: fig. 4A) and Cyprinodontea. **(0=postmaxillary process present; 1=postmaxillary process absent; 0.50)**

44 Premaxillary alveolar arm (Chernoff, 1986b).– The plesiomorphic condition of the premaxillary alveolar arm in atheriniforms is a pointed distal end. The distal end of the premaxilla is variably broadened in some Atherinoidei groups such as *Atherion*, *Pseudomugil*, *Notocheirus*, and *Craterocephalus* (Patten, 1978). A derived condition of the premaxilla is found in atherinopsids in which the distal end is notably dilated (over twice the width of the proximal region of the alveolar arm) with a mostly convex posteroventral border (Figs 17, 18; Chernoff, 1986b). Reduction of the dilation is found in some membradins (Chernoff, 1986a) and a concave distal border is present in *Leuresthes* (Schultz, 1948: fig. 4D). **(0=premaxillary alveolar arm pointed or slightly broad; 1=premaxillary alveolar arm broadly dilated; 1.00)**

45 Premaxilla-dentary coronoid ligament (Patten, 1978).– A relatively long ligament connecting the coronoid process of the dentary with the adjoined tips of the upper jaw bones is the

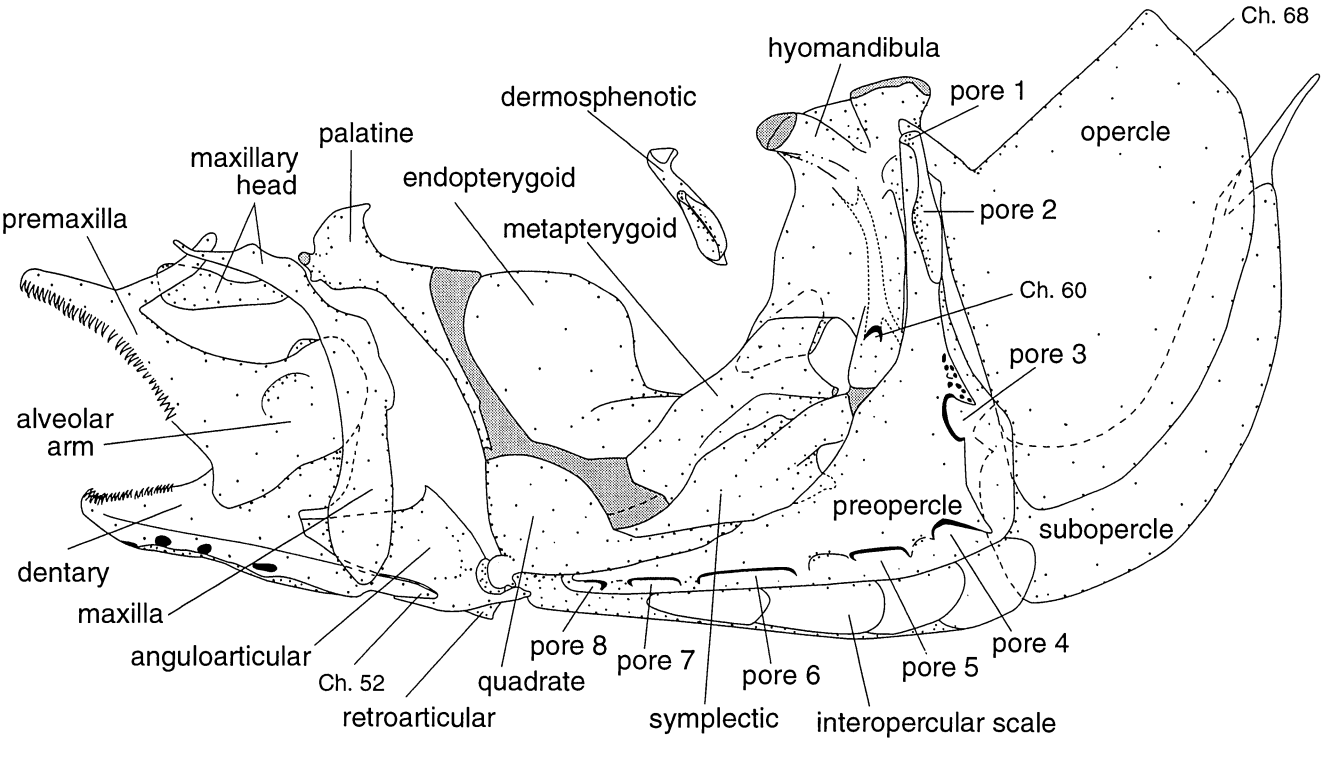

Fig. 17. Lateral view of the left jaws and suspensorium of *Odontesthes retropinnis* (UMMZ 231950).

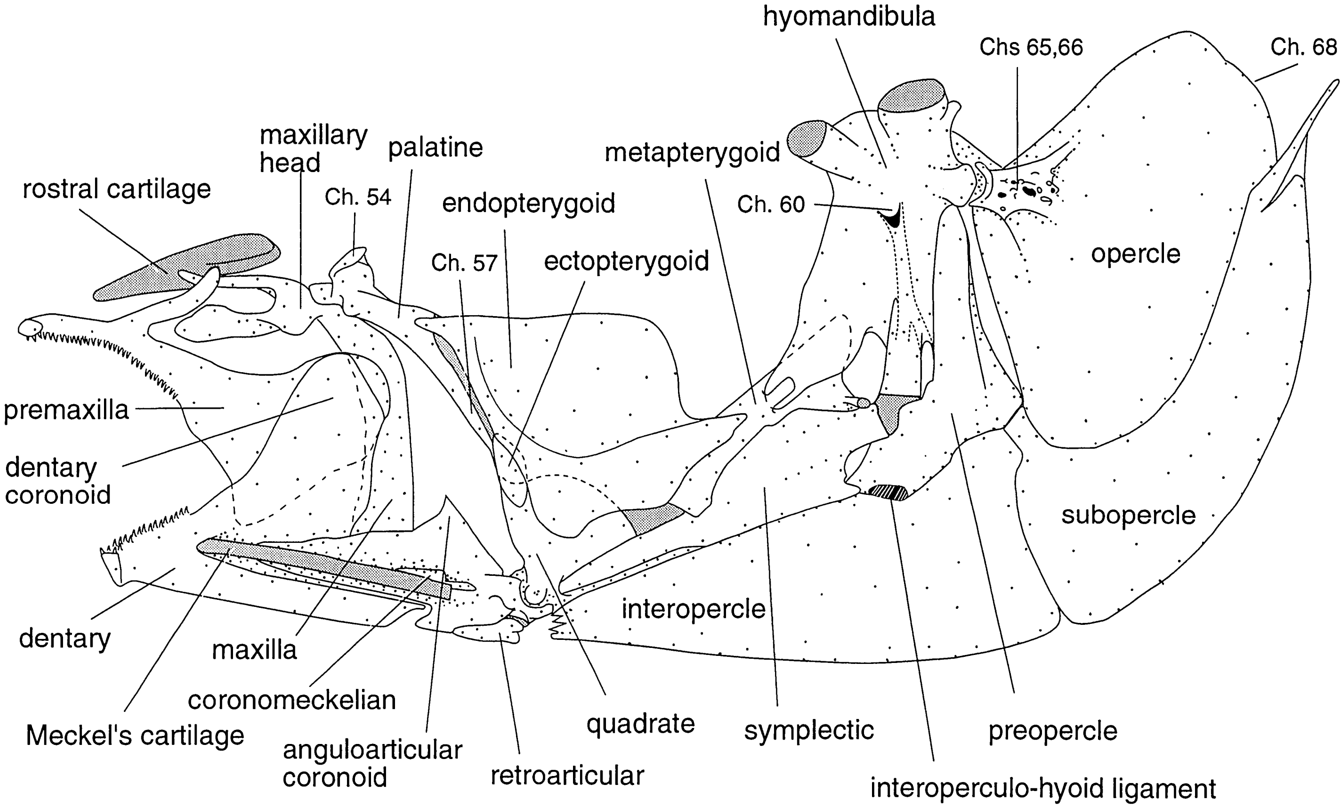

Fig. 18. Medial view of the left jaws and suspensorium of *Odontesthes retropinnis* (UMMZ 231950).

plesiomorphic condition for atheriniforms. A derived condition of atherinopsids is for the ligamentous connection between the postero-dorsal corner of the dentary coronoid and the posterior end of the premaxillary alveolar arm to be extremely short (Fig. 22). The ligament is so short that movement between the two bones is restricted to rotation relative to each other. This allows the lowering mandible to pull the premaxillae forward and down during opening of the mouth (De la Hoz & Vial, 1988; 1994; De la Hoz, 1994). **(0=premaxilla-dentary coronoid ligament long; 1=premaxilla-dentary coronoid very short; 1.00)**

A short ligament between the premaxilla and coronoid process of the dentary has derived independently in *Pseudomugil* and *Craterocephalus* (Dyer & Chernoff, 1996), though not as short as in atherinopsids.

46 Maxilla-anguloarticular coronoid ligament.– The maxilla and premaxilla are closely adjoined at their distal tips in atheriniform outgroups and are connected only to the coronoid process of the dentary by a long ligament (see Ch. 45). A derived condition present in Menidiinae, Atherinopsini, and *Odontesthes* is presence of a ligamentous attachment from the maxilla to the coronoid process of the anguloarticular (Fig. 22). **(0=no ligament between maxilla and anguloarticular coronoid; 1=ligament between maxilla and anguloarticular coronoid present; 0.50, 0.83)**

47 Maxilla-premaxilla distal ligament (White, 1985).– The distal ends of the maxilla and premaxilla are connected by a short ligament in atheriniform outgroups allowing a limited movement between them. The derived condition of atherinopsids is a long ligament between the distal end of the maxilla and the lateral face of the premaxilla (Fig. 22), allowing a greater amount of relative movement between the upper jaw bones. The generalized atherinopsid condition is to have the ligament attached to the mid-region of the premaxillary alveolar arm. Derived states of the ligament's premaxillary attachment are: to the anteroventral corner of the alveolar arm in *Labidesthes*, *Colpichthys*, and *Basilichthys* (Fig. 22; De la Hoz & Aldunate, 1994; De la Hoz *et al.*, 1994: figs 18-20); to the mid-ventral region in *Atherinella* and some species of *Chirostoma*; and to the dorsal border of the alveolar dilation in *Leuresthes*, anterior to the attachment of the premaxilla-dentary coronoid ligament (Ch. 45). All other atherinopsids have the ligamentous connection to the lateral face of the alveolar arm of the premaxilla at positions intermediate between those of *Colpichthys* and *Leuresthes*. **(0=maxilla-premaxilla ligament very short; 1=maxilla-premaxilla ligament elongated, attached to mid-region of premaxillary alveolar arm; 2=maxilla-premaxilla ligament elongated, attached to anteroventral corner of premaxillary alveolar arm; 0.50, 0.80; add)**

48 Labial ligament fold (Chernoff, 1986b).– The labial ligament connects the mandibular lip with the distal or posterolateral end of the upper jaw. This ligament unfolds as the mandible is lowered and the upper jaw is displaced anteriorly. The plesiomorphic atherinomorph condition is for the labial ligament to be folded between the mandible and the premaxilla (Jordan & Hubbs, 1919: figs 1-10, 41, 42). A derived condition is found in cyprinodontiforms, menidiines, and sorgentinins, in which the labial ligament is folded on the lateral face of the

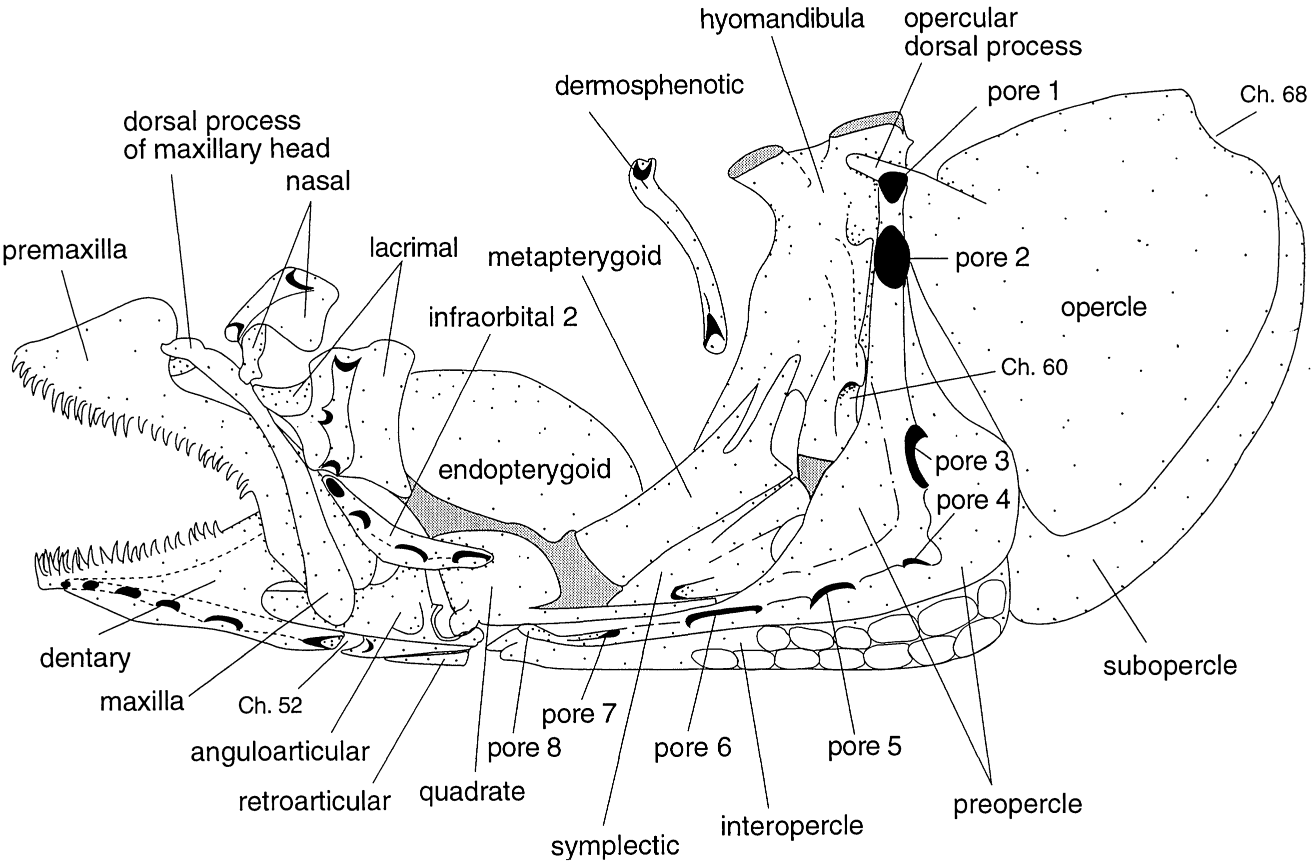

Fig. 19. Lateral view of the left jaws, infraorbitals, and suspensorium of *Basilichthys australis* (UMMZ 215507).

premaxilla (Fig. 22; Jordan & Hubbs, 1919: figs 27-35; Schultz, 1948: figs 8, 9). In menidiines and *Odontesthes* this fold is broad and overlaps the premaxilla (Fig. 23A). The *Basilichthys microlepidotus* species group has a greatly reduced overlap (Fig. 23B), whereas in the *B. semotilus* species group there is no upturned fold and a much narrower labial ligament (Fig. 23C). **(0=labial ligament folded internal to premaxilla; 1=labial ligament folded lateral to premaxilla; 2=labial ligament with lateral fold greatly reduced; 3=labial ligament lateral but not folded; 0.75, 0.90; add)**

The only references I was able to find on this striking feature are Gosline (1963: 24) and Rosen (1964: 233). Gosline noted that cyprinodontiforms and amblyopsids have the lower lip folded over the upper jaw, a "curious reversal of the usual upper lip configuration [which] does not occur elsewhere among the prepercoid groups". Rosen reported the presence of a lateral fold in all cyprinodontiforms, some exocoetoids, and all atheriniforms except *Basilichthys australis.* Because Gosline's only atheriniform was *Atherinops affinis* and Rosen did not include an atherinopsinin species in his comparative material, they were led to opposing generalizations about the condition in atheriniforms.

49 Cusps on oral-jaw teeth (White, 1985).– Presence of unicuspid teeth is the plesiomorphic condition for atheriniforms. Presence of bicuspid teeth in *Atherinops* and *Colpichthys* is unique in atheriniformes. In *Atherinops* both cusps are of about the same size whereas in *Colpichthys* the lateral cusp is longer (Todd, 1976: fig. 2; White, 1985: fig. 22). Bicuspid teeth are also present in posterior rows of mugilids and some derived cyprinodontoids. **(0=unicuspid teeth; 1=bicuspid teeth; 0.67, 0.00 / 1.00)**

50 Tooth rows on oral jaws.– Plesiomorphic for atheriniforms is presence of more than three rows of teeth on oral jaws as seen in mugilids, cyprinodontiforms, beloniforms, and atherinoids except for notocheirids which have two rows only. A similar condition occurs in membradins in which *Membras* and *Atherinella* have the plesiomorphic condition, but *Melanorhinus* has only two rows. Two states are found in Atherinopsini: (i) *Colpichthys* and *Atherinops* have two rows of teeth; and (ii) *Atherinopsis* and *Leuresthes* have three rows. Adult sorgentinins have three rows of teeth except for *O. hatcheri* and the *Basilichthys semotilus* species group that have more than three rows (De la Hoz *et al.*, 1994: fig. 6), and *Odontesthes perugiae, O. retropinnis,* and the subgenus *Austromenidia* that have two rows of teeth. Modification of oral jaw teeth in *O. incisa* render an ambiguous coding and is discussed in Dyer (1993: 346). **(0=more than three rows of teeth on jaws in adults; 1=three rows of teeth on jaws in adults; 2=two rows of teeth on jaws in adults; ?=polymorphic; 0.29, 0.58; n-add)**

Colpichthys and *Atherinops* have been described as having a single row of bifid teeth (Jordan & Hubbs, 1919; Crabtree, 1989). Only one row of teeth is visible, however, because the anterior row is embedded in the lip and only the posterior row protrudes beyond the skin.

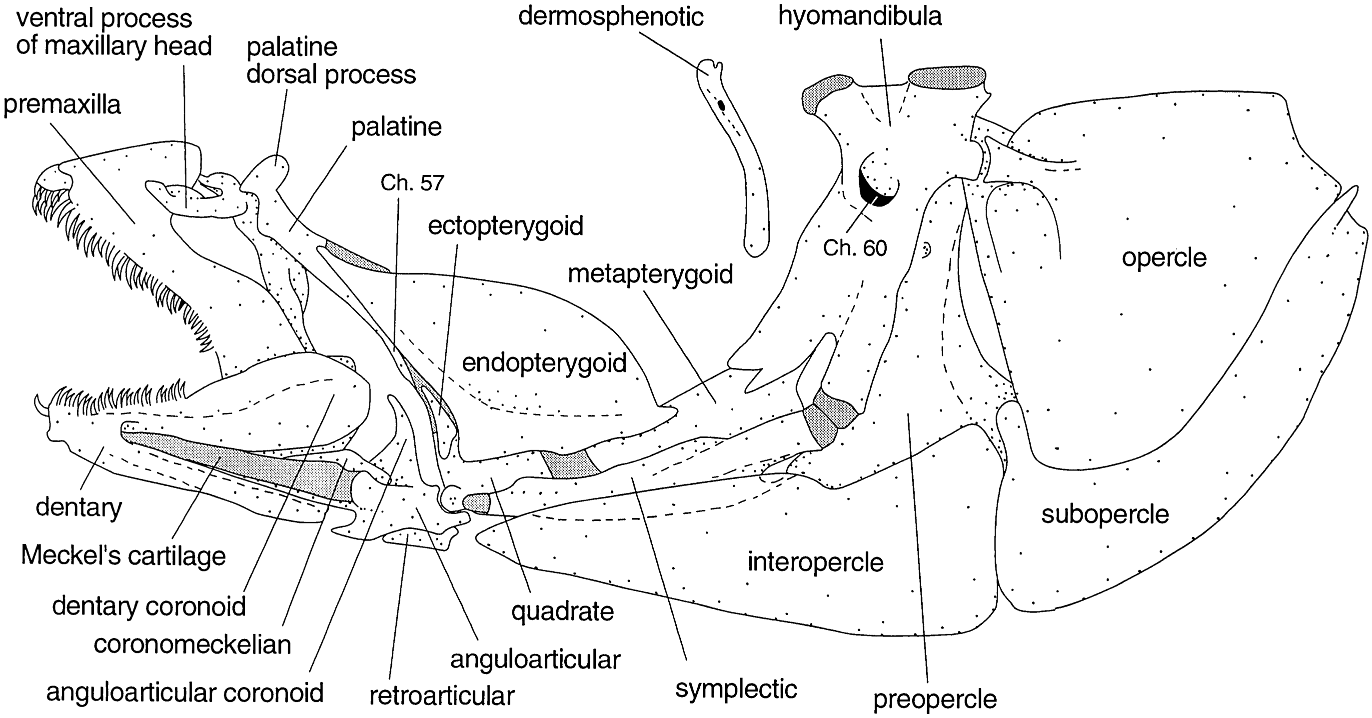

Fig. 20. Medial view of the left jaws and suspensorium of *Basilichthys australis* (UMMZ 215507).

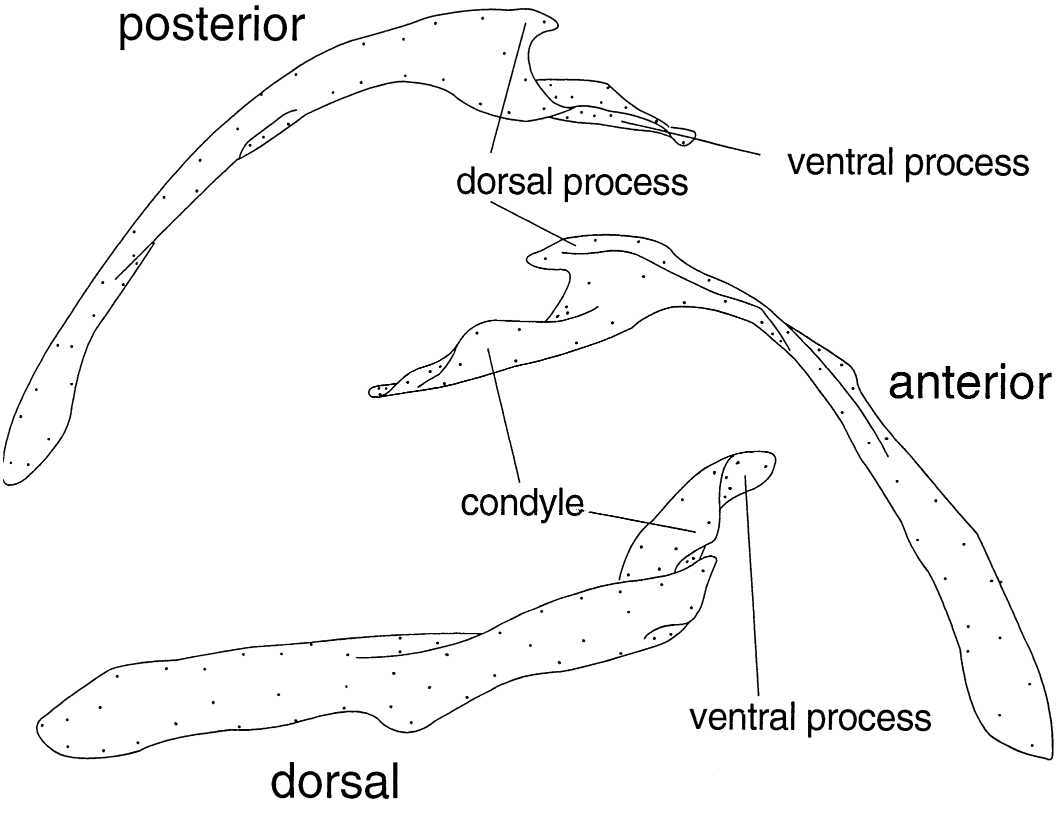

Fig. 21. Left maxilla in posterior, anterior, and dorsal views of *Basilichthys* (CAS 45197).

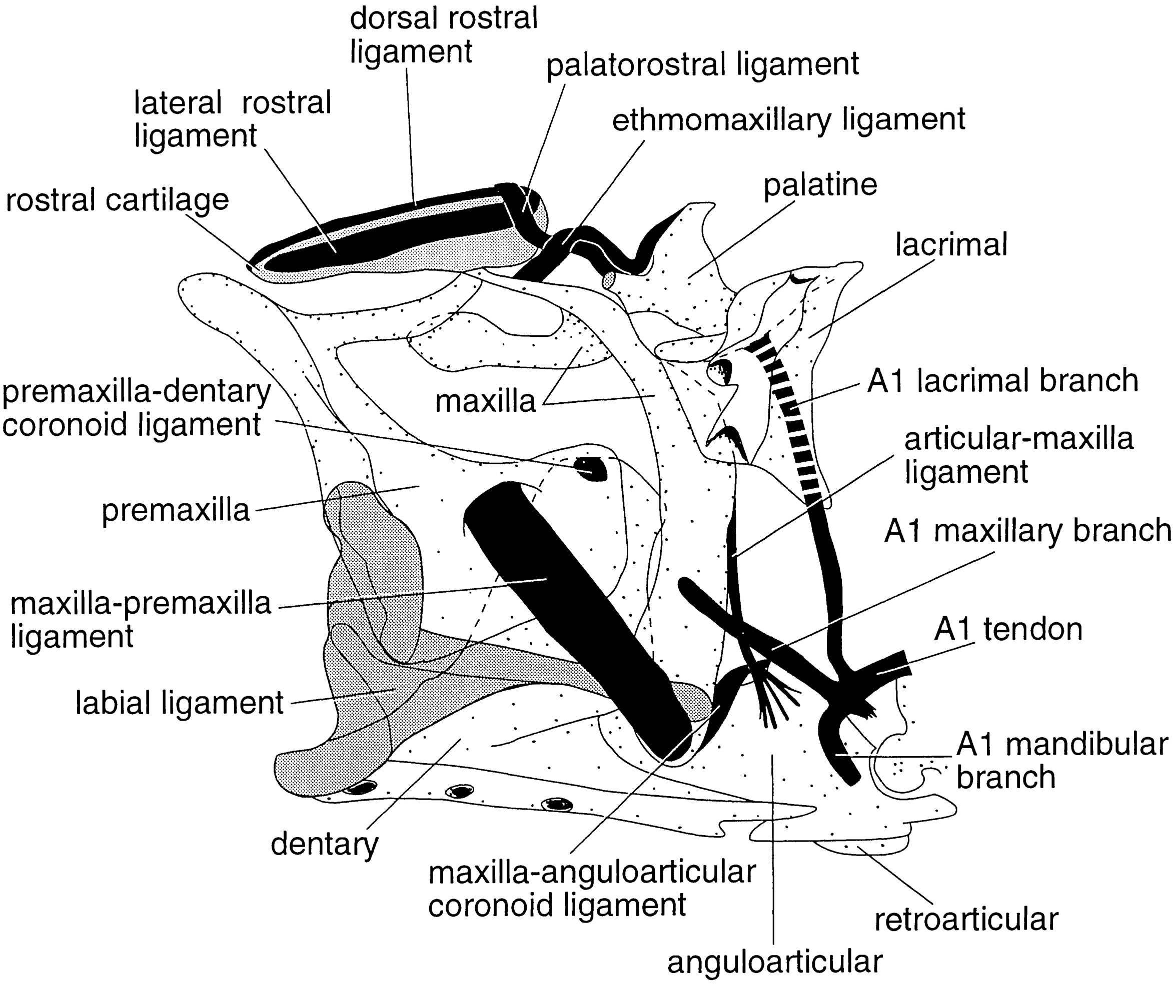

Fig. 22. Diagram of jaw ligaments in lateral view of *Odontesthes retropinnis* (UMMZ 231950).

51 Dentary coronoid process.– The coronoid process of the dentary is usually rounded and extended dorsally in atheriniforms, well beyond the coronoid process of the anguloarticular. Even when the dentary coronoid is not so well developed dorsally (e.g., *Labidesthes*), the anguloarticular coronoid is usually reduced to a relatively short spine (Figs 17, 18). *Basilichthys* has a derived condition in which the dorsal border of the dentary coronoid process is flattened and at the same level of a dorsally enlarged anguloarticular coronoid (Figs 11, 20, 25). A similar condition is found in pseudomugilins (Saeed *et al.*, 1989). **(0=dentary coronoid process rounded and taller than anguloarticular coronoid; 1=dentary coronoid process flattened dorsally and at level with tip of anguloarticular coronoid; 1.00)**

52 Dentary gnathic spine.– The posteroventral region of the dentary articulates medially with the anterior process of the anguloarticular. The posterior end of the dentary sensory canal projects posteriorly towards the anguloarticular in a gnathic ramus or spine, bridging the gap between both bones (Figs 17, 18). A derived condition found in *Basilichthys* is absence of the gnathic spine (Figs 11, 19, 20, 24, 25; De la Hoz & Tosti-Croce, 1981: fig. 6). **(0=gnathic spine present; 1=gnathic spine absent; 1.00)**

53 Mandibular branch of A1 muscle tendon.– The A1 division of the adductor mandibulae muscle of atherinopsids is attached anteriorly by a tendon to the medial face of the ventral half of the maxilla, and a long dorsal branch of the A1 tendon to the subnasal shelf of the lacrimal (Dyer & Chernoff, 1996). A derived condition found only in atheriniforms is a ventral or mandibular branch attached ventrally to the anguloarticular, anterior to the articulation with the quadrate (Fig. 22; De la Hoz & Aldunate, 1994; De la Hoz *et al.*, 1994). In atherinoids, the mandibular branch is found in *Atherion*, melanotaeniines, *Telmatherina*, and atherinines (Dyer & Chernoff, 1996: fig. 8). In atherinopsids, the mandibular branch is found in menidiines, *Leuresthes*, and *Odontesthes* (Fig. 26). In menidiines the mandibular tendon branches posterior to the lacrimal branch as in atherinoids (Fig. 26A). In *Leuresthes* and *Odontesthes*, however, the mandibular tendon branches anterior to the lacrimal branch (Figs 22, 26B). **(0=no A1 mandibular branch; 1=A1 mandibular branch present, posterior to lacrimal tendon; 2=A1 mandibular branch present, anterior to lacrimal branch; 0.75, 0.90; n-add)**

Suspensorium and associated ligaments

54 Palatine dorsal process (dorsal crest, Chernoff, 1986a,b).– Presence of a palatine dorsal process is a plesiomorphic

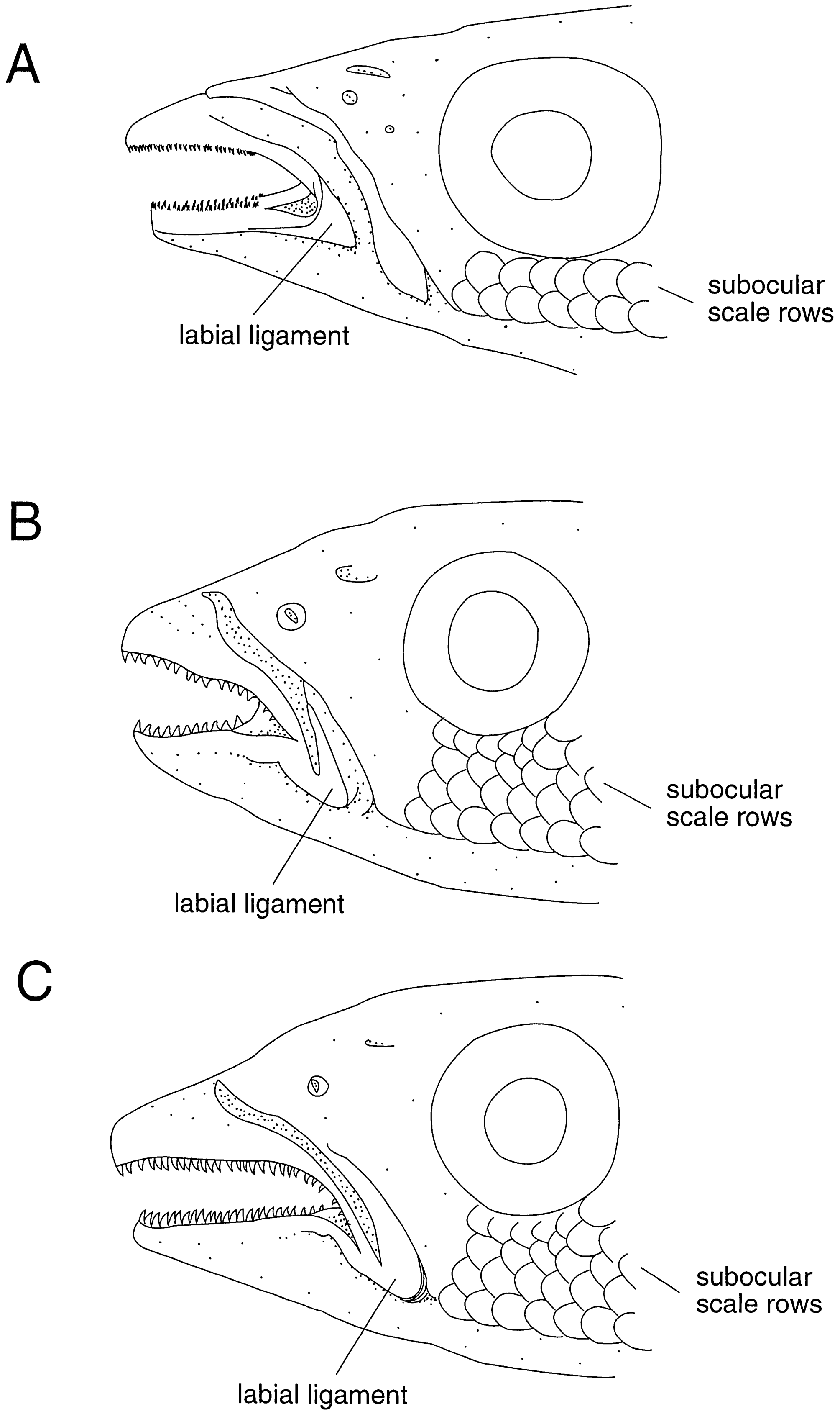

Fig. 23. Lateral view of the snout region; A, *Odontesthes perugiae* (UMMZ 221328); B, *Basilichthys microlepidotus* (UMMZ 215514); C, *Basilichthys semotilus* (UMMZ 217957).

atherinomorph feature; its absence is diagnostic of Atherinoidei (Dyer & Chernoff, 1996). A derived condition for atherinopsids is presence of a dorsal ridge that connects the anterior and dorsal processes of the palatine (Fig. 27A). A further derived condition of atherinopsines is the development of a shelf medial to the dorsal ridge such that the dorsal process appears folded over the ethmoid cartilage block (Chernoff, 1986b) and the dorsal process is pointed distally (Fig. 27B). In *Basilichthys* the dorsal crest is tall, rounded, and spoon shaped, lacking the dorsal ridge and lateral protuberances associated with the ethmomaxillary ligament attachment (Fig. 27C). **(0=dorsal process present; 1=dorsal process with dorsal ridge; 2=dorsal process pointed and folded over ethmoid block; 3=dorsal process spoon shaped and folded over ethmoid block; 0.75, 0.86; add)**

55 Ethmomaxillary ligament palatine attachment (Chernoff, 1986b).– Presence of an ethmomaxillary ligament between the dorsal process of the maxilla and the ethmoid region is considered a plesiomorphic feature in atheriniforms. The plesiomorphic condition for Cyprinodontea is ambiguous because of the derived conditions found in that group. Atherinopsids display a derived condition in that the ligament is attached to the dorsal crest of the palatine (Ch. 54), and is usually divided into maxillopalatine and ethmopalatine segments (Figs 4, 22). *Basilichthys* is the only atherinopsid that lacks the palatine attachment; rather, the wide and undivided ethmomaxillary ligament overlies the medially-folded dorsal crest of the palatine without any connecting fibers (Fig. 5; De la Hoz & Vial, 1994). **(0=ethmomaxillary ligament attached posteriorly to ethmoid region only; 1=ethmomaxillary ligament with intermediate palatine attachment; ?=polymorphic; 0.50, 0.80)**

A uniquely derived condition found in *Colpichthys regis* is presence of a ring ligament attached to the palatine dorsal process forming a loop through which the ethmomaxillary ligament traverses with no attachment to the palatine.

56 Palatorostral ligament.– Presence of a strong palato-premaxillary ligament between the base of the anterior process of the palatine and the posterodorsal end of the premaxillary ascending processes is a plesiomorphic condition for atherinomorphs. This ligament extends dorsal to the ethmomaxillary ligament forming the so-called crossed ligaments (Schaeffer & Rosen, 1961; Rosen, 1964; Stiassny, 1986). Crossed ligaments are absent in Cyprinodontea (Parenti, 1981) but, contrary to Rosen (1964), well developed crossed rostral ligaments are present in some atheriniforms, namely, in sorgentinins. In mugilids, the palato-premaxillary ligament is attached to the base of the palatine's anterior process and overlaps the ethmomaxillary ligament, but in sorgentinins this ligament is attached to the posterior end of the rostral cartilage rather than to the premaxilla (Figs 4, 22, 26B; De la Hoz & Vial, 1994). A strong palatorostral ligament with this configuration is unique to Sorgentinini. Faint ligamentous fibers attached to the posterior end of the rostral cartilage are present in atherinopsinins and menidiines, but the fibers that extend to the palatine are ventral to the ethmomaxillary ligament. This form of palatorostral ligament is well developed only in the *Atherinella pachylepis* species group and is considered independently derived from that present in sorgentinins. **(0=palatorostral ligament absent; 1=palatorostral ligament present; 0.50, 0.88)**

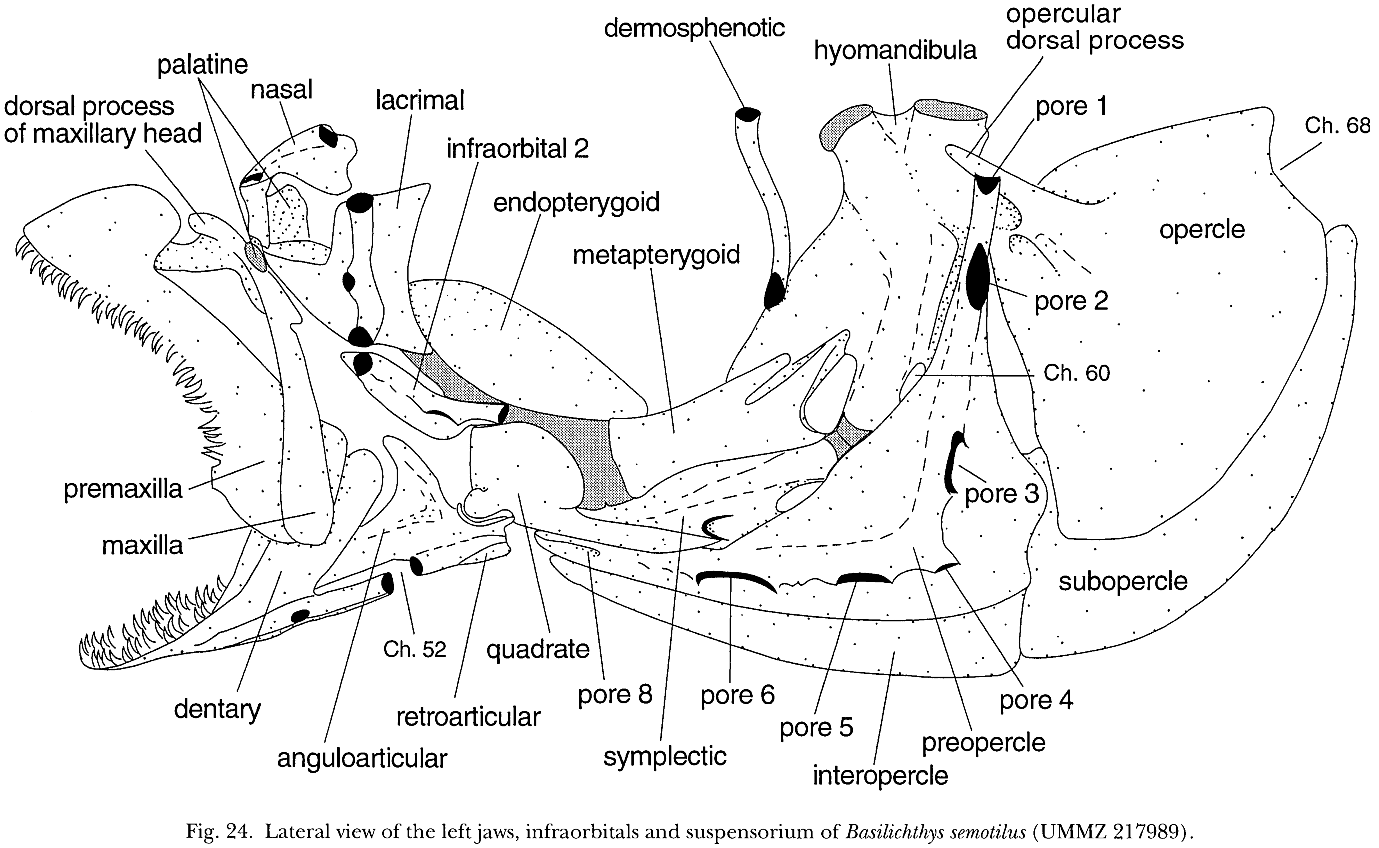

Fig. 24. Lateral view of the left jaws, infraorbitals and suspensorium of *Basilichthys semotilus* (UMMZ 217989).

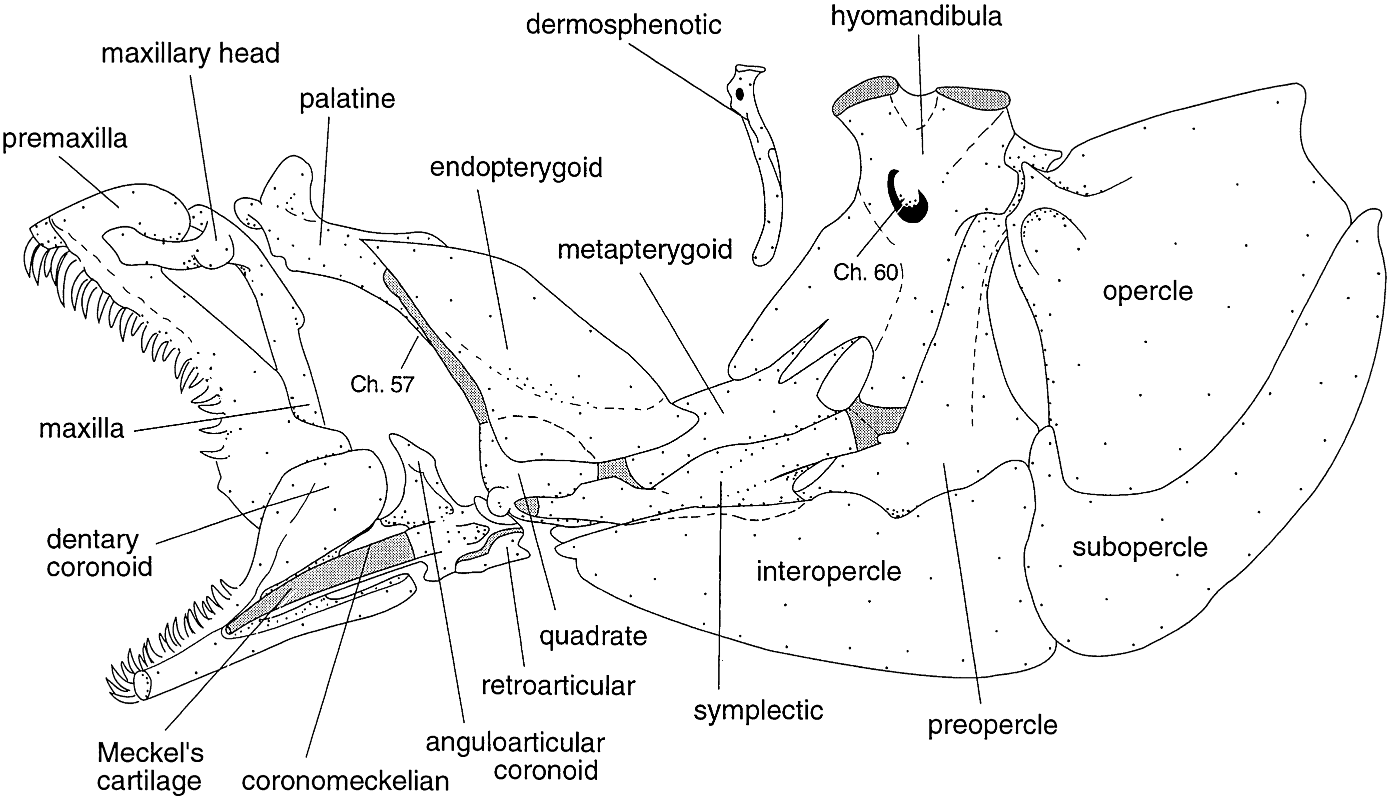

Fig. 25. Medial view of the left jaws and suspensorium of *Basilichthys semotilus* (UMMZ 217989).

57 *Palatine posteroventral spine*.– The posteroventral projection of the palatine extended along the anterior face of the cartilaginous palatoquadrate arch (Fig. 27), but short of the quadrate bone (Figs 20, 25), is regarded as a plesiomorphic feature for atherinomorphs. A derived feature is the extension of this posteroventral spine to contact the quadrate (Figs 17, 18). The derived condition is present in beloniforms, menidiines, *Atherinopsis*, *Leuresthes*, and *Odontesthes* species except for *O. humensis*. The condition in *O. perugiae* species group is ambiguous. **(0=palatine spine not contacting quadrate; 1=palatine spine extended to quadrate; ?=polymorphic; 0.25, 0.63)**

58 *Ectopterygoid*.– The ectopterygoid in mugilids and outgroups is a relatively wide bone folded around the anterior face of the palatoquadrate cartilage, dorsal to the quadrate and ventral to the palatine spine. In atherinopsids, the ectopterygoid is a laminar bone on the medial face of the quadrate and palatoquadrate cartilage (Figs 18, 20). Absence of this laminar bone from the medial side of the suspensorium is a derived condition observed in *Basilichthys* and *O. nigricans* (Fig. 25). Absence of this feature is variable in the *B. microlepidotus* species group and coded as polymorphic in the data matrix (Table 3). In the *B. microlepidotus* species group 54% of the 50 specimens examined lacked the ectopterygoid on both sides, 20% lacked it on one side only, and 26% had it on both sides. **(0=ectopterygoid present; 1=ectopterygoid absent; 0.60, 0.33)**

59 *Endopterygoid teeth*.– Presence of teeth on the ventrolateral surface of the endopterygoid is considered plesiomorphic in atheriniforms, though absent in Cyprinodontea. Size and position of the tooth patches, however, is variable. Within menidiines, teeth are present only in *Membras* and *Atherinella*. Chernoff (1986a) discussed the variable nature of these teeth in the *Atherinella crystallina* complex and attributes this variability to interpopulational gene flow. In Atherinopsinae, endopterygoid teeth are present in most species as well developed or reduced tooth patches. Tooth patches are consistently absent in *Basilichthys* (Figs 20, 25), *Odontesthes hatcheri*, *O. humensis*, and the subgenus *Cauque*. **(0=endopterygoid teeth present; 1=endopterygoid teeth absent; 0.20, 0.43)**

60 *Hyomandibular nerve*.– The plesiomorphic condition for atherinomorphs is for the hyomandibular nerve to penetrate the hyomandibula dorsomedially and ventrolaterally. In atheriniforms, the hyomandibular nerve divides into hyoid and mandibular branches external to the hyomandibular bone, usually at the ventral foramen (Fig. 19). The hyoid nerve branches posteriorly and either penetrates the hyomandibula again or lies between the preopercle and hyomandibula to exit posteromedially (Dyer & Chernoff, 1996: fig. 15A). A derived condition is present in *Leuresthes*, membradins, *Atherion*, *Notocheirus*, and *Odontesthes* species except for *O. hatcheri*, in which the hyomandibular nerve is divided inside the hyomandibula (Figs 17, 18). Another derived condition is presence of a dorsal foramen perforating the hyomandibula dorsally in mugilids, atherinomorines, *Iso*, and *Colpichthys*. **(0=hyomandibular nerve divided external to hyomandibula or at ventral foramen; 1=hyomandibular nerve divided inside of hyomandibula; 2=dorsal foramen of hyomandibular nerve perforates hyomandibula; ?=polymorphic; 0.40, 0.67; n-add)**

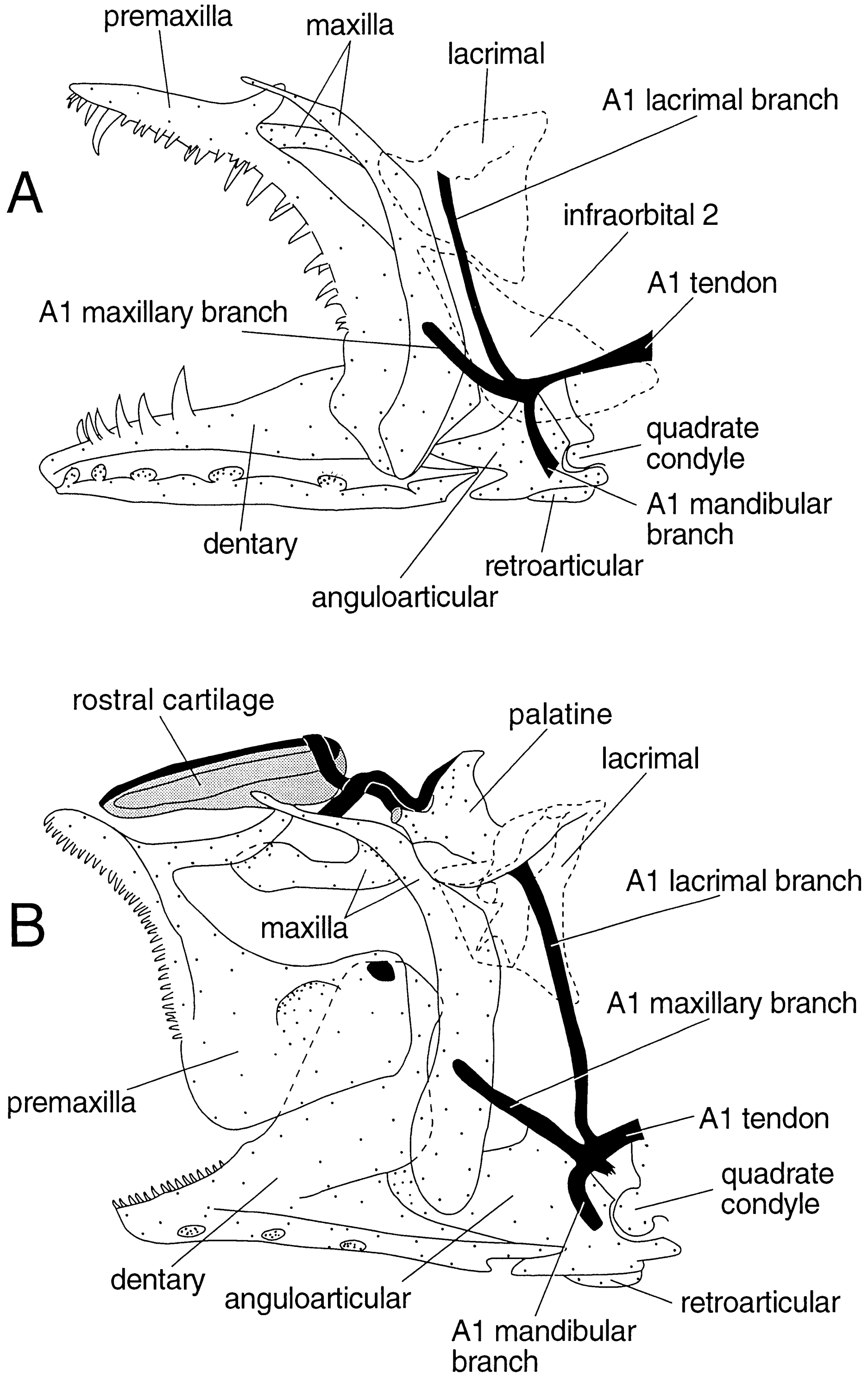

Fig. 26. Diagram in lateral view of the A1 tendon complex of the adductor mandibulae muscle; A, *Chirostoma labarcae* (UMMZ 193463); B, *Odontesthes retropinnis* (UMMZ 231950).

61 Preopercular sensory canal.– The plesiomorphic atheriniform condition is an open preopercular sensory canal, as found in Cyprinodontea, atherinoids, and mugilids (Fig. 28A, 28B). The preopercular sensory canal of the vertical shaft is enclosed by bone between pores two and four in menidiines (Fig. 28C), *Atherinops* (Fig. 28D), and *Atherinopsis* (Chernoff, 1986b). *Melanorhinus*, *Poblana*, *Leuresthes*, *Colpichthys*, and Sorgentinini have both the horizontal and vertical shafts of the preopercular canal enclosed by bone, though a bony bridge is usually lacking between pores one and two (Fig. 17), and between pores seven and eight (Fig. 19). **(0=preopercular sensory canal open; 1=vertical shaft of preopercular sensory canal**

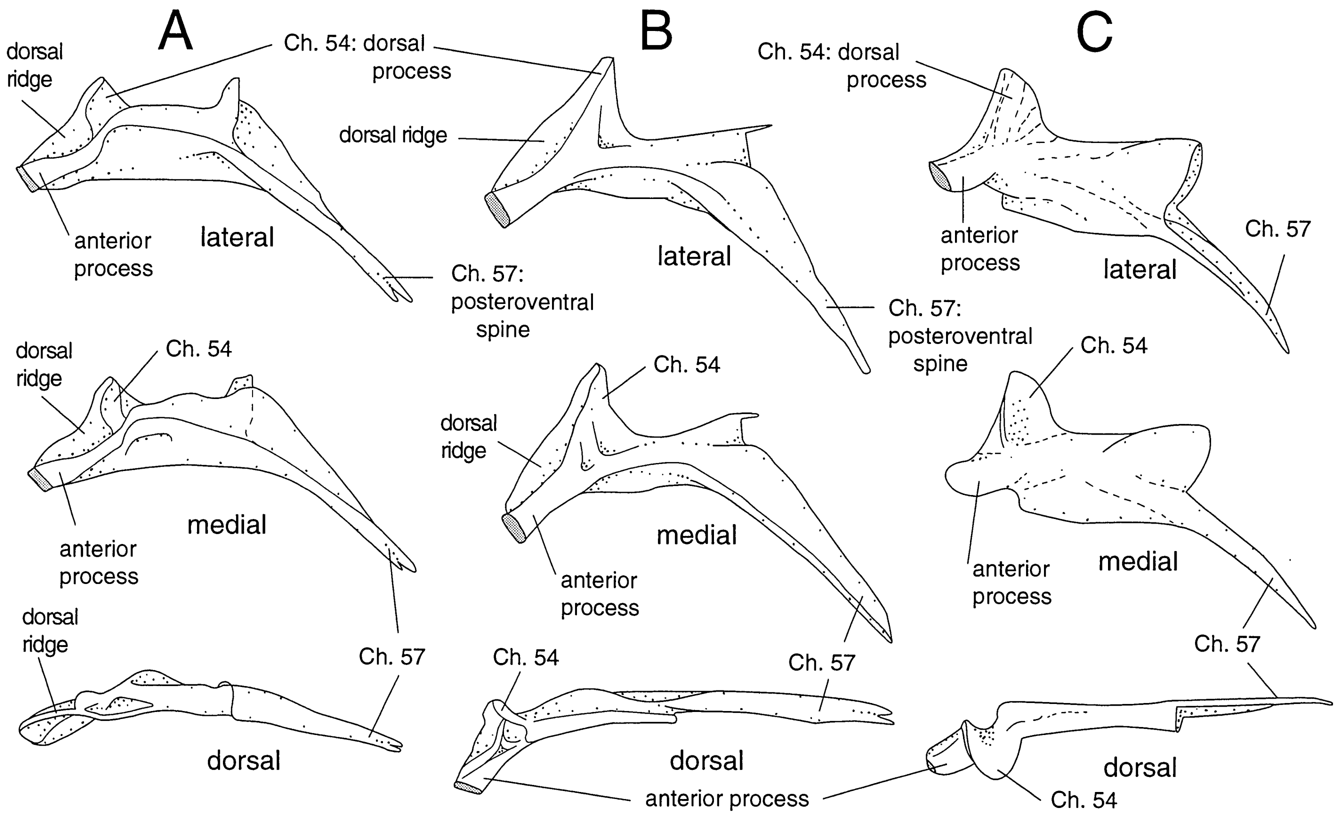

Fig. 27. Lateral, medial, and dorsal views of the left palatine; A, *Menidia beryllina* (UMMZ 107098); B, *Atherinops affinis* (UMMZ 232001); C, *Basilichthys australis* (UMMZ 215508).

enclosed by bone; 2=vertical & horizontal shafts of preopercular sensory canal enclosed by bone; 0.50, 0.80; add)

A greatly enlarged sensory canal system of the head is diagnostic of the subgenus *Cauque*. *Chirostoma labarcae* has the vertical shaft fully enclosed by bone with a bony enclosure between pores four and five on the horizontal shaft.

62 Preopercular sensory canal between pores one and two.– The plesiomorphic condition of atheriniforms is for the preopercular sensory canal between pores one and two to be open (Figs 17, 18). A relatively derived condition present in *Melanorhinus*, some species of *Chirostoma*, *Basilichthys*, and *Odontesthes nigricans* is the bony enclosure of the sensory canal between preopercular pores one and two (Figs 19, 24). Other menidiines have the dorsal shaft folded to a greater extent than atherinoids, but not fully enclosed (Fig. 24B, 28C). **(0=preopercular pores 1 & 2 open; 1=preopercular pores 1 & 2 enclosed; 0.50, 0.67)**

63 Preopercular canal pores on horizontal shaft.– The preopercular sensory canal has three pores on the vertical shaft and five pores on the horizontal shaft in atherinopsids (Figs 17, 19, 28C). A derived condition found in the *Basilichthys semotilus* species group is presence of only four pores on the horizontal shaft, apparently by loss of the pore seven (Figs 11, 24). **(0=preopercular horizontal shaft with 5 pores; 1=preopercular horizontal shaft with 4 pores; ?=unknown; 1.00)**

Six pores are present on the horizontal shaft of *Poblana*.

64 Opercular dorsal process.– Presence of a blade-like laminar flange on the lateral face of the dorsal process of the opercle is a plesiomorphic feature of atheriniforms (Fig. 29). The dilatator operculi muscle is attached to the medial face of this laminar flange which is extended posteroventrally on to the lateral face of the opercle. A derived condition found in *Atherinopsis*, *Basilichthys*, *Odontesthes nigricans* and the subgenus *Austromenidia*, is a rounded dorsal process of the opercle lacking a lateral laminar flange (Figs 19, 24). **(0=opercular dorsal process blade-like; 1=opercular dorsal process not blade-like; 0.25, 0.57)**

65 Opercular fenestration (White, 1985).– A smooth surface at the base of the opercular process is a plesiomorphic feature of atheriniforms (Fig. 29). Presence of fenestration at the anterodorsal corner of the opercle is a unique trait within atheriniforms, and is present in *Odontesthes* except for *O. incisa* (Fig. 18). **(0=no opercular fenestra; 1=opercular fenestra present on medial face; 2=opercular fenestra present on medial and external faces [Dyer, 1993: 350]; 0.33, 0.78; add)**

66 Medial lamina between opercular struts.– The medial face of the opercle has two strut-like thickenings that converge on the hyomandibular condyle of the opercle. The ventral strut is extended along the anterior border of the opercle and the posterior strut is directed posteriorly (Figs 20, 25). Presence of both struts is a plesiomorphic trait and in atherinopsids there is a semicircular space between them (Fig. 25). A derived condition is present in *Odontesthes* species except for *O. perugiae* and

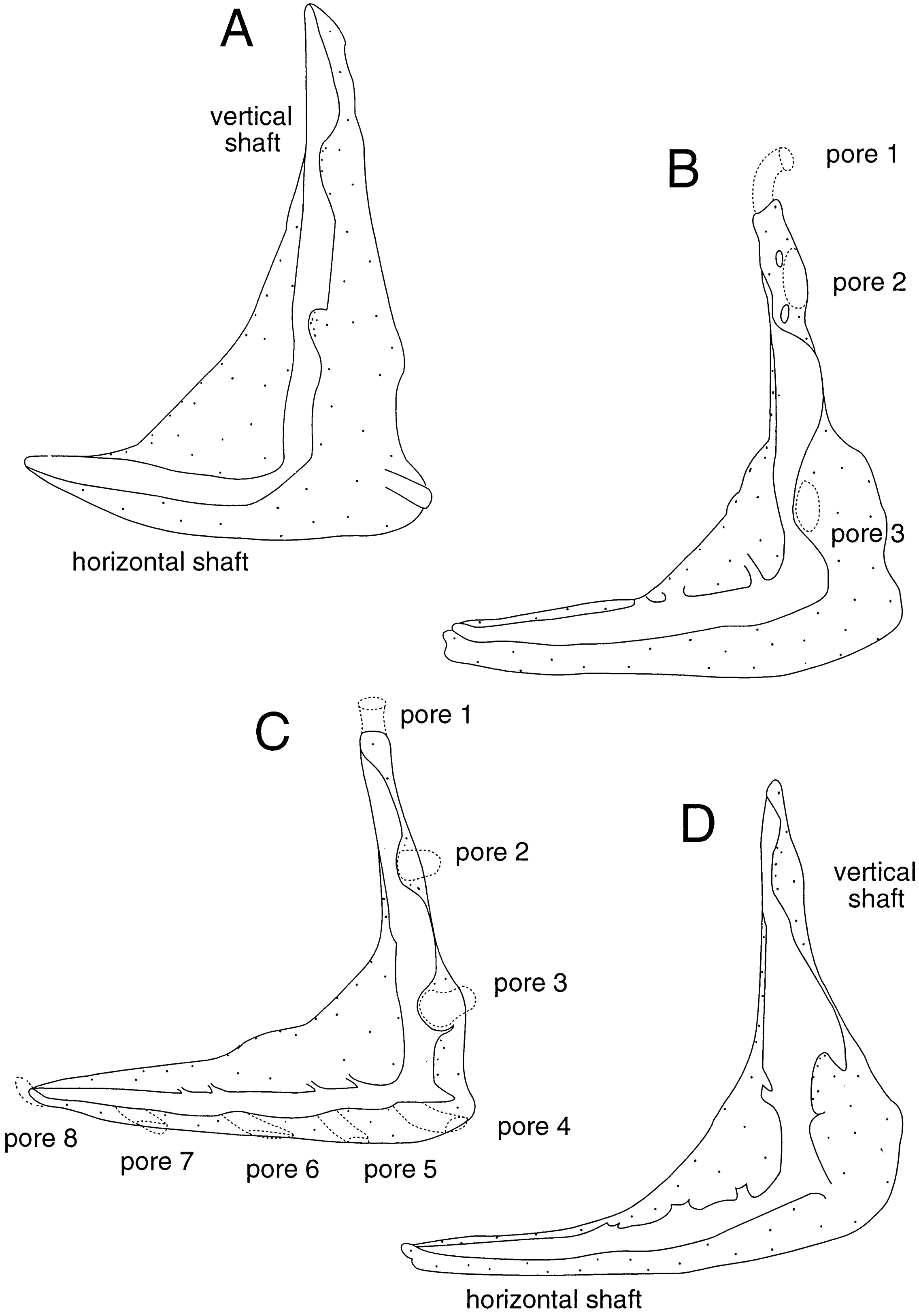

Fig. 28. Lateral view of the left preopercle; A, *Agonostomus monticola* (UMMZ 199463); B, *Atherinomorus bleekeri* (FMNH 57459); C, *Menidia beryllina* (UMMZ 203149); D, *Atherinops affinis* (UMMZ 72212).

O. incisa, in which both struts are interconnected by a greatly fenestrated medial laminar bone (Fig. 18). **(0=no medial lamina between posterior and ventral struts; 1=presence of fenestrated medial lamina between posterior and ventral struts; 0.33, 0.80)**

The posterior strut is greatly reduced to absent in *Oryzias*, notocheirids, *Atherion*, *Chirostoma* (Fig. 29) and *Melanorhinus*.

67 Opercular dorsal border.– The plesiomorphic condition of atheriniforms is for the dorsal border of the opercle to be continuous with the laminar flange of the dorsal process. The derived condition characteristic of atherinopsids is for the dorsal border to be displaced medial to the dorsal process (Figs 19, 20, 29), except in *Odontesthes hatcheri*, *O. perugiae*, and *O. retropinnis* (Figs 17, 18). **(0=dorsal border of opercle continuous with laminar flange of dorsal process; 1=dorsal border of opercle displaced medially; 0.33, 0.67)**

68 Opercular posterodorsal border.– The posterodorsal border of the opercle is concave in atherinomorph outgroups (Fig. 29). A straight or convex posterodorsal border of the opercle is a derived condition present in Cyprinodontea, Atherinoidei, *Labidesthes*, *Membras gilberti*, *Melanorhinus microps*, Atherinopsini, and *Odontesthes* (Figs 17, 18). In atherinopsids, the opercular posterodorsal border is concave in menidiines and *Basilichthys* (Figs 19, 20, 24, 25, 29). **(0=opercle posterodorsal border concave; 1=opercle posterodorsal border straight; 2=opercle posterodorsal border convex; 0.67, 0.77; add)**

69 Opercular posteroventral border.– **(0=opercle posteroventral border convex; 1=opercle posteroventral border concave; 1.00)**

Branchial basket

70 First infrapharyngobranchial.– Presence of an ossified first infrapharyngobranchial is the plesiomorphic condition for atherinomorphs. A derived condition of *Atherion* and Atherinopsini is for the first infrapharyngobranchial to be cartilaginous (Fig. 30). Absence of first infrapharyngobranchial is a further derived condition of Cyprinodontea, *Notocheirus*, and Membradini (Chernoff, 1986b). A cartilaginous nodule found at the distal end of epibranchial 1 in the cyprinodontiforms *Floridichthys carpio, Cualac tessellatus* and *Cynolebias elongatus*, were interpreted as a first infrapharyngobranchial by Parenti (1981: 417). **(0=infrapharyngobranchial 1 ossified; 1=infrapharyngobranchial 1 cartilaginous; 2=infrapharyngobranchial 1 absent; 0.40, 0.50; add)**

71 Cranial processes of second infrapharyngobranchial (Chernoff, 1986b).– The generalized outgroup and atherinopsid condition of infrapharyngobranchial 2 is presence of a cranial process of medium width that runs roughly parallel to infrapharyngobranchial 3 and is articulated with it in a medial groove. Atherinopsini has a clearly derived condition in that the cranial process of infrapharyngobranchial 2 is pointed (with the distal chondral surface of articulation greatly reduced) and

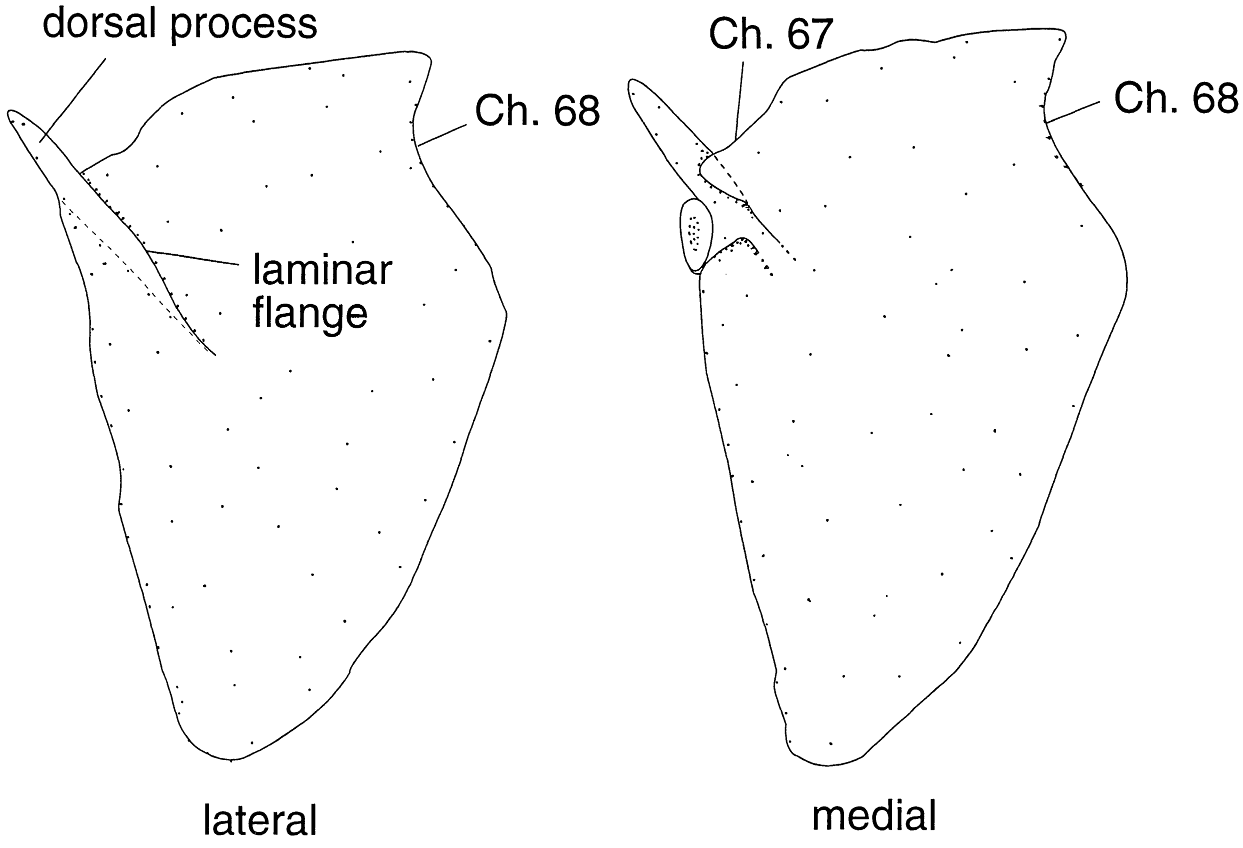

Fig. 29. Lateral and medial views of the opercle of *Chirostoma labarcae* (UMMZ 193463).

at right angles to the cranial process of infrapharyngobranchial 3 (Fig. 30; Chernoff, 1986b: fig. 7D). **(0=infrapharyngobranchial 2 cranial process of median width, mostly parallel to cranial process of infrapharyngobranchial 3; 1=infrapharyngobranchial 2 cranial process pointed, perpendicular to cranial process of infrapharyngobranchial 3; 1.00)**

72 *Third epibranchial uncinate process* (White, 1985).– The plesiomorphic atheriniform condition of epibranchial 3 is for the uncinate process to be placed roughly in the middle of the bone, and a relatively straight and cylindrical shaft between the uncinate process and the articulation of epibranchial 3 with infrapharyngobranchial 3. The third epibranchial of Atherinopsini is derived in that the uncinate process is more laterally attached and elongated (Fig. 30). A further derived condition of epibranchial 3 is for the shaft medial to the uncinate process to be flattened and twisted in *Atherinopsis* and *Leuresthes* (Fig. 30B; White, 1985: fig. 20). **(0=epibranchial 3 cylindrical, with short and mid-placed uncinate process; 1=epibranchial 3 cylindrical, with a long and laterally-placed uncinate process; 2=epibranchial three flattened and twisted, with a long and laterally-placed uncinate process; 1.00 / 0.67, 0.75; add)**

73 *Fourth ceratobranchial tooth plate* (Chernoff, 1986b; White, 1985).– Tooth patches are not present on ceratobranchial 4 in mugilids, beloniforms, *Notocheirus*, and atherinopsines. A tooth patch is present on the proximal end of ceratobranchial 4 in cyprinodontiforms, atherinoids except *Notocheirus*, and menidiines. The "tooth plates" in *Colpichthys* described by White (1985: fig. 4C) are enlarged gill-raker plates supporting hair-like denticles, unlike those present in other atheriniforms and not fused with ceratobranchial 4. In *Colpichthys*, the medial and lateral rows of gill-raker plates contact each other at the dorsal mid-line except anteriorly, where the lateral row of rakers is extended across to the medial side. **(0=no tooth patch on ceratobranchial 4; 1=tooth patch present on ceratobranchial 4; 1.00)**

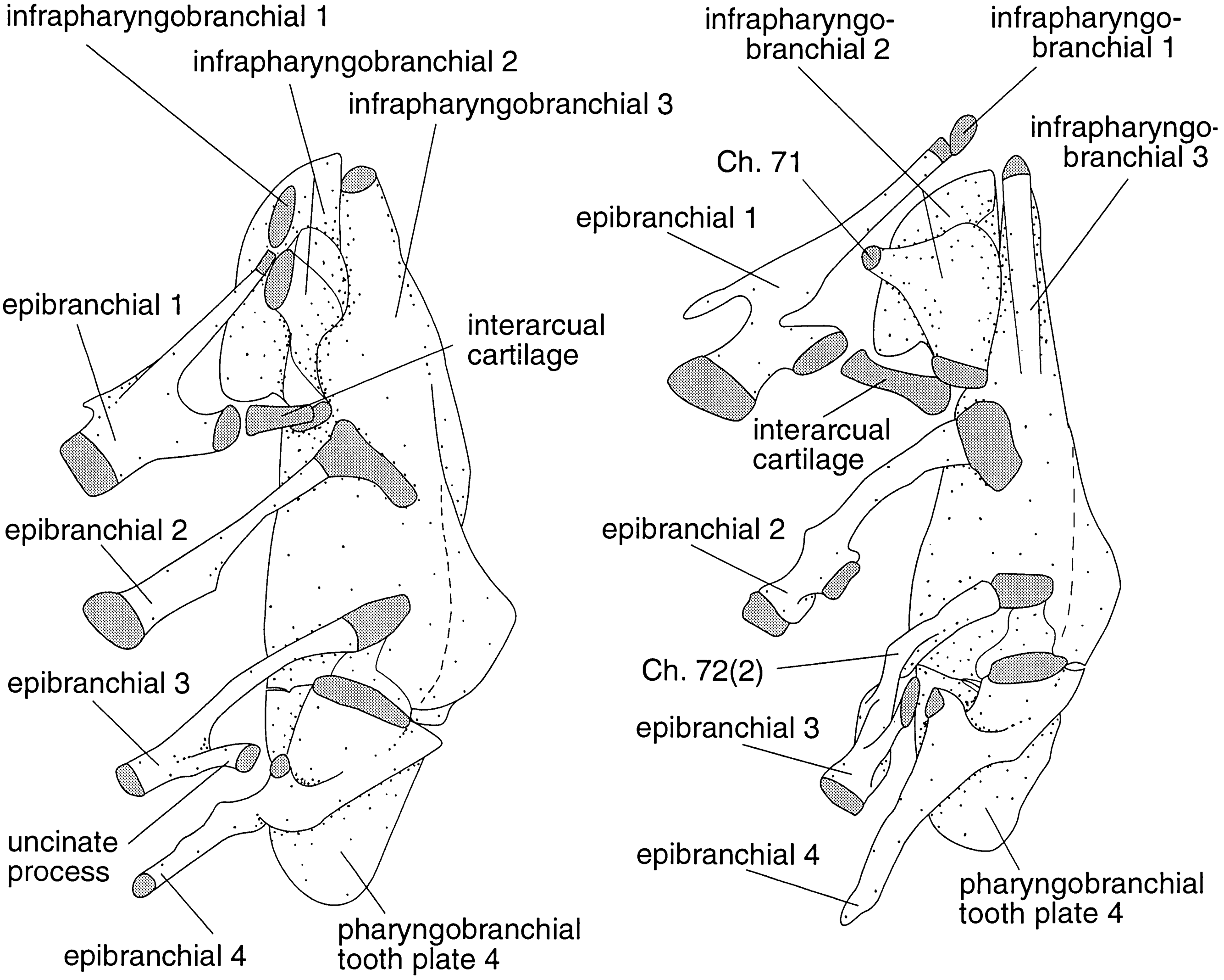

Fig. 30. Dorsal view of the left upper pharyngeal jaw; A, *Atherinops affinis* (UMMZ 72212); B, *Leuresthes tenuis* (UMMZ 65910).

In atherinoids, the tooth plate is fused to ceratobranchial 4 in *Iso*, *Atherion*, phallostehids, and craterocephalines. The tooth plate is over but not fused to ceratobranchial 4 in melanotaeniids, atherinomorines, and atherinines.

74 Urohyal ventral plate.– Plesiomorphically, the ventral border of the urohyal widens posteriorly into an oval-shaped plate (Fig. 31A). This ventral plate is absent in *Atherinops* and *Atherinopsis* (Fig. 31B). This plate is also absent in *Craterocephalus eyresii* species group (Crowley & Ivantsoff, 1992). **(0=urohyal ventral plate present; 1=urohyal ventral plate absent; 0.50, 0.00)**

Pectoral girdle and fin

75 Cleithrum dorsomedial wing.– The anterior border of the dorsal-medial wing of the cleithrum is extended ventrally towards a central medial wing of the cleithrum. The plesiomorphic condition is for the dorsomedial wing to extend ventrally as far as the scapula-coracoid articulation or beyond (Fig. 32A). A derived condition is for the anterior border of the dorsomedial wing to be more curved or involuted, and extended ventrally as far as the scapular foramen at the most (Fig. 32B). The derived condition is present in Menidiinae, *Colpichthys*, and *Odontesthes* species except for *O. hatcheri*, *O. humensis*, *O. perugiae*, and the subgenus *Cauque*. **(0=anterior border of cleithrum dorsomedial wing tapered ventrally to scapula-coracoid articulation or beyond; 1=anterior border of cleithrum dorsomedial wing curved ventrally, extended to scapular foramen at most; 0.20, 0.64)**

76 Baudelot's ligament posterodorsal attachments.– The plesiomorphic condition for atheriniforms is for Baudelot's ligament to be attached posterodorsally to the dorsomedial wing of the cleithrum and anteroventrally to the neurocranium. A derived condition found in atherinopsids, except for *Menidia* and *Labidesthes*, is for Baudelot's ligament to be also attached posterodorsally with the parapophysis and epineural of the first vertebra (Fig. 33). **(0=Baudelot's ligament attached posteriorly to cleithrum only; 1=Baudelot's ligament attached posteriorly to cleithrum, and to parapophysis and epineural of first vertebrae; 1.00)**

77 Pectoral struts (White, 1985).– Dorsal enclosure of the pectoral abductor muscles by the cleithrum is a plesiomorphic feature of Atherinomorpha (Dyer & Chernoff, 1996). A derived feature of atherinopsids is presence of struts, oval in cross-section, between the lateral and medial extensions of the cleithrum (not between cleithrum and scapula as in White, 1985). **(0=no pectoral struts; 1=pectoral struts present; 1.00)**

78 Pectoral-fin spur (Stiassny, 1993).– Presence of a pectoral spur (rudimentary pectoral-fin spine), dorsal and proximal to the second unbranched ray, is the generalized condition in atherinomorphs and mugilids (Stiassny, 1993). Lack of this spur is characteristic of *Notocheirus*, atherinopsids (Fig. 11), and *Gulaphallus*. Stiassny (1993: 210) proposed that the lack of a pectoral spur in atherinopsids is due to ontogenetic fusion of this element with the median hemitrichium of the unbranched pectoral-fin ray. Evidence supporting the fusion of these elements is presence of pectoral spurs in specimens of *Basilichthys* under 30 mm SL (UMMZ 215491; CAS 45197). Conversely, the lack of a pectoral spur in *Notocheirus* and *Gulaphallus* seems to be due to absence of this element because the dorsal ray does not have the characteristic protruding thickness as do atherinopsids (Fig. 11). **(0=pectoral-fin spur present, 1=pectoral-fin spur fused to second pectoral-fin ray, not separate; 1.00)**

79 Ventral postcleithrum position.– The ventral postcleithrum situated anterior to the first pleural rib is the plesiomorphic condition for atheriniforms (Dyer & Chernoff, 1996). A derived condition of atherinopsids and atherinids is for the ventral postcleithrum to be placed between pleural ribs one and two (Fig. 32A). **(0=ventral postcleithrum anterior to pleural rib one; 1=ventral postcleithrum between pleural ribs one and two; 2=ventral postcleithrum between pleural ribs one and three [Dyer, 1993: 353]; ?=polymorphic; 0.67, 0.91; add)**

Atherinopsids share with atherinids and *Dentatherina* an expanded and laminar ventral postcleithrum, connected to the dorsal postcleithrum by a dorsal ramus (Dyer & Chernoff, 1996). Atherinopsids have, in addition, an anterior ramus that attaches mostly to the first pleural rib (Fig. 32; Dyer & Chernoff, 1996: fig. 17).

Pelvic girdle and fin

80 Pelvic bone medial plate (Chernoff, 1986b).– The plesiomorphic condition of atherinomorphs is for the medial plate of the pelvic bone to extend to the anterior end of the longitudinal shaft. In atheriniforms, the pelvic medial plate does not reach the anterior end (Dyer & Chernoff, 1996) except for atherinids, phallostethids, *Atherinella schultzi* and *A. marvelae*, *Leuresthes*, and the subgenus *Cauque* (Fig. 34D). **(0=pelvic medial plate extending to anterior tip; 1=pelvic medial plate not reaching anterior tip; 0.33, 0.50)**

81 Pelvic bone median process.– The plesiomorphic condition of the pelvic median process is a deep, strong, percoid-type articulation between pelvic bones, as found in mugilids (Stiassny, 1990, 1993; Stiassny & Moore, 1992; Johnson & Patterson, 1993: 619). Atherinomorphs exhibit the plesiomorphic acanthomorph condition of flattened pelvic median processes that overlap at the midline (Fig. 34A; Stiassny & Moore, 1992; Saeed *et al.*, 1994). This condition is regarded as a reversal in the context of relationships proposed by Johnson & Patterson (1993). In atherinopsines except for *Leuresthes*, the overlap of the median processes is greatly reduced to absent (Fig. 34C, 34D; De la Hoz & Tosti-Croce, 1981). **(0=pelvic median process percoid-like; 1=pelvic median process flat and overlapping at midline; 2=pelvic median process flat, slightly overlapping or abutting; 0.67, 0.86; add)**

Median fins

82 Position of first dorsal fin.– Origin of the first dorsal fin well in advance of the anus is considered a plesiomorphic feature of atheriniforms. The first dorsal-fin origin located over or posterior to a vertical from the anus, is a derived condition present in atherinoids, menidiines except for *Melanorhinus*, and in *Atherinops*, *Colpichthys hubbsi*, *Leuresthes*, *Odontesthes perugiae*, *O. retropinnis*, *0. bonariensis*, *O. argentinensis*, and *O. incisa* (Fig. 35). **(0=first dorsal fin well in advance of anus; 1=first dorsal-fin origin over or posterior to anus; 0.38)**

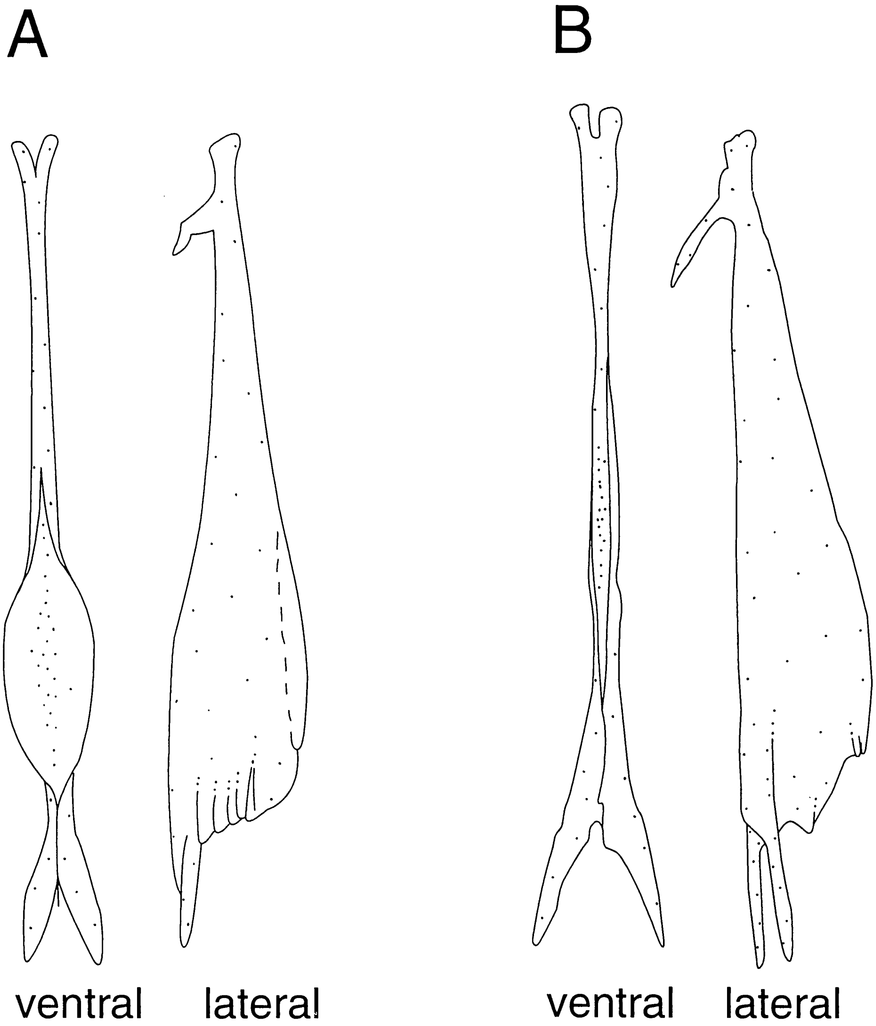

Fig. 31. Lateral and ventral views of the urohyal; A, *Odontesthes regia* (UMMZ 215521); B, *Atherinops affinis* (UMMZ 72212).

In *Colpichthys*, the first dorsal fin is located anterior to the anus in *C. regis* and posterior to the anus in *C. hubbsi*. In atherinoids, the first dorsal fin is anterior to the anus in *Iso*, *Atherion*, and in a few melanotaeniids and atherinids. The posterior position of the first dorsal fin relative to the anus in Atherines is mostly because of an anterior displacement of the anus, effected by presence of the anal plate and elongation of the anal-fin base (Dyer & Chernoff, 1996).

83 Length of spines of first and second dorsal fins.– In atheriniforms and atherinomorph outgroups, the length of the anterior spine of the first dorsal fin is greater than the spinous ray of the second dorsal fin. A derived condition of *Basilichthys* is for the anterior spine of the first dorsal fin to be shorter than the spinous ray of the second dorsal fin (Fig. 36). This feature is especially noticeable in the *B. semotilus* species group which has the first dorsal fin greatly reduced, sometimes absent. **(0=first spine of D1 longer than first spine of D2; 1=first spine of D1 shorter than first spine of D2; 1.00)**

84 Interdorsal pterygiophores.– A series of pterygiophores without associated fin rays between the dorsal fins (interdorsals) is a feature characteristic of some gadiforms (Markle, 1989: fig. 13; Okamura, 1989: figs 3, 4), mugilids, and most atheriniforms (Parenti, 1993: fig. 8). Interdorsals appear to be absent in *Iso* and pseudomugilins (Dyer & Chernoff, 1996), though strictly the last pterygiophore of the first dorsal fin always lacks its corresponding ray (Figs 35-38). *Notocheirus* and Cyprinodontea lack a first dorsal fin and have no rayless pterygiophores anterior to the dorsal fin. The interdorsal pterygiophores of atherinopsids are present as laminar plates, without a ventral shaft, reduced to nodules (ossified or cartilaginous) posteriorly along the dorsal ligament that connects both fins in the vertical septum (Figs 35-38). A continuous series of interdorsal pterygiophores is present in atherinoids except for *Iso*, in most menidiines, *Colpichthys*, and in the sorgentinins *Basilichthys* (Fig. 36), *Odontesthes hatcheri*, *O. humensis*, and the subgenus *Cauque*. All other sorgentinins examined have a gap in the series of interdorsal pterygiophores (Figs 37, 38). **(0=continuous series of interdorsal pterygiophores with ventral shaft; 1=continuous**

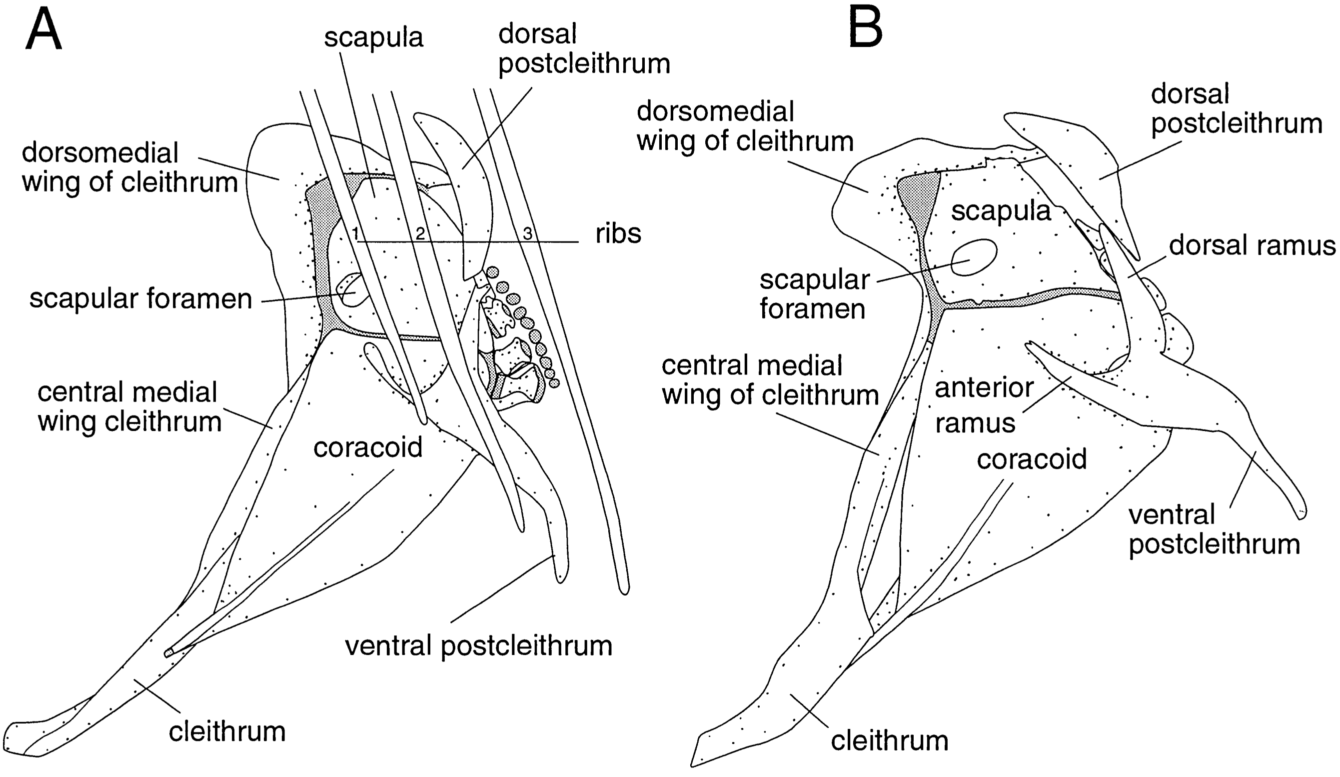

Fig. 32. Medial view of left pectoral girdle; A, *Odontesthes brevianalis* (UMMZ 215459); B, *Odontesthes regia* (UMMZ 215521).

series of interdorsal pterygiophores without ventral shaft; 2=shaftless interdorsal pterygiophore series discontinuous; ?=ambiguous [Dyer, 1993: 354]; 0.50, 0.82 / 0.40, 0.73; add)

85 Number of interdorsal pterygiophores.– Interdorsal pterygiophores (Ch. 84) are found in varying numbers in mugilids and atheriniforms (Parenti, 1993; Dyer & Chernoff, 1996). Mugilids have three or four interdorsal bones. In atherinoids, *Iso* has three interdorsals, *Atherion* and *Dentatherina* have more than six, melanotaeniids have four or fewer, and atherinids have more than five. Menidiines have six to nine interdorsals except for small species of *Menidia* (*colei*, *parva*, etc.) and some species of *Chirostoma* (*labarcae*, *arge*, etc.) and *Poblana*. Atherinopsines with six or more interdorsals include *Colpichthys*, *Odontesthes hatcheri*, *O. humensis*, *O. incisa*, and *Basilichthys* (some specimens have four or five longer bones which seem to be a product of fusion of two elements; Fig. 36). The remainder of atherinopsines have three to six interdorsals, usually four or five (Figs 35, 37, 38). **(0=six or fewer interdorsals; 1=more than six interdorsals; ?=polymorphic [Dyer, 1993: 355]; 0.25, 0.63 / 0.20, 0.50)**

Axial skeleton

86 Number of precaudal and caudal vertebrae.– The plesiomorphic condition found in mugilids, cyprinodontiforms, atherinoids, menidiines, and atherinopsinins is for the number of precaudal vertebrae to be equal to or fewer than the caudal vertebrae. Within atherinopsines the derived condition of having more precaudal vertebrae than caudal vertebrae is present in two states. In *Basilichthys* there are roughly ten more precaudal vertebrae than caudal vertebrae, i.e., precaudal vertebrae account for over 57% of the total number of vertebrae (Fig. 36). Exocoetoids also have at least 60% precaudal vertebrae. *Odontesthes* species have more than 50% precaudal vertebrae except for *O. incisa*, *O. nigricans*, *O. platensis*, and the subgenus *Austromenidia* which have more caudal than precaudal vertebrae. Romer's definition of caudal vertebrae is used (Romer & Parsons, 1986; see Ch. 95 and below in Discussion: Axial skeleton). **(0=precaudal vertebrae under 50% of total vertebrae; 1=precaudal vertebrae more than 50%; 2=precaudal vertebrae over 57%; ?=polymorphic [Dyer, 1993: 356]; 0.67, 0.90; add)**

87 First pleural rib.– **(0=first pleural rib long, attached to ventral postcleithrum; 1=first pleural rib short, not attached to ventral postcleithrum; 0.50, 0.75)**

88 Posterior pleural ribs.– Pleural ribs are attached to the parapophyses of vertebrae three, to the posterior precaudal vertebra, and sometimes to the anterior caudal vertebra. The plesiomorphic condition of atheriniforms is for the posterior ribs to be anterior to the dorsal tip of the first anal-fin pterygiophore (Fig. 38). Presence of two or more pleural ribs posterior to the dorsal tip of the first anal-fin pterygiophore (Figs 35, 37) is a derived feature of melanotaeniids and atherinopsids except for *Membras*, *Melanorhinus*, *Odontesthes platensis*, *O. nigricans*, *O. incisa*, and the subgenus *Austromenidia*. **(0=pleural ribs anterior to first anal-fin pterygiophore; 1=presence of two or more pleural ribs posterior to first anal-fin pterygiophore; 0.50, 0.89)**

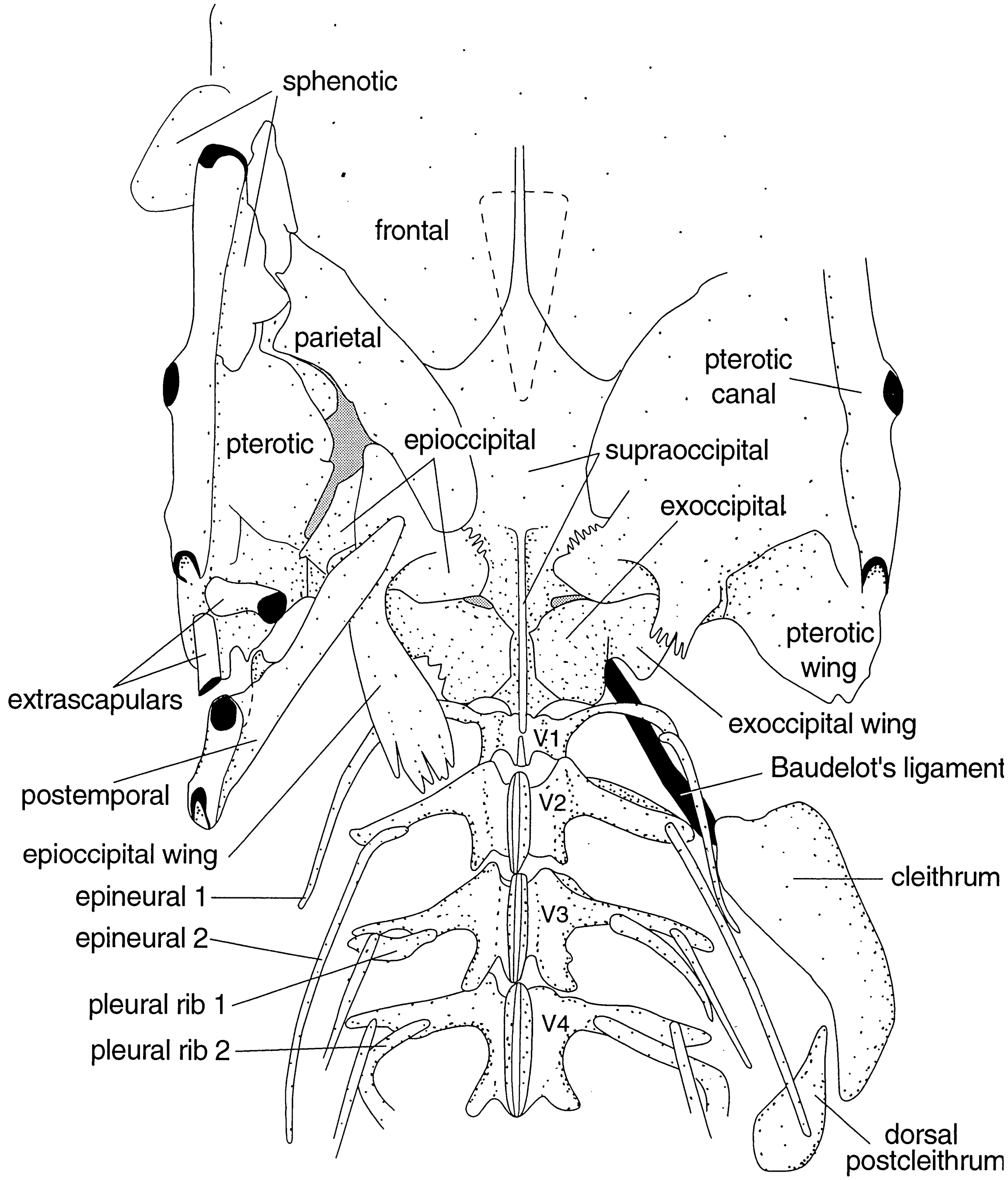

Fig. 33. Dorsal view of the occipital region of the head, pectoral girdle, and anterior vertebrae of *Odontesthes brevianalis* (UMMZ 215459). Left pectoral girdle and right postemporal, extrascapulars, and exoccipital wing removed.

89 Posterior extension of swimbladder into a haemal funnel (White, 1985).– The swimbladder is extended posteriorly to the first caudal vertebrae in atheriniforms and outgroups. A derived feature of atherinopsines except for *Colpichthys hubbsi, Odontesthes incisa*, and *O. nigricans*, is the posterior extension of the swimbladder into a funnel formed by modifications of haemal hypophyses (Fig. 39; Ch. 90) or haemal arches (Fig. 36; Ch. 91), respectively (Schultz, 1948; White, 1985). A similar modification of this sort has evolved independently in some species of atherinines (Patten, 1978; Schultz, 1948), some gadiforms (Ford, 1937; Clothier, 1950), in sillaginids (McKay, 1992), and in some cheiline labrids (Westneat, 1993). **(0=no swimbladder funnel; 1=swimbladder funnel present; 0.67, 0.86)**

90 Haemal-hypophysis funnel (White, 1985).– The haemal hypophysis in atheriniforms and outgroups extends ventrally with no expansions or modifications. A derived feature of atherinopsinins is the posteroventral expansion of haemal hypophyses over the swimbladder to form a swimbladder funnel (Ch. 89), separated by a bony bridge from the dorsal blood ves-

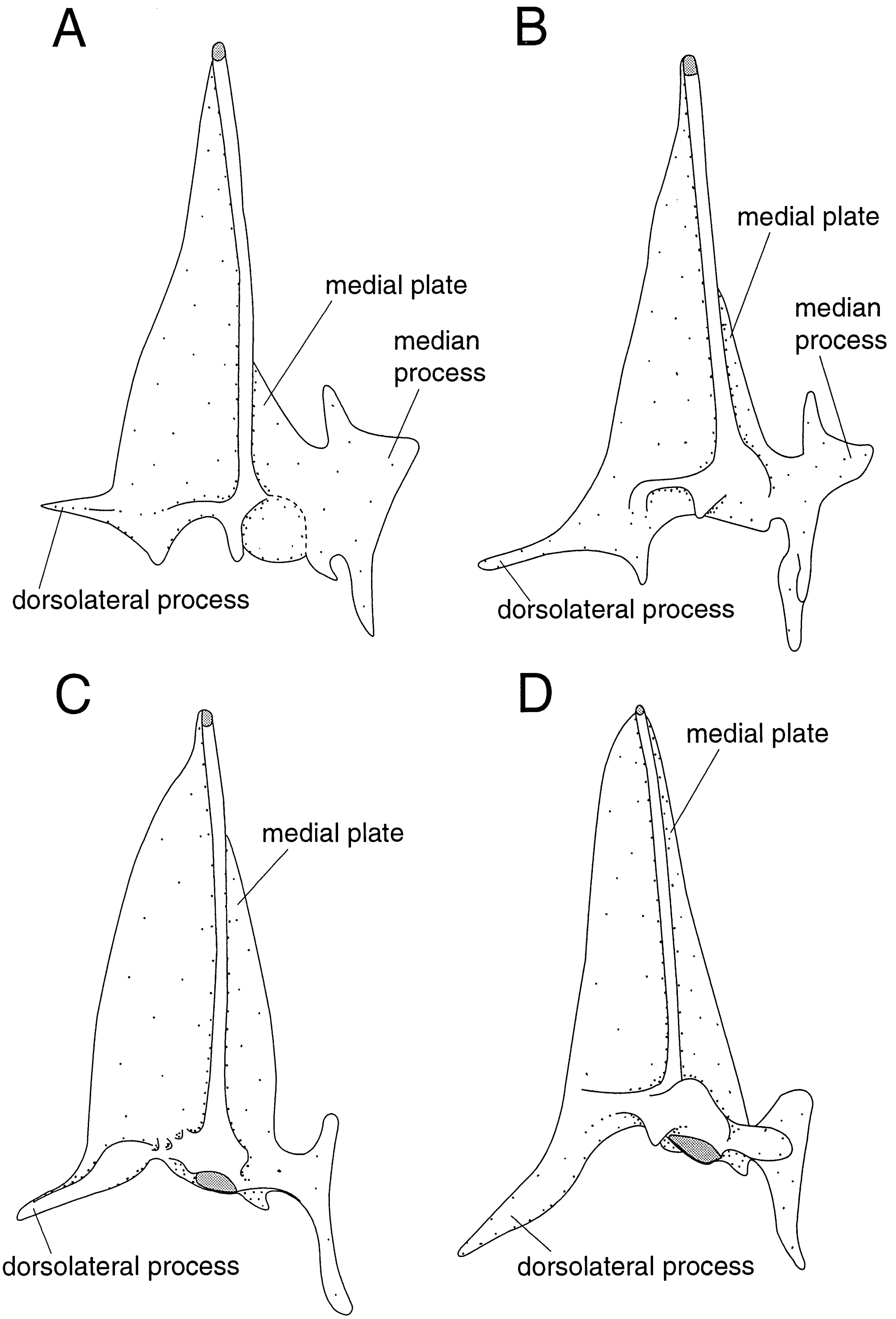

Fig. 34. Ventral view of the left pelvic girdle; A, *Atherinella brasiliensis*; B, *Menidia*; C; *Basilichthys* (UMMZ 215508); D, *Odontesthes brevianalis* (UMMZ 215459). (A & B modified from Chernoff, 1986a)

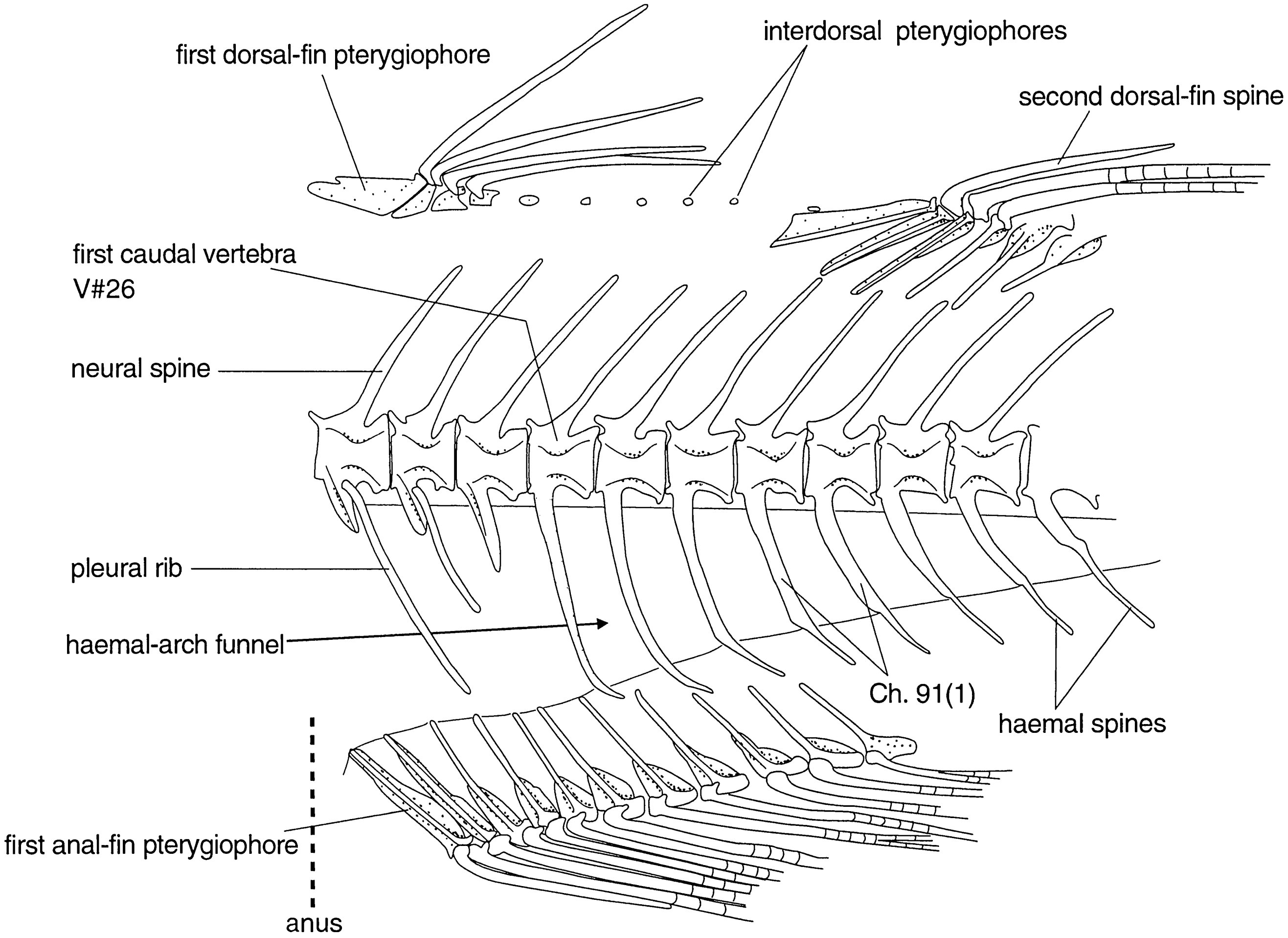

Fig. 35. Lateral view of median fins and axial skeleton of *Odontesthes retropinnis* (UMMZ 231950).

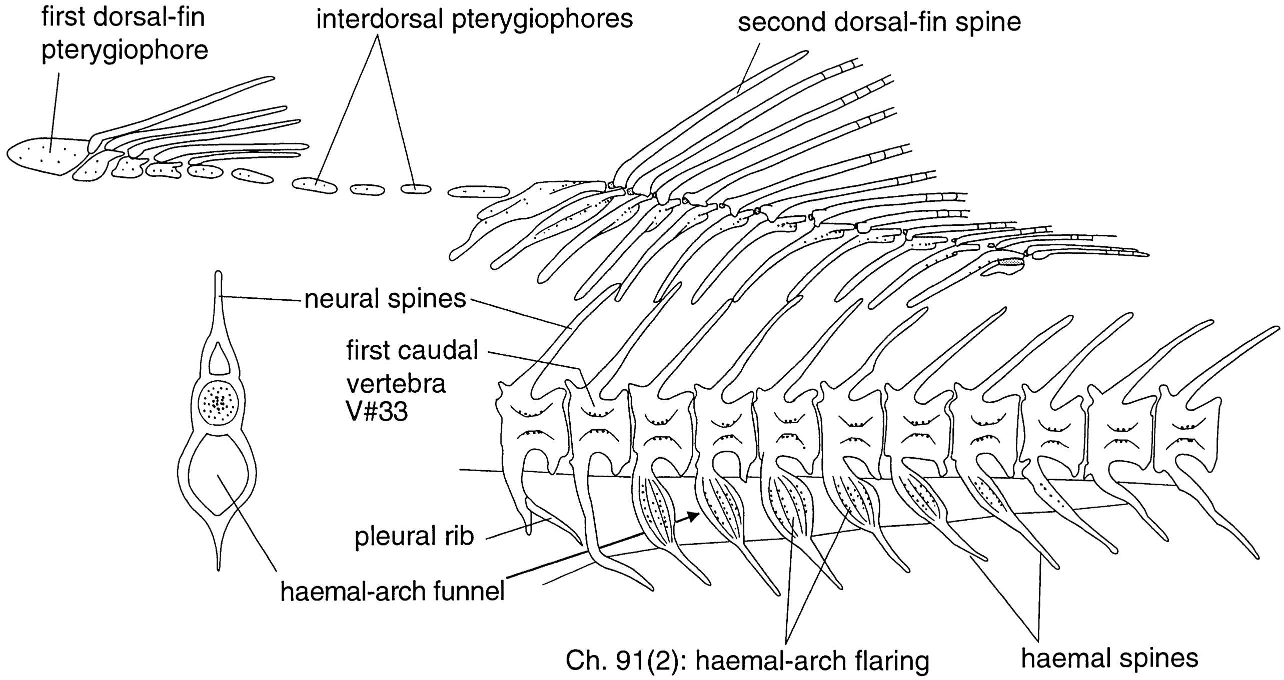

Fig. 36. Frontal view of caudal vertebra, and lateral view of dorsal fins and axial skeleton of *Basilichthys* sp. (UMMZ 215519).

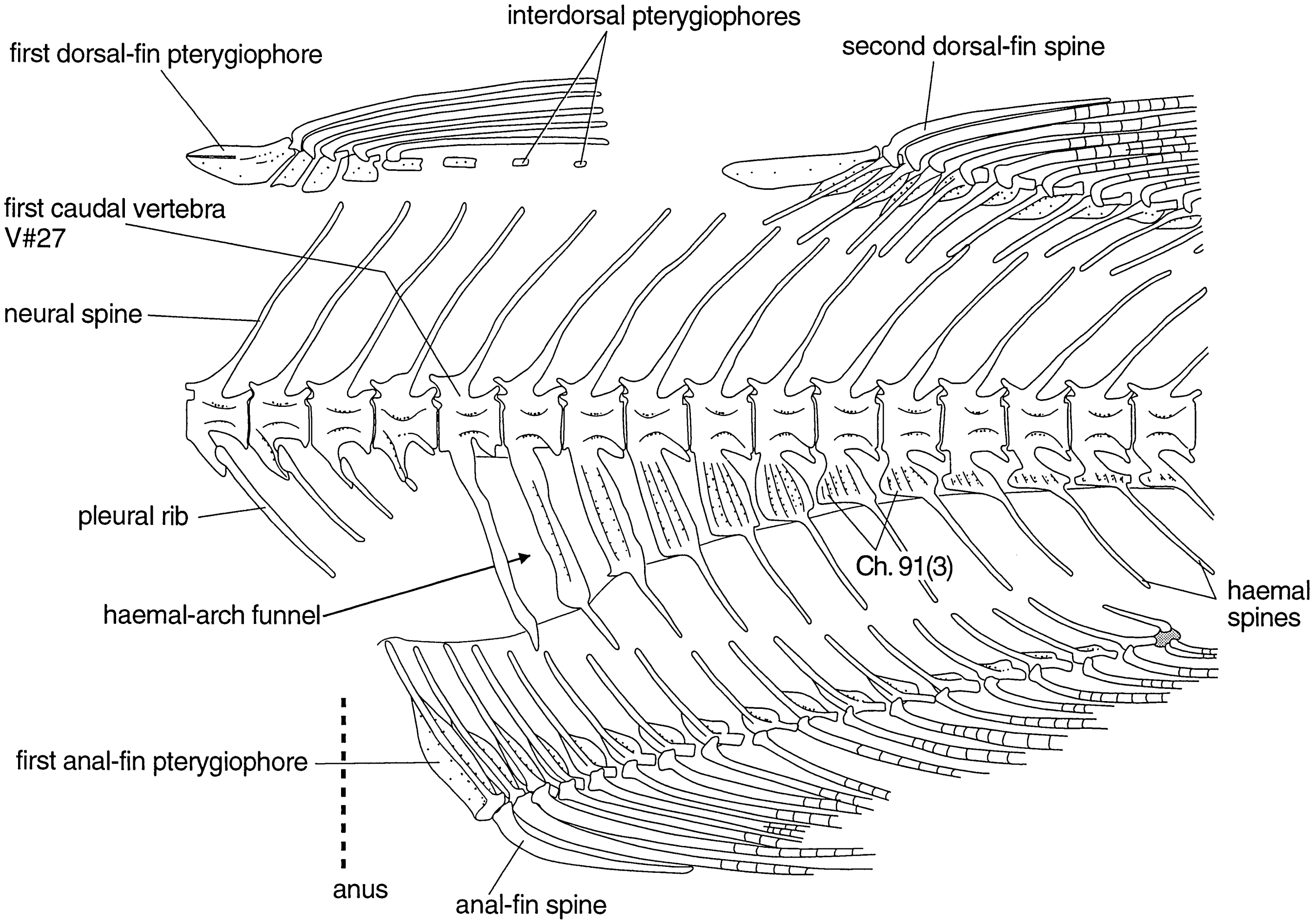

Fig. 37. Lateral view of median fins and axial skeleton of *Odontesthes bonariensis* (UMMZ 218609).

sels (Fig. 39; White, 1985: fig. 11). Haemal-hypophysis expansions are reduced to just two or three vertebrae in *Colpichthys hubbsi* (Crabtree, 1989). **(0=no haemal-hypophysis funnel; 1=haemal-hypophysis funnel present; 1.00)**

The haemal funnel of atherinopsinins resembles that of sillaginids (McKay, 1992) and *Atherinason hepsetoides*, including the separation of the blood vessels from the swimbladder by a bony bridge (Patten, 1978: 123 & fig. 32C; McKay, 1992: figs 6 & 7).

91 *Haemal-arch funnel and expansions* (White, 1985).– The haemal arches in atheriniforms and outgroups have no expansions or modifications. A derived feature of sorgentinins except for *Odontesthes incisa* and *O. nigricans* is the posterior projection of the swimbladder, together with the major blood vessels, into expanded haemal arches (Figs 35-38; White, 1985: fig. 11; De la Hoz & Tosti-Croce, 1981: fig. 12). The haemal-arch funnel of sorgentinins is present in four conditions, each state inclusive of the previous: *O. hatcheri* and *O. retropinnis* have a haemal funnel but lack any form of flaring or projections (Fig. 35); sorgentinins except for the four species mentioned above, have flaring expansions of the haemal arches (Fig. 36); *Odontesthes* species except the four species mentioned above, have an anterior projection from the spine base of the haemal arches in the posterior region of the haemal funnel (Fig. 37); and *O. smitti*, *O. regia*, *O. gracilis* (subgenus *Austromenidia)* have anterior and posterior projections restricted to the base of the haemal arches in the posterior region of the haemal funnel (Fig. 38). The flaring of the haemal arches is most developed anteriorly except for the most anterior one (Figs 36-38). **(0=no haemal-arch funnel; 1=haemal-arch funnel present; 2=haemal-arch flaring present; 3=anterior haemal-arch projections present; 4=anteroposterior haemal-arch projections present, restricted to ventral half of haemal arch [Dyer, 1993: 358]; 0.40, 0.81; add)**

92 *Posterior extension of the haemal-arch funnel.*– **(0=haemal-arch funnel extended posteriorly to end of anal fin or beyond; 1=haemal-arch funnel extended to mid-anal fin; 0.50, 0.67)**

93 *Haemal-arch funnel floor shape.*– **(0=haemal-arch funnel floor gradually tapering posteriorly, bulged ventrally; 1=haemal-arch funnel floor abruptly tapering posteriorly, bulged dorsally; 1.00)**

94 *Haemal-spine length.*– Haemal spines of the anterior haemal arches are primitively long. A derived condition present in *Odontesthes hatcheri*, *O. humensis*, *O. bonariensis*, *O. perugiae*, and *O. retropinnis* is for the first three haemal spines to be short (Figs 35, 37). **(0=anterior haemal spines long; 1=anterior haemal spines short; 0.50, 0.75)**

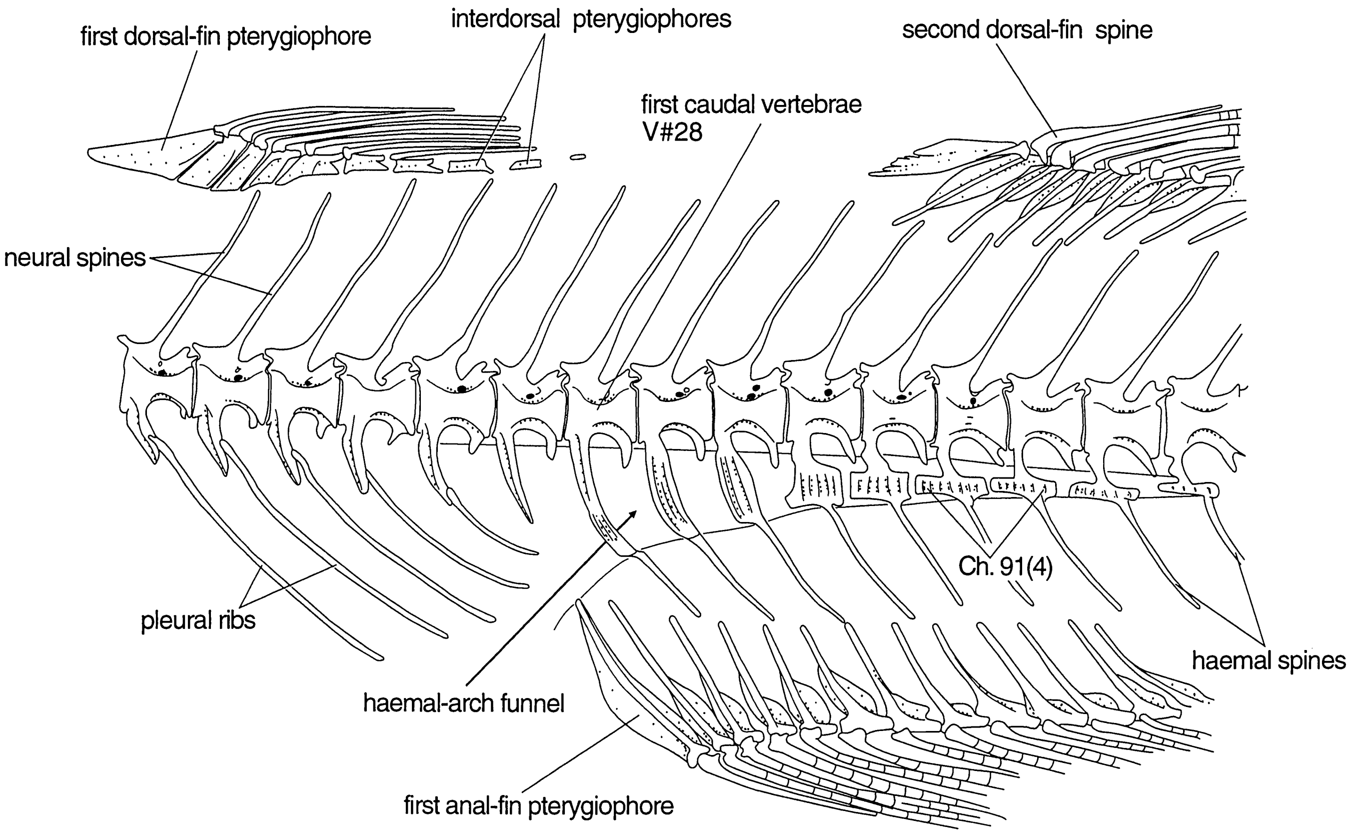

Fig. 38. Lateral view of median fins and axial skeleton of *Odontesthes regia* (UMMZ 215521).

95 Position of first caudal vertebra.– The first caudal vertebra (see below, Discussion: Axial skeleton) located anterior to a vertical from the anal-fin origin is a plesiomorphic feature for atheriniforms (Fig. 38). The derived condition is for the first caudal vertebra to be located posterior to a vertical from the anal-fin origin and dorsal to the anterior half of the anal fin. This derived condition is found in menidiines except for *Melanorhinus* and small *Menidia* species, and in *Odontesthes hatcheri, O. humensis, O. perugiae,* and *O. retropinnis* (Fig. 35). A further derived condition found in *Basilichthys* is for the first caudal vertebra to lie dorsal to the posterior half of the anal fin. **(0=first caudal vertebrae anterior to anal-fin origin; 1=first caudal vertebrae dorsal to anterior half of anal fin; 2=first caudal vertebrae dorsal to posterior half of anal fin; ?=polymorphic [Dyer, 1993: 359]; 0.50, 0.80; add)**

Scales

96 Imbrication of dorsal head scales (Thompson, 1916).– The plesiomorphic condition found in atheriniforms is for the dorsal scales of the head, over the frontals, to have regular imbrication, i.e., anterior border imbedded in the skin and posterior border free. A uniquely derived condition found in *Basilichthys* is for scales in the interorbital region to have reversed imbrication (Fig. 16). In the *B. microlepidotus* species group the occiput scale (transition scale between regular and reversed imbrication) is in a nuchal position (Fig. 16A), whereas in the *B. semotilus* species group the occiput scale is located at the level of the postorbital rim (Fig. 16B). **(0=dorsal head scales with regular imbrication; 1=reversed imbrication of dorsal head scales with occiput scale in nuchal position; 2=reversed imbrication of dorsal head scales with occiput scale at postorbital rim; 1.00; add)**

Thompson (1916: 464) was first to describe this distinctive and highly unusual feature of *Basilichthys*, which was subsequently used by Jordan & Hubbs (1919), Hildebrand (1946), and Arratia (1981). Thompson (1916) also described the presence of this feature in *Menidia albumus* Günther (=*Odontesthes nigricans*) restricted to the anterior two or three rows of scales. I was unable to confirm this observation on the type specimens or on any other available specimens of *O. nigricans.*

97 Number of suborbital scale rows.– Three rows of scales below the orbit in adult specimens is considered the plesiomorphic condition for atheriniforms. Three suborbital scale rows are found in mugilids, cyprinodontiforms, *Notocheirus,* Atherinopsini except *Atherinops, Odontesthes hatcheri, O. humensis, O. bonariensis, O. incisa,* and *O. gracilis.* Two suborbital rows are found in menidiines, *Atherinops, Odontesthes perugiae* (Fig. 23A), and *O. retropinnis.* Four suborbital scale rows are found in *Basilichthys* (Fig. 23B, 23C), *Odontesthes argentinensis, O. platensis, O. nigricans, O. regia, O. smitti,* and the subgenus *Cauque.* **(0=three suborbital scale rows; 1=four suborbital scale rows; 2=two suborbital scale rows; ?=polymorphic; 0.29, 0.58; n-add)**

98 Interopercle scales.– Presence of scales along the entire length of the interopercle is a plesiomorphic feature of atheriniforms (Fig. 17). A derived condition found in *Basilichthys, Odontesthes nigricans, O. humensis,* and the subgenus

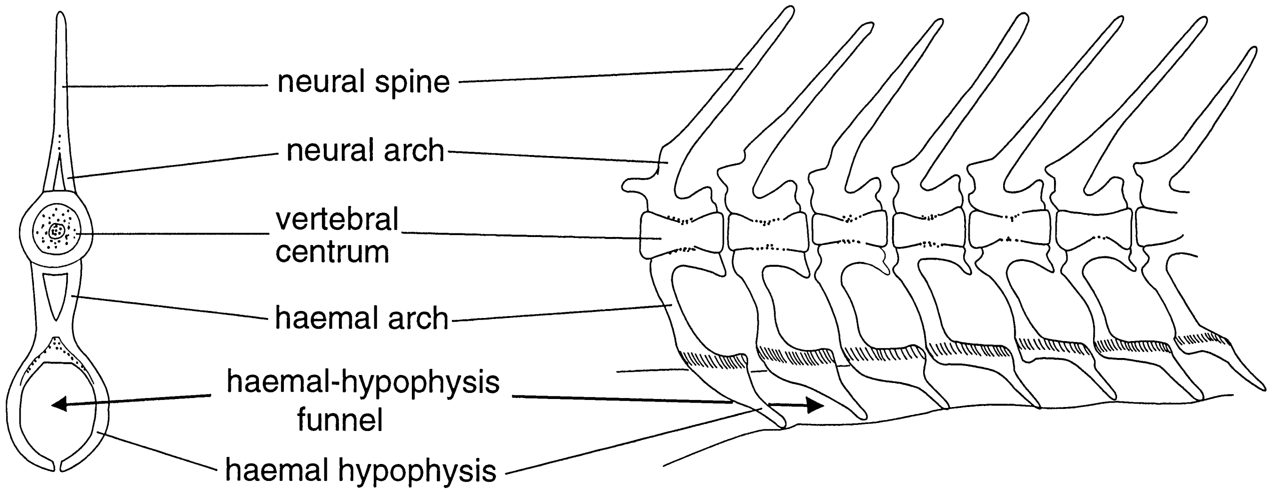

Fig. 39. Lateral and frontal views of anterior caudal vertebrae of *Atherinops* (modified from White, 1985).

Cauque is presence of scales on the posterior half only of the interopercular bone (Fig. 19). **(0=interopercle fully scaled; 1=interopercle with scales on posterior half only; 0.25, 0.40)**

Populations of the *B. semotilus* species group from Río San Juan, Cajamarca, and Río Rimac, Lima, and some populations of *B. australis* have a few scales on the anterior half of the interopercle, but they do not extend to the anterior end of the bone as in the plesiomorphic condition.

In Cyprinodontea, the interopercle is not exposed laterally and lacks scales. *Atherion* and *Iso* also lack interopercular scales.

99 Cleithrum scales.– No scales on the lateral shaft of the cleithrum is a plesiomorphic feature of atheriniforms. A derived condition is presence of large scales along the entire length of the cleithral lateral shaft (Fig. 40). This derived condition is present in atherinopsinins except for *Atherinops*, and in *Odontesthes* species *O. hatcheri*, *O. argentinensis*, subgenus *Cauque*, *O. nigricans*, *O. incisa*, *O. platensis*, and the subgenus *Austromenidia*. **(0=no scales on cleithrum shaft; 1=scales present along cleithrum shaft; 2=small scales only present along cleithrum shaft [Dyer, 1993: 361]; 0.29, 0.67; add)**

100 Scales on second dorsal fin.– Second dorsal fin without scales is a plesiomorphic feature of atheriniforms. Presence of scale rows between rays at the anterior base of the second dorsal fin, though present in mugilids, is considered derived in *Leuresthes*, *Basilichthys semotilus*, *Odontesthes humensis*, *O. perugiae*, *O. retropinnis*, *O. bonariensis*, and *O. argentinensis*. **(0=no scales between rays on second dorsal fin; 1=scales present between anterior rays of second dorsal fin; 0.20, 0.43)**

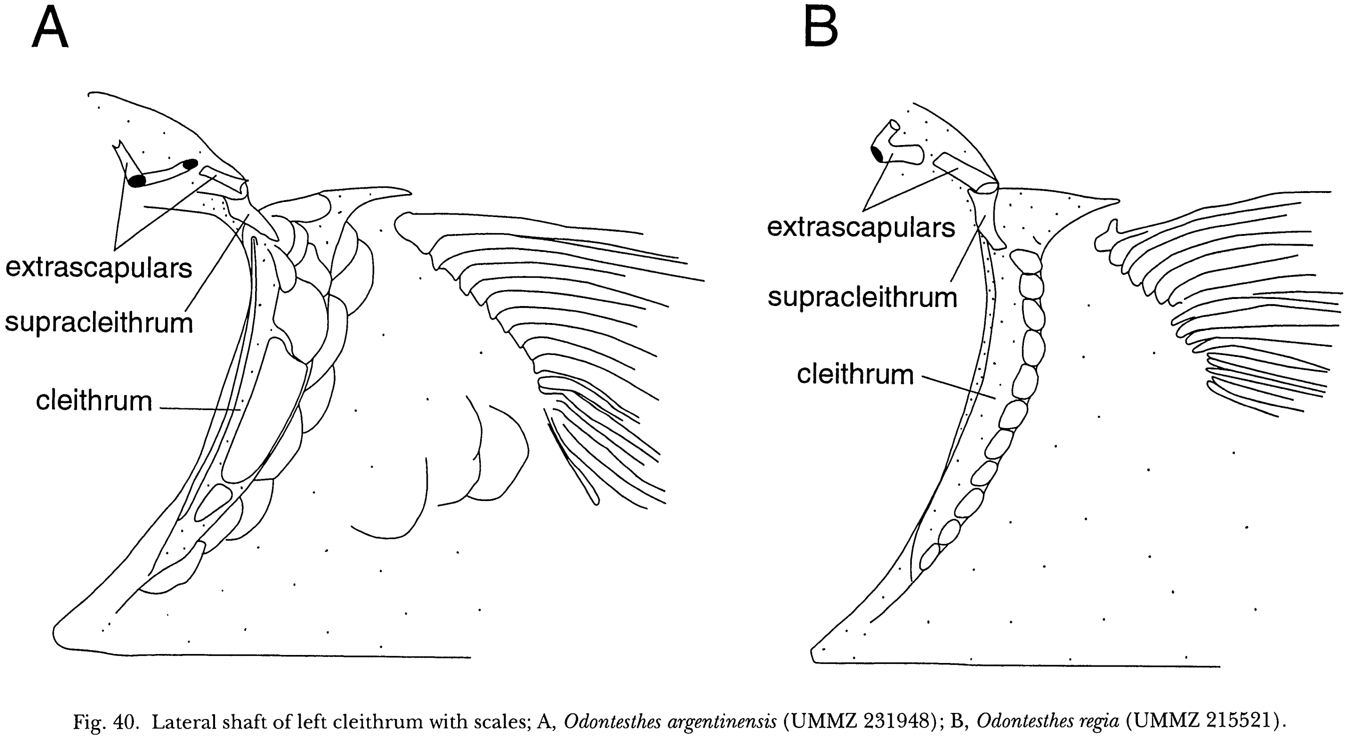

Fig. 40. Lateral shaft of left cleithrum with scales; A, *Odontesthes argentinensis* (UMMZ 231948); B, *Odontesthes regia* (UMMZ 215521).

This feature is not to be confused with the sheath of body scales raised along the base of the second dorsal fin present in *Membras* and *Melanorhinus* (Chernoff, 1986b: 237).

101 Scales on anal fin.– Anal fin without scales is considered a plesiomorphic feature for atheriniforms. The derived presence of rows of scales between rays at the anterior base of the anal fin is found in mugilids, in atherinopsinins except for *Colpichthys*, in *Basilichthys semotilus*, and in *Odontesthes hatcheri, O. humensis, O. perugiae, O. retropinnis, O. bonariensis, O. argentinensis*, and subgenus *Cauque*. This feature is not to be confused with the sheath of body scales raised along the base of the anal fin present in most membradins (Chernoff, 1986b: 237). **(0=no scales on anal fin; 1=scales present between anterior rays of anal fin; 0.20, 0,64 / 0.17, 0.55)**

102 Scale size.– The size of scales is usually estimated by the number of scales on the lateral sensory line or, in the case of silversides, along the lateral band. Because the number of lateral scales is associated with the number of vertebrae, which is quite variable, the number of scale rows that extend over the dorsum between the lateral bands is considered a more accurate estimate of scale size among closely related species. Relatively large scales is the plesiomorphic condition in atheriniforms. Small scales are a derived condition and are found in some species of *Chirostoma*, in *Atherinopsis*, and in the sorgentinins *Basilichthys, Odontesthes hatcheri, O. nigricans*, subgenus *Cauque, O. platensis*, and the subgenus *Austromenidia*. **(0=large scales [≤11 dorsal scales]; 1=small scales [≥12 dorsal scales]; 0.20, 0.60)**

103 Posterior border of scales.– **(0=body scales cycloid with posterior border smooth; 1=predorsal scales crenate; 2=all body scales crenate; 0.50, 0.60; add)**

104 Monophyly of Atherinomorpha (Stiassny, 1990, 1993; Parenti, 1993).– Of a list of 18 characters compiled from Parenti (1993) and Stiassny (1993), five unique features are selected to diagnose atherinomorphs: (1) spermatogonia restricted to distal end of testicular tubules; (2) pelvic girdles lacking median suture and dorsolateral processes associated with pleural ribs (Fig. 34); (3) supracleithrum reduced and saddled on cleithral dorsal enclosure rather than laterally; (4) enlarged fourth epibranchial and fourth infrapharyngobranchial (Fig. 30); and (5) olfactory sensory epithelium arranged in sensory islets. The above-listed characters were used to provide Ch. 104 with a weight of five in the analysis. **(1.00)**

105 Monophyly of Atheriniformes (Dyer & Chernoff, 1996).– Of a list of ten characters listed by Dyer & Chernoff (1996) as diagnostic of atheriniforms, three unique characters are selected for the purpose of this study: (1) larval pigmentation pattern and preanal length; (2) lacrimal branch of A1 muscle tendon long, attached to subnasal shelf of lacrimal bone (Figs 22, 26); and (3) presence of a pelvic-rib ligament. The above-listed characters were used to provide Ch. 105 with a weight of three in the analysis. **(1.00)**

106 Monophyly of Menidiinae (Chernoff, 1986b).– Of a list of eight characters proposed by Chernoff (1986b), seven are corroborated as diagnostic of Menidiinae: (1) parapophysis of vertebra 1 enlarged; (2) epineural 1 short, attached posteriorly to dorsomedial wing of cleithrum; (3) infrapharyngobranchial 2 with deep medial groove; (4) infrapharyngobranchial 2 tooth plate short and wide; (5) vagus nerve foramen with posterior wall (Fig. 13); (6) urohyal pedicel with wide dorsal surface; and (7) pelvic bone with ventral cradle for fin rays. The above-listed characters were used to provide Ch. 106 with a weight of seven in the analysis. **(1.00)**

Allozyme characters

107 - 123 Character-state coded allozyme data (Crabtree, 1987).– The following is a list of the characters taken from Crabtree (1987) in the order of his table 4. The name of each allozyme character is followed by its acronym in brackets and the number of character states. Character states are coded quantitatively and qualitatively, and as in Table 3, qualitative coding is in parenthesis only when the two coding schemes differ.

107: Adenylate kinase [Ak-A:4] (**1.00**); *108:* Aminopeptidase [Ap-A:2] (**1.00**); *109:* Aspartate aminotransferase [M-Aat-A:5] (**1.00**); *110:* Aspartate aminotransferase [S-Aat-A:6] (**1.00, 0.0**); *111:* Dipeptidase [Dip-A:5(7)] (**0.80, 0.0/1.00 (1.00, 0.0)**); *112:* Esterase [Est-1:5] (**1.00, 0.0**); *113:* Glucose-6-phosphate isomerase [Gpi-A:6] (**1.00, 0.0**); *114:* Glucose-6-phosphate isomerase [Gpi-B:7] (**1.00, 0.0**); *115:* Glutamate dehydrogenase [Gtdh-A:4(5)] (**1.00**); *116:* Glycerol-3-phosphate dehydrogenase [G3pdh-A:8(9)] (**1.00, 0.0**); *117:* Isocitrate dehydrogenase [M-Icdh-A:3] (**1.00, 0.0**); *118:* L-lactate dehydrogenase [Ldh-A:9] (**1.00, 0.0**); *119:* Malate dehydrogenase [S-Mdh-A:4] (**0.75, 0.50**); *120:* Malate dehydrogenase [S-Mdh-B:5(7)] (**1.00(1.00, 0.0)**); *121:* Phosphoglucomutase [Pgm-A:8(9)] (**1.00, 0.0**); *122:* Pyruvate kinase [Pk-A:8] (**1.00, 0.0**); and *123:* Superoxide dismutase [Sod-A:6] (**1.00**). **(?=unknown; all n-add)**

SYSTEMATICS

Claims of monophyly are supported solely by diagnostic features, i.e., characters that are unambiguously derived at that node (whether unique or homoplasious) in the context of the proposed hypothesis of phylogenetic relationships. A complete list of diagnostic and supporting characters is presented in Appendix 2. Most nodes have an additional suite of characters that are ambiguously optimized at that node but are, nevertheless, deemed informative of the group's historical identity (Dyer & Chernoff, 1996). Rather than choosing a single optimization criterion for all characters prior to the phylogenetic analysis, each ambiguous character state is optimized *a posteriori* by distinguishing types of ambiguity (Appendix 3).

Monophyly of Atherinopsidae

Atherinopsidae comprises the New World silverside subfamilies Menidiinae and Atherinopsinae. Atherinopsids have traditionally been considered a part of Atherinidae (Jordan & Hubbs, 1919; Schultz, 1948; Patten, 1978; White, 1985; Chernoff, 1986b), but here and in Dyer & Chernoff (1996) they are considered instead as the sister group to all other atheriniforms. A total of 20 diagnostic characters support Atherinopsidae as monophyletic: sphenotic postorbital process wide at base (Ch. 18), dermosphenotic not articulated to postorbital process (Ch. 19) and with sensory canal enclosed (Ch. 20), presence of pterotic wing (Ch. 29) and exoccipital wing (Ch. 30), postemporal with anterior process (Ch. 36), premaxilla with narrow anterior joint (Ch. 39), premaxillary alveolar arm greatly expanded (Ch. 44), premaxilla-dentary coronoid ligament very short (Ch. 45), presence of a maxilla-anguloarticular ligament (Ch. 46), premaxilla-maxilla ligament long (Ch. 47), ethmomaxillary ligament with palatine attachment (Ch. 55), vertical shaft of preopercular canal enclosed (Ch. 61), dorsal border of opercle displaced medially from dorsal process (Ch. 67), Baudelot's ligament posteriorly attached to cleithrum, parapophysis and epineural of vertebrae 1 (Ch. 76), presence of pectoral struts in cleithral dorsal enclosure (Ch. 77), pectoral-fin spur fused to second ray (Ch. 78), ventral postcleithrum between pleural ribs one and two (Ch. 79), interdorsals without a ventral shaft (Ch. 84), pleural ribs posterior to first anal-fin pterygiophore (Ch. 88). Characters 18, 30, 39, 44, 45, and 77 are unique features of Atherinopsidae. Additional supporting characters are presence of the anterior vomerine shelf (Ch. 4), the secondary trigeminofacial arch (Ch. 25), labial ligament folded lateral to premaxilla (Ch. 48), the dorsal process of the palatine (Ch. 54), palatine extended posteroventrally to quadrate (Ch. 57), many interdorsal bones (Ch. 85), and first caudal vertebra dorsal to anterior half of anal fin (Ch. 95). Additional supporting characters proposed by Dyer & Chernoff (1996) are maxillary branch of the A1 muscle tendon attached to the distal half of the maxilla and pelvic girdle attached to pleural rib 6 or more posteriorly.

The present assemblage of menidiine and atherinopsine genera was first recognized at the family level by Jordan & Hubbs (1919). Patten (1978) proposed Atherinopsinae and Menidiinae as phylogenetic sister taxa, a hypothesis later corroborated by White (1985) and Chernoff (1986b). Saeed & Ivantsoff (1991) discussed the differences between New and Old World silversides, and informally grouped the latter with melanotaeniids and phallostethids. New World silversides, or Atherinopsidae, was formally proposed by Saeed *et al.* (1994) and Dyer & Chernoff (1996). Saeed *et al.* (1994) grouped atherinopsids and notocheirids as sister taxa in a New World superfamily, a hypothesis unsupported by parsimony criteria (Dyer & Chernoff, 1996).

Monophyly of Menidiinae

Menidiinae comprises seven genera in two tribes: Membradini (*Atherinella, Membras, Melanorhinus*) and Menidiini (*Menidia, Chirostoma, Poblana, Labidesthes*). Chernoff (1986b) diagnosed Menidiinae with eight characters, seven of which are recognized herein (Ch. 106; Appendix 2); exoccipital with wings (Ch. 30) is considered in this study to be diagnostic of Atherinopsidae. Six additional diagnostic characters were found (Chs 3, 25, 53, 73, 75, 97), the first two of which are unique. White (1985: 6) mentioned a single dorsal projection of the vomer in *Menidia*, but did not mention that this unique feature is present in all menidiines (Ch. 3; Fig. 3A). Also unique to menidiines is the bony enclosure of the jugular vein posterior to the trigeminofacial arch (Ch. 25; Fig. 13). Other diagnostic characters are presence of the A1 mandibular branch (Ch. 53), tooth patches fused with ceratobranchial four (Ch. 73), anterior border of cleithrum dorsomedial wing curved ventrally, extended to scapular foramen at most (Ch. 75), and two suborbital scale rows (Ch. 97). Additional supporting characters for menidiines is a postemporal sensory canal with three pores and no extrascapulars (Ch. 35), premaxillary ascending process with narrow base (Ch. 38), palatine spine extended to quadrate (Ch. 57), and origin of the first dorsal fin posterior to the anus (Ch. 82).

Monophyly of Menidiini was supported by Chernoff (1986b) with two characters: a fused upper hypural plate and no pelvic axillary scale, however the latter is ambiguous because it is also lacking in atherinopsines. Another two features found to diagnose menidiins are absence of a dermosphenotic medial flange (Ch. 22) and absence of endopterygoid teeth (Ch. 59). Monophyly of Membradini is supported by six features, four of which are unique (Chernoff, 1986b; Appendix 2). Another two diagnostic features of this group are the hyomandibular nerve divided inside of the hyomandibula (Ch. 60) and absence of infrapharyngobranchial 1 (Ch. 70).

Monophyly of Atherinopsinae

Atherinopsinae comprises six genera in two tribes (Fig. 1): Atherinopsini (*Atherinops, Atherinopsis, Colpichthys, Leuresthes)* and Sorgentinini (*Basilichthys, Odontesthes*). Atherinopsines form a monophyletic group diagnosed by eight characters: ethmoid cartilage folded ventral to vomer midline (Ch. 6), nasal ventral process overlaps subnasal shelf (Ch. 11), nasal sensory canal detached anteriorly (Ch. 12), postocular shelf at dorsal half of dermosphenotic (Ch. 23), basisphenoid belofragm short (Ch. 26), Baudelot's ligament ossified (Ch. 34), palatine dorsal process pointed and folded over ethmoid block (Ch. 54), and presence of a swimbladder haemal funnel (Ch. 89). Characters 6, 34, and 54 are unique to Atherinopsinae. Additional supporting characters are presence of a dorsal median ridge on the vomer (Ch. 1), ventral condyle of lateral ethmoid ossified (Ch. 15), pterotic-exoccipital wings contiguous (Ch. 31), postemporal canal with two pores and extrascapular with three pores (Ch. 35), vertical and horizontal shafts of preopercular sensory canal enclosed by bone (Ch. 61), and pelvic median process reduced or absent (Ch. 81).

The present generic composition of Atherinopsinae was proposed by Schultz (1948) and the first phylogenetic hypothesis of relationships diagnosed the subfamily with five characters (Chs 11, 15, 34, 54, 73; White, 1985). Chernoff (1986b) provided two more features (Chs 36, 71) in support of a monophyletic Atherinopsinae, but of the list of seven features combined from White and Chernoff, only three (Chs 11, 34, 54) are considered as diagnostic of Atherinopsinae in this study. White's hypothesis of atherinopsine intrarelationships (Fig. 41) was tentatively supported with allozyme data (Crabtree, 1987), though no diagnostic features were provided for Atherinopsinae.

Monophyly and systematics of Atherinopsini

Atherinopsini comprises the North American taxa *Atherinops, Atherinopsis, Colpichthys,* and *Leuresthes.* This group is diagnosed by seven characters: two dorsal laminae of the vomer (Ch. 3), dermosphenotic with three sensory canal pores (Ch. 21), supraoccipital crest "trifid" (Ch. 28), cartilaginous first

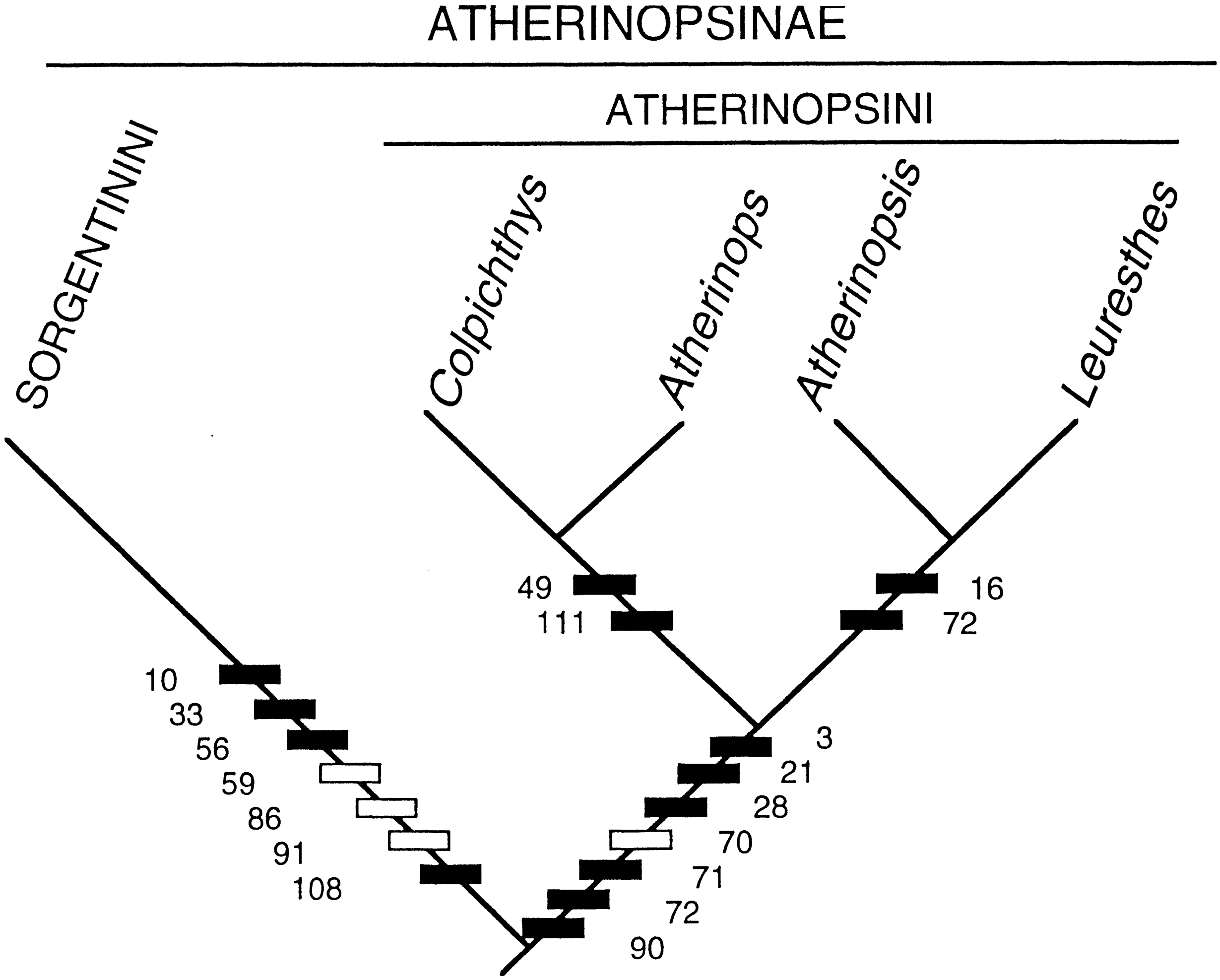

Fig. 41. Hypothesis of relationships within atherinopsinins proposed by White (1985) (L=404). Unique characters within atheriniforms are opposite black bars and homoplasious characters independently derived elsewhere are opposite white bars.

infrapharyngobranchial (Ch. 70), cranial process of infrapharyngobranchial 2 pointed and at right angles to infrapharyngobranchial 3 (Ch. 71), uncinate process of epibranchial 3 in a lateral position and long (Ch. 72), and presence of a haemal-hypophysis funnel (Ch. 90). All features except for Characters 70 and 90 are unique in atheriniforms. Additional supporting characters are a wide postemporal anterior process (Ch. 36), presence of an upper jaw frenum (Ch. 37), three rows of teeth or less on oral jaws (Ch. 50), discontinuous series of interdorsal bones (Ch. 84), presence of scales on cleithrum shaft (Ch. 99), and the allozymes M-Aat-A (Ch. 109) and Est-1 (Ch. 112).

The morphological data of White (1985) and the distance-treated allozyme data of Crabtree (1987) both supported a sister-group relationship between *Atherinops* and *Colpichthys*, and between *Atherinopsis* and *Leuresthes* (Fig. 41). The character-state allozyme data yielded a slightly different topology in that the *Atherinopsis* - *Leuresthes* clade was more closely related to the *Basilichthys* - *Odontesthes* clade, with no significant difference between the quantitative and qualitative coding schemes. In the present analysis, both morphological and allozyme characters were combined in a single data matrix (Table 3). The phylogenetic analysis using quantitatively-coded allozyme characters resulted in two equally parsimonious trees (Figs 2, 42), however, the qualitatively-coded allozyme data resulted in a single most-parsimonious tree (Figs 2A, 42A). Both topologies differ from White's hypothesis (Fig. 41), though admittedly, the latter is only one step longer than the two trees resulting from this analysis (Fig. 2A, 2B). This is an indication that the hypotheses of atherinopsinin interrelationships are not as robust as would seem from the results of White (1985) and Crabtree (1987). Morphology alone renders a single tree (Length=321, CI=0.53, RI=0.78) with the same topology of Figures 2A and 42A.

Relationships depicted in Figure 42A show *Atherinops* more closely related to the *Atherinopsis* - *Leuresthes* clade and *Colpichthys* is the sister group to that assemblage. The *Atherinops*, *Atherinopsis*, and *Leuresthes* clade is diagnosed by three characters (Chs 84, 85, 101), and the *Atherinopsis* - *Leuresthes* clade is diagnosed by seven features (Chs 16, 25, 50, 57, 72, 109, 119) of which two anatomical features (Chs 16, 72) and one enzymatic character (Ch. 109) are unique. The alternative equally parsimonious cladogram is the mirror image of the tree described above (Fig.

42B), in which *Atherinopsis* is sister to the *Atherinops* - *Colpichthys* clade and *Leuresthes* is the next sequential outgroup. The *Atherinops*, *Atherinopsis*, and *Colpichthys* clade is diagnosed by three characters (Chs 12, 37, 40) and the *Atherinops* - *Colpichthys* clade is diagnosed by six features (Chs 25, 49, 50, 57, 109, 119) of which one is unique (Ch. 49).

Colpichthys Hubbs, 1918a

Type species: *Atherinops regis* Jenkins & Evermann, 1889
C. regis (Jenkins & Evermann, 1889)
C. hubbsi Crabtree, 1989

Diagnosis: oral jaws with asymmetrical bicuspid teeth (see Ch. 49), notch in the dorsal process of maxilla (White, 1985), presence of a hyomandibular nerve foramen (Ch. 60), few gill rakers (<20 lower limb) on the first branchial arch, external row of gill rakers on anterior portion of fourth ceratobranchial expanded medially in a plate-like form (White, 1985), infrapharyngobranchial teeth hair-like (White, 1985), ventral extension of anterior border of cleithrum dorsomedial wing not reaching scapular foramen (Ch. 75), female with ovipositor (Crabtree, 1989), and eggs lacking filaments (Crabtree, 1989).

Additional descriptive features: Atherinopsinins with a maxilla-premaxillary ligament attached to the anteroventral corner of premaxilla (Ch. 47), a subterminal mouth, presence of a secondary trigeminofacial arch (Ch. 25), horizontal shaft of preopercular sensory canal enclosed by bone (Ch. 61), a continuous series of six or more interdorsal bones (Chs 84, 85), large scales on cleithrum shaft (Ch. 99), no scales on the anal fin (Ch. 101), and the allozymes S-Aat-A (Ch. 110), Gpi-A (Ch. 113), and Pgm-A (Ch. 121).

A unique feature of *C. regis* is presence of a ring ligament on the palatine around the ethmomaxillary ligament (see Ch. 55). *Colpichthys hubbsi* is diagnosed by absence of a haemal funnel (Chs 89, 90) and the first dorsal fin posterior to a vertical from the anus (Ch. 82). For additional features of *Colpichthys* species see Crabtree (1989).

Distribution: Endemic to the Gulf of California. *Colpichthys hubbsi* is restricted to the area of the Colorado River delta north of 31° N latitude and *C. regis* is found north of 28° N latitude in the upper and central Gulf of California.

Atherinops Steindachner, 1875

Type species: *Atherinopsis affinis* Ayres, 1860
A. affinis (Ayres, 1860)
=*A. insularum* Gilbert, 1891
=*A. magdalenae* Fowler, 1903
=*A. oregonia* Jordan & Snyder, 1913.
=*A. littoralis* Hubbs, 1918b
=*A. cedroscensis* Hubbs, 1918b
=*A. guadalupae* Hubbs, 1918b

Diagnosis: Frills of skin between the maxilla and premaxilla (White, 1985), two rows of subocular scales (Ch. 97), and the allozyme Sod-A (Ch. 123).

Additional descriptive features: Atherinopsinins with two

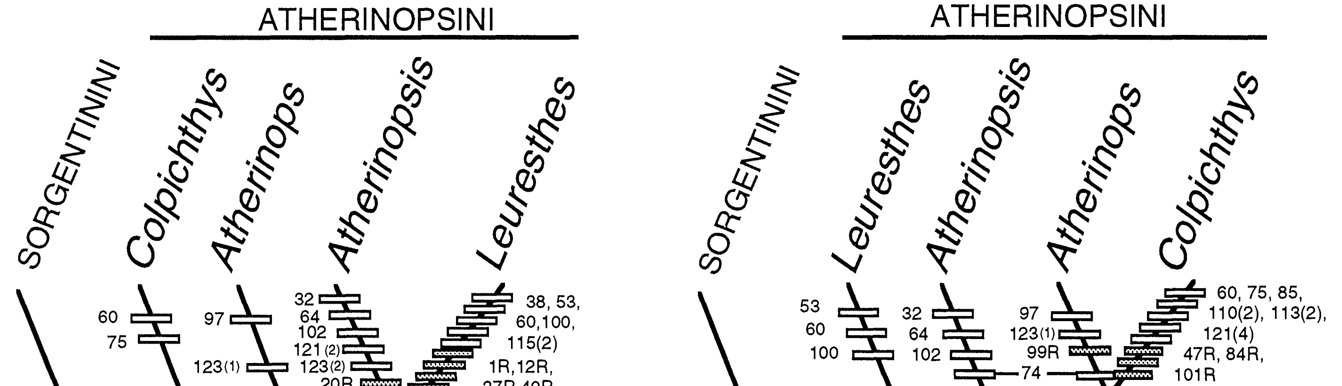

Fig. 42. Alternative equally parsimonious hypotheses of relationships among atherinopsinin genera. Unique characters within atheriniforms are opposite black bars; reversed characters (with an "R") are opposite grey bars; and homoplasious characters independently derived elsewhere are opposite white bars. Diagnostic characters and additional support is listed in Appendix 2; A, *Colpichthys* is sister to *Atherinops*, *Atherinopsis*, and *Leuresthes*; B, *Leuresthes* is sister to *Atherinopsis*, *Atherinops*, and *Colpichthys*.

rows of bicuspid teeth (cusps symmetrical or slightly asymmetrical) arranged in a single exposed row (Chs 49, 50), gill rakers 20-25 on lower limb, absence of a urohyal ventral plate (Ch. 74), origin of the first dorsal fin over anus (Ch. 82), and lack of scales on the cleithrum shaft (Ch. 99).

Distribution: Ranges from Vancouver Island, B.C., Canada, to the Gulf of California.

Various species, subspecies and their intergrades were described by Hubbs (1918b) as a way to delineate the variation of meristics and body proportions that *Atherinops* displays along the West coast of North America. Because no features are known to clearly distinguish one form from another, I consider all nominal species to be junior synonyms of *Atherinops affinis.*

Atherinopsis Girard, 1854

Type species: *Atherinopsis californiensis* Girard, 1854
A. californiensis Girard, 1854
=*A. sonorae* Osburn & Nichols, 1916

Diagnosis: Modification of the ventral process of the maxilla for the attachment of premaxillary and rostral-cartilage ligaments (maxillary anterior pocket; White, 1985: fig. 23A), dermosphenotic canal not enclosed by bone (Ch. 20), pterotic and epioccipital wing bases contiguous under the epaxial musculature of the temporal fossa (Ch. 32), dorsal process of opercle not blade-like (Ch. 64), small scales (Ch. 102), and the allozymes Pgm-A (Ch. 121) and Sod-A (Ch. 123).

Additional descriptive features: Atherinopsinins with the lateral ethmoid contacting the parasphenoid (Ch. 16), epibranchial three with twisted shaft medial to the uncinate process (Ch. 72), and absence of a urohyal ventral plate (Ch. 74).

Distribution: From Yaquina Bay, Oregon, south to the west coast of Baja California Sur.

Leuresthes Jordan & Gilbert, 1880

Type species: *Atherinopsis tenuis* Ayres, 1860
=*Hubbsiella* Breder, 1936
Type species: *Menidia clara* Evermann & Jenkins, 1891
L. tenuis (Ayres, 1860)
=*L. crameri* Jordan & Evermann, 1896
L. sardina (Jenkins & Evermann, 1888)
=*L. clara* (Evermann & Jenkins, 1891)

Diagnosis: Maxilla-premaxilla distal ligament attached to the dorsal border of the premaxillary alveolar dilation (see Ch. 47), mandibular branch of A1 muscle tendon present anterior to lacrimal branch (Ch. 53), hyomandibular nerve divided inside of hyomandibula (Ch. 60), pelvic median plate extending to anterior tip (Ch. 80), scales present between anterior rays of second dorsal fin (Ch. 100), and unique lunar cycle beach-spawning habits (Moffat & Thomson, 1975).

Additional descriptive features: Atherinopsinins lacking a vomerine dorsomedial ridge (Ch. 1), anterior detachment of the nasal sensory canal reduced (Ch. 12), highly protractile premaxillae without an upper jaw frenum (Ch. 37), long premaxillary ascending process with narrow base (Ch. 38), a well developed dorsal process of the maxilla (Ch. 40), horizontal shaft of preopercular sensory canal enclosed by bone (Ch. 61), pelvic medial process well developed (Ch. 81), and origin of the first dorsal fin placed posteriorly to vertical through anus (Ch. 82), and the allozyme Gtdh-A (Ch. 115).

The feature that most readily distinguishes both species of *Leuresthes* is the number of lateral scale rows, with 51-60 in *L. sardina* and 69-80 in *L. tenuis* (Moffatt & Thomson, 1975). White (1985) reported that both species of *Leuresthes* lack strongly developed teeth in the oral jaws as adults, and reported the absence of teeth in the cleared and stained specimens he studied. Oral jaw teeth present in the material I studied are minute in *L. tenuis,* whereas in *L. sardina* teeth are small but readily visible. The spawning habits of *L. tenuis* are strictly nocturnal whereas *L. sardina* spawns diurnally and nocturnally (Moffatt & Thomson, 1975).

Distribution: *Leuresthes tenuis* is found from Monterrey Bay south to Baja California Sur, whereas *L. sardina* is endemic to the Gulf of California north of Bahía Concepción and Guaymas.

Monophyly and systematics of Sorgentinini

Sorgentinini comprises the South American taxa *Basilichthys* and *Odontesthes,* a sister-group relationship diagnosed by eight characters: ethmomaxillary ligament attached to ethmoid cartilage block only (Ch. 10), presence of basioccipital fenestration (Ch. 33), a palatorostral ligament dorsal to the ethmomaxillary ligament (Ch. 56), absence of an endopterygoid tooth patch (Ch. 59), precaudal vertebrae over 50% of total vertebrae (Ch. 86), presence of an haemal-arch funnel (Ch. 91), and the allozymes Ak-A (Ch. 107) and Ap-A (Ch. 108). The first three morphological features are unique in atherinomorphs.

The morphological data of White (1985) and the enzymatic data of Crabtree (1987) both supported a sister-group relationship between *Basilichthys* and *Odontesthes.* The representative material they had available, however, underestimated significantly the species and anatomical diversity present in the South American clade. The present study includes for the first time the complete taxonomic diversity of the group, with four or five species in *Basilichthys* and at least 17 species in *Odontesthes.*

Odontesthes Evermann & Kendall, 1906

Type species: *Odontesthes perugiae* Evermann & Kendall, 1906
=*Kronia* Miranda-Ribeiro, 1915
Type species: *Kronia iguapensis* Miranda-Ribeiro, 1915
=*Pseudothyrina* Miranda- Ribeiro, 1915
Type species: *Pseudothyrina jheringi* Miranda-Ribeiro, 1915
=*Austromenidia* Hubbs, 1918a
Type species: *Basilichthys regillus* Abbott, 1899
=*Cauque* Eigenmann, 1927
Type species: *Chirostoma mauleanum* Steindachner, 1896
=*Patagonia* Eigenmann, 1927
(preoccupied; misspelling of *Patagonina*)
=*Patagonina* Eigenmann, 1927
Type species: *Menidia hatcheri* Eigenmann, 1909
=*Austroatherina* Marrero, 1950 (*nomen nudum*)
Type species: no type designation.
=*Bachmannia* Nani, in Szidat & Nani, 1951
(preoccupied)

Type species: *Basilichthys smitti* Lahille, 1929
=*Sorgentinia* Pianta de Risso & Risso, 1953
Type species: *Atherina incisa* Jenyns, 1842
=*Tupa* De Buen, 1953
Type species: *Atherinichthys platensis* Berg, 1895
=*Yaci* De Buen, 1953
Type species: *Yaci retropinnis* De Buen, 1953

Diagnosis: Mesethmoid absent (Ch. 9), trigeminal foramen enlarged and enclosed by prootic, sphenotic, and pleurosphenoid (Ch. 24), ventral and dorsal processes of maxillary head of about equal length (Ch. 41), mandibular branch of A1 muscle tendon present anterior to lacrimal branch (Ch. 53), opercle fenestrated (Ch. 65) with medial lamina between struts (Ch. 66), and anterior haemal spines short (Ch. 94).

Additional descriptive features: Sorgentinins lacking dorsal laminae on vomerine anterior face (Ch. 3), nasal sensory canal greatly detached anteriorly (Ch. 12), secondary trigeminofacial arch present (Ch. 25), pterotic and exoccipital wing bases contiguous (Ch. 31), highly protractile premaxillae without an upper jaw frenum (Ch. 37), premaxillary ascending process with a narrow base (Ch. 38), labial ligament broadly folded lateral to premaxilla (Ch. 48), and scales present between anterior rays of anal fin (Ch. 101).

Distribution: Coastal marine and freshwater drainages of southern temperate South America. Marine forms range from the southern tip of Tierra del Fuego to northern Peru, including the Juan Fernandez Archipelago, in the southeastern Pacific and to southeastern Brazil, including the Falkland Islands, in the southwestern Atlantic. Brackish and freshwater forms range from Patagonia to northern Central Chile along the Pacific drainages, and to Rio Grande do Sul, southeastern Brazil, along the Atlantic drainages.

Comments: This genus is the most species rich and widespread of atherinopsine genera, comprizing 20 to 25 recognized species. White (1985) diagnosed *Odontesthes* with three characters (Chs 9, 37, 65) and remarked that this group was in need of revision. Of the several junior synonyms of *Odontesthes* still in use, *Austromenidia* (Hubbs, 1918a) and *Cauque* (Eigenmann, 1927) are the only taxa comprising two or more species. Other genus-level names such as *Kronia* (Miranda-Ribeiro, 1915), *Patagonina* (Eigenmann, 1927), *Sorgentinia* (Pianta de Risso & Risso, 1953), and *Yaci* De Buen (1953) are thus far monotypic. The relationships and systematics of *Odontesthes* species and those of the subgenus *Austromenidia* are treated elsewhere (Dyer, 1993: 331-590).

Basilichthys Girard, 1854

Type species: *Atherina microlepidotus* Jenyns, 1842
=*Protistius* Cope, 1874
Type species: *Protistius semotilus* Cope, 1874
=*Gastropterus* Cope, 1878
Type species: *Gastropterus archaeus* Cope, 1878
=*Pisciregia* Abbott, 1899
Type species: *Pisciregia beardsleei* Abbott, 1899

Diagnosis (Fig. 43): Vomer with two slightly elevated parasagittal laminae (Ch. 3), vomer slightly concave ventrally (Ch. 5), a single median tooth patch (Ch. 7), lacrimal condyle of lateral ethmoid does not reach ventral edge of lateral ridge (Ch. 13), dermosphenotic medial flange reduced or absent (Ch. 22), pterotic and epioccipital wing bases contiguous under temporal fossa epaxial musculature (Ch. 32), maxilla with condyle on ventral process (Ch. 42), maxilla-anguloarticular coronoid ligament absent (Ch. 46), labial ligament with reduced lateral fold (Ch. 48), dentary coronoid process flat dorsally at level with anguloarticular coronoid (Ch. 51), dentary gnathic spine absent (Ch. 52), dorsal palatine process spoon-shaped (Ch. 54), ethmomaxillary ligament not attached to palatine dorsal process (Ch. 55), preopercular sensory canal between pores one and two enclosed by bone (Ch. 62), dorsal process of opercle not blade-like (Ch. 64), posterodorsal border of opercle concave (Ch. 68), first spine of first dorsal fin shorter than spine of second dorsal fin (Ch. 83), precaudal vertebrae over 57% of total vertebrae (Ch. 86), first caudal vertebra over posterior half of anal fin (Ch. 95), dorsal head scales with reversed imbrication (Ch. 96), four suborbital scale rows (Ch. 97), and interopercle with scales on posterior half only (Ch. 98).

Additional descriptive features: Sorgentinins with a single median patch of vomerine teeth (Ch. 8), an isolated, oval mesethmoid (Ch. 9), nasal sensory canal slightly detached (Ch. 12), lateral ethmoid with bony ventral condyle (Ch. 15), single trigeminofacial arch (Ch. 25), supraoccipital crest bifid (Ch. 28), exoccipital wing reduced to spiny processes (Ch. 30), wide anterior process of the postemporal (Ch. 36), frenum between the forehead and upper jaws (Ch. 37) and restricted premaxillary protrusion, premaxillary ascending process with a wide base (Ch. 38), maxillary dorsal process reduced (Ch. 40), maxilla-premaxilla distal ligament elongated and attached to anteroventral corner of alveolar arm (Ch. 47), palatine spine not contacting quadrate (Ch. 57), six or more interdorsals (Ch. 85) in a continuous series (Ch. 84), haemal arches with flaring expansions only (Ch. 91), and body scales small (Ch. 102).

Distribution: Restricted to freshwater drainages of the western Andes from Lambayeque, northern Peru, to Chiloé Island in southern Chile (Fig. 44). I have neither collected nor encountered museum specimens that support literature reports of this group's presence in marine environments (Mann, 1954) or freshwater drainages east of the Andes (Lahille, 1929; Aramburu & Ringuelet, 1967). Urzúa *et al.* (1977), however, reported the occasional capture of *Basilichthys* in the Port of San Antonio, Chile, by local sport fishermen. Though specimens of *Basilichthys australis* can survive accidental transplants directly from freshwater to seawater aquaria, I regard the presence of *Basilichthys* in marine waters as rare and incidental occurrences.

Parenti (1984: 110) refers in a footnote to a small specimen of *Basilichthys* (FMNH 94184: 17.5 mm SL) collected near Lake Titicaca, Peru. Examination of an X-ray plate of the specimen, kindly provided by Parenti, confirm it as *Basilichthys. Odontesthes bonariensis* was introduced into Lake Titicaca much later than the 1918 collection date of this specimen. This specimen continues to be the only record of this genus in the Puno Region and either represents the sole representative of a now extinct population or species, or is a misplaced specimen from a previous collection of the Irwin expedition in the Arequipa region.

Comments: The species composition of *Basilichthys* has been problematic ever since its description (Girard, 1854, 1855). Based on Girard's descriptions alone the name *Basilichthys* has

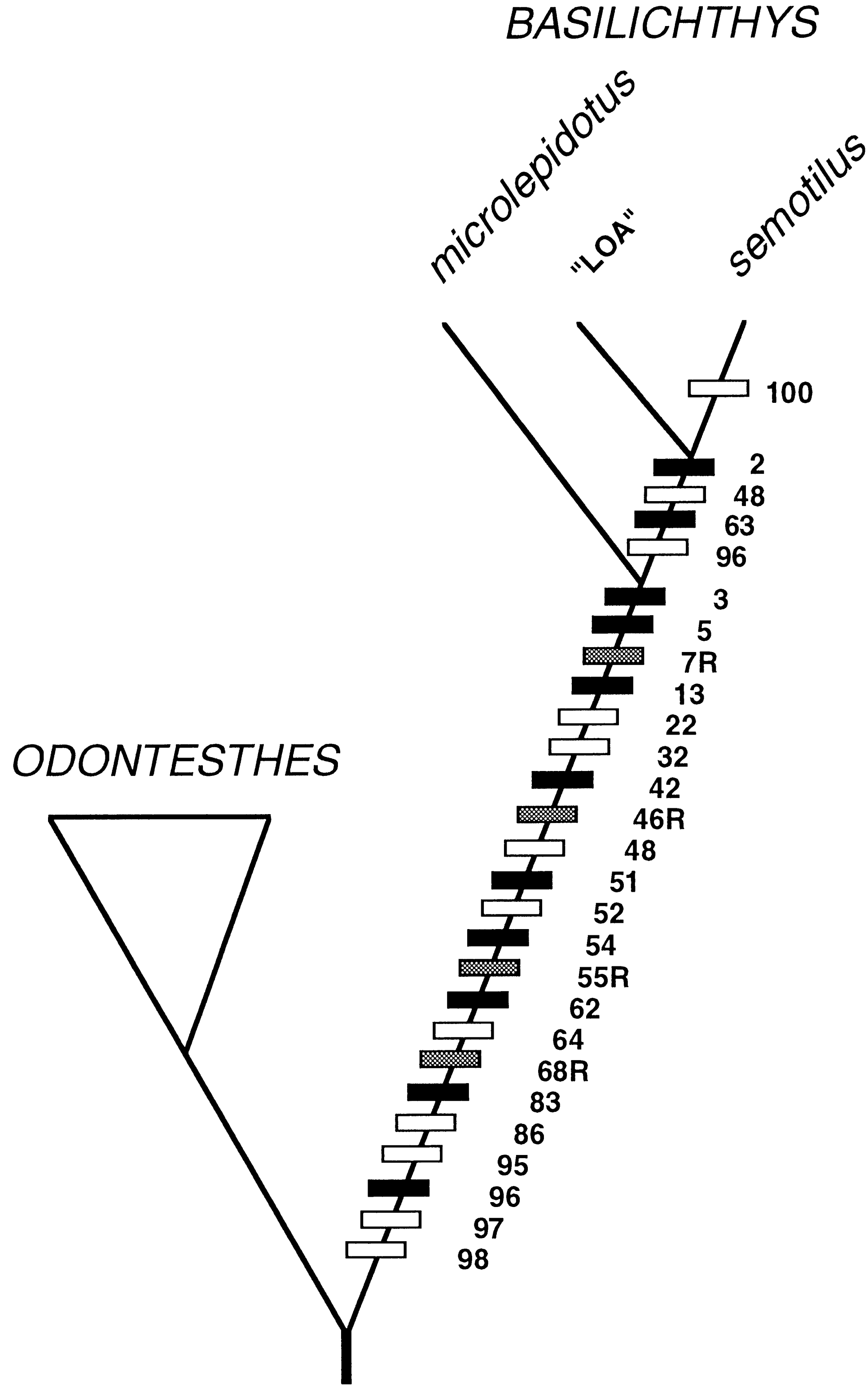

Fig. 43. Monophyly of *Basilichthys*, showing the undescribed species from Río Loa as part of the *semotilus* species group. Unique characters within atheriniforms are opposite black bars; reversed characters (with an "R") are opposite grey bars; and homoplasious characters independently derived elsewhere are opposite white bars. Diagnostic characters and additional support is listed in Appendix 2.

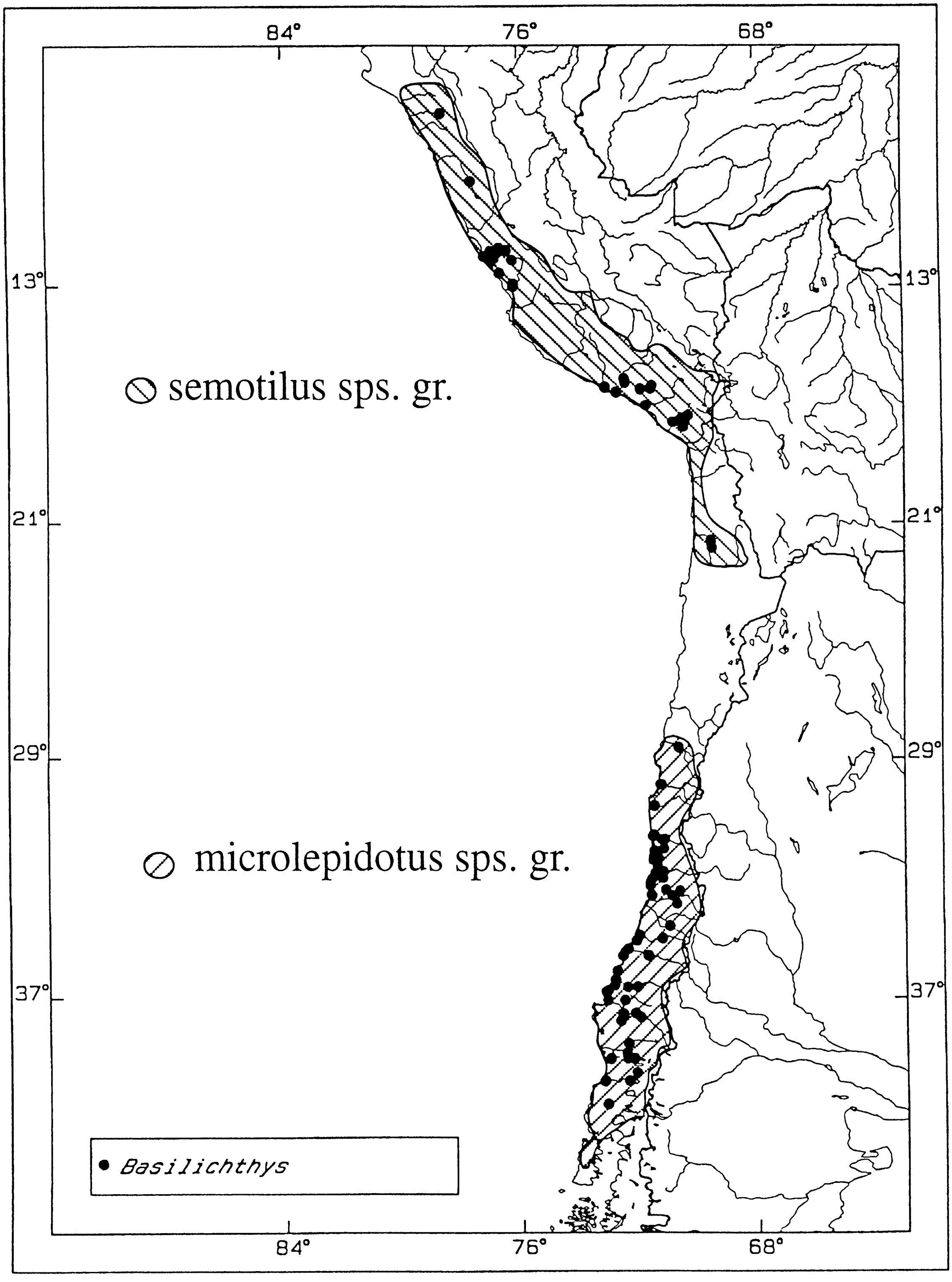

Fig. 44. Distribution map of *Basilichthys*. Dots indicate localities of collections examined. Shaded areas mark the distribution range of the species groups.

been used by different authors either to group sorgentinins without upper jaw protrusion (Jordan & Hubbs, 1919; Eigenmann, 1927; De Buen, 1950; Mann, 1954), sorgentinins without vomerine teeth (Evermann & Kendall, 1906), or all sorgentinins (Lahille, 1929; Aramburu & Ringuelet, 1967; Ringuelet *et al.*, 1967). *Basilichthys* is restricted to the western freshwater drainages of Chile and Peru, despite some recent publications that continue to follow the old nomenclature of Lahille (1929) and Ringuelet *et al.* (1967). A good example of this taxonomic misunderstanding is when the Patagonian silverside *Odontesthes hatcheri* (Eigenmann) is referred to as *Basilichthys microlepidotus.*

microlepidotus species group

Basilichthys microlepidotus (Jenyns, 1842)
Type locality: Valparaíso, Chile.
Basilichthys australis Eigenmann, 1927
Type locality: from Río Maipo to Río Rahue, Chile.

Diagnosis:

Additional descriptive features: *Basilichthys* species with nasal ventral process not overlapping the subnasal shelf (Ch. 11), labial ligament with a reduced lateral fold (Ch. 48), three rows of teeth on jaws (Ch. 50), and all dorsal head scales reversed in imbrication (Ch. 96).

Distribution: From Río Huasco, III Region (28°-29°S), to Chiloé Island, X Region (42°-43°S), Chile (Fig. 44). Eigenmann (1927) cites reports of *Basilichthys* in Río Copiapó but none have been collected despite numerous attempts (De la Hoz, pers. comm.). The southern limits of the range was extended from Puerto Montt to Chiloé Island by Campos *et al.* (1984).

Comments: Distinction between the two species is problematic. The northern populations look quite different from the southern populations, but those of the central Aconcagua and Maipo river drainages overlap in their counts and measurements. Both species are virtually identical in an allozyme survey of 37 loci (Gajardo, 1988). Morphometrically they are indistinguishable or only statistically separated by mean values of some meristics, namely longitudinal scale row counts (Gajardo, 1987), the same feature used by Eigenmann (1927) in his description of *B. australis.* The only qualitative evidence that argues for the existence of two species is karyotypic, in which the modal chromosome number for *B. microlepidotus* is 2n=46 and that of *B. australis* is 2n=48 (Gajardo, 1992). The chromosome number of *Odontesthes bonariensis* is 2n=48 (Arai & Koike, 1980) as is true generally of atheriniforms such as *Menidia*, *Melanotaenia*, and *Atherion* (Gajardo, 1992), suggesting the karyotypically derived condition is that of *B. microlepidotus.*

A number of papers have described the feeding (Urzúa *et al.*, 1977; Bahamondes *et al.*, 1979) and reproductive biology (Moreno *et al.*, 1977; Vila & Soto, 1981; Vila *et al.*, 1981) of *B. australis*, but only one of *B. microlepidotus* (Comte & Vila, 1992). Differences were found between these species, but are attributed to the very different environments and flow regimes of the localities compared (Comte & Vila, 1992).

semotilus species group

Basilichthys semotilus (Cope, 1874)
Type locality: Andes, Peru.
=*B. beardsleei* (Abbott, 1899)
Type locality: Callao, Peru.
Basilichthys archaeus (Cope, 1878)
Type locality: Arequipa, Peru.
Basilichthys sp.
Type locality: Río Loa, Chile.

Diagnosis (Fig. 43): Vomer with dorsomedial spine (Ch. 2), labial ligament fold greatly reduced or absent (Ch. 48), four preopercular sensory canal pores on horizontal shaft (Ch. 63), and head scales of interorbital region only reversed in imbrication (Ch. 96).

Additional descriptive features: *Basilichthys* species with anterior elongation of basisphenoid to interorbital cartilage (Ch. 26), more than three rows of teeth on oral jaws (Ch. 50), upper jaw relatively more prognathous, ectopterygoid always absent (Ch. 58), and first dorsal fin relatively smaller, sometimes absent.

Distribution: From Río Reque, Lambayeque (7°S), to Río Sama, Tacna (22°S), in Peru, and in Río Loa, Iquique (22°S), I Region, Chile (Fig. 44). Eigenmann (1927) cites reports of *Basilichthys* in Río Loa and Río Camarones in northern Chile and refers them to *B. semotilus.* Though *Basilichthys* is indeed present in Río Loa no specimens have been collected in Río Camarones (De la Hoz, pers. comm.). The northern extent of the range was previously considered as the Río Rimac, and expected to be in the Río Santa (Eigenmann, 1922). The presence of *Basilichthys* in Río Santa is confirmed by A. Sifuentes and H. Ortega (UMMZ 218074), the range is extended to Río Jequetepeque (UMMZ 218050), and with unconfirmed reports of its presence in Río Reque (R. Alva, pers. comm.). Collections north of Lima, in Río Santa (Carhuaz) and Río San Juan (upper Río Jequetepeque), were made at elevations of 2000 m or greater, whereas collections at lower elevations are devoid of *Basilichthys* (Eigenmann, 1922; Dávila, 1973).

Comments: The population present in Río Loa is separated by approximately 1000 kms from its nearest congener in the Río Sama, Tacna, Peru. The Río Loa population is an undescribed species which, based on the preliminary data presented here, is the sister species to the remainder of the *semotilus* species group. This undescribed species is under severe threat of extinction because of a contamination event in 1996, the origin of which is to be determined. This population is so far endemic to the Río Loa and restricted to a portion of river downstream from the city of Calama and a major copper-mining industry.

The *semotilus* species group, exclusive of the Río Loa population, is diagnosed with scales present between the anterior rays of the second dorsal and anal fins (Chs 100, 101). *Basilichthys beardsleei* was described based on a single large specimen collected from the market at Callao and assumed to be marine (Abbott, 1899). *B. archaeus* is tentatively considered to be distinct from *B. semotilus* based on the morphology of the jaws, but so far neither species has been phylogenetically diagnosed.

A relatively large collection was made along the western drainages of the Andes of Peru between the Jequetepeque and Sama rivers in 1988. This collection suggests *B. archaeus* is possibly endemic to altitudes over 2000 m in the Arequipa region. *Basilichthys* is found only in the uppermost reaches of the Santa, Chicama, and Jequetepeque rivers. This suggests that potential areas of endemism for freshwater fishes in the western Andes ocurr in an altitudinal rather than latitudinal gradient.

KEY TO THE ATHERINOPSINE GENERA AND SPECIES OF ATHERINOPSINI

1a. Upper jaw frenum present (premaxillary protrusion restricted; Figs 16, 23 B,C) 2

1b. Upper jaw frenum absent (premaxillaries freely protractile; Fig. 23A) 6

2a(1). Dorsal head scales with reversed imbrication (anterior margin free; Fig. 16); four subocular scale rows, and reduced labial ligament folded lateral to premaxilla (Fig. 23 B,C); first dorsal fin small, anterior to anus .... *Basilichthys*

(Pacific freshwater drainages of Andes of Chile and Peru)

2b. Dorsal head scales with normal imbrication (posterior margin free); two or three suborbital scale rows (Fig. 23 A); labial ligament folded medial to premaxilla; first dorsal fin anterior or posterior to anus 3

3a(2). Two or three rows of conical teeth on oral jaws; gillrakers on lower limb of first branchial arch 30 or more; isthmus straight, lacking posterior widening of urohyal ventral plate (Fig. 31B); first dorsal fin anterior to anus .... *Atherinopsis californiensis*

(Northeastern Pacific, from Oregon to Baja California Sur)

3b. A single row of exposed bicuspid teeth on oral jaws; gillrakers on lower limb of first branchial arch 25 or less; isthmus straight or with widening of urohyal ventral plate (Fig. 31) 4

4a(3). Frills of skin on margin of labial ligament between maxilla and premaxilla; tooth cusps symmetrical or slightly asymmetrical; gillrakers on lower limb of first branchial arch 20-25; two rows of subocular scales; horizontal shaft of preopercular sensory canal not enclosed by bone (Fig. 28D); scales absent on cleithrum; isthmus straight, lacking posterior widening of urohyal ventral plate (Fig. 31B); first dorsal fin over or posterior to anus; anal fin with scales between anterior rays; females with no ovipositors .... *Atherinops affinis*

(Northeastern Pacific, from British Columbia to Gulf of California)

4b. No frills of skin on margin of labial ligament between maxilla and premaxilla; tooth cusps asymmetrical, lateral cusp longer; gillrakers on lower limb of first branchial arch 15-19; three rows of subocular scales; horizontal shaft of preopercular sensory canal enclosed by bone (Fig. 17); large scales present on cleithrum (Fig. 40A); isthmus with posterior widening of urohyal ventral plate (Fig. 31A); first dorsal fin anterior or posterior to anus; anal fin without scales between anterior rays; females with ovipositors 5

5a(4). Origin of first dorsal fin anterior to anus; dorsolateral series of scales 40-47; haemal funnel present .... *Colpichthys regis*

(Gulf of California, north of 28° N latitude)

5b. Origin of first dorsal fin posterior to anus; dorsolateral series of scales 47-57; haemal funnel absent .... *Colpichthys hubbsi*

(Gulf of California, Colorado River delta north of 31° N latitude)

6a(1). Oral teeth well developed; labial ligament folded lateral to premaxilla (Fig. 23A); dermosphenotic with one external pore (Fig. 12 B,C); scales large and small (9-15 dorsal scales); first dorsal fin anterior, over, or posterior to anus; no beach spawning habits .... *Odontesthes*

(coastal marine and freshwater drainages of southern South America)

6b. Oral teeth small, minute, or absent; labial ligament folded medial to premaxilla; dermosphenotic with two external pores (Fig. 12A); scales large (9 dorsal scales); first dorsal fin posterior to anus; beach spawning habits 7

7a. Number of dorsolateral scale rows 51-60; diurnal and nocturnal beach spawning habits .... *Leuresthes sardina*

(Gulf of California endemic)

7b. Number of dorsolateral scale rows 69-80; strictly nocturnal beach spawning habits .... *Leuresthes tenuis*

(Northeastern Pacific, from central California to Baja California Sur)

DISCUSSION

SYSTEMATICS

Taxonomic results obtained in the present study are identical to those proposed by White (1985), i.e., the tribes and genera are monophyletic. Different results were obtained, however, regarding the generic relationships within Atherinopsini. Two equally parsimonious hypotheses of relationships result from the data collected in this study (Fig. 2). As depicted in Figures 2A and 42A, *Colpichthys* is the sister group to all atherinopsinins whereas in Figures 2B and 42B, *Leuresthes* is the sister group to all atherinopsinins. Either of these hypotheses is only one step shorter than White's (1985) hypothesis in which *Atherinops* is sister to *Colpichthys* and *Atherinopsis* is sister to *Leuresthes* (Fig. 41). Inability to make the multistate enzymatic characters binary (Chs 107-123) precludes an attempt to choose between the two trees using the successive weighting procedure (Carpenter, 1988). Morphology alone and the qualitatively-coded allozyme characters result in a single tree with *Colpichthys* as sister to other atherinopsinins (Fig. 2A). Clearly the intergeneric relationships among atherinopsinins are not stable with the evidence collected thus far and more comparative work is needed to resolve the conflict of data.

The list of diagnostic features provided by White (1985), Chernoff (1986b), and Crabtree (1987) has changed for the taxa included in this analysis (Appendix 2). These changes include the addition of new diagnostic characters and the change in status from diagnostic to ambiguously optimized (Chs 15, 35, 37, 43, 48, 73, 80) in the present hypothesis.

The number of derived characters shared between *Basilichthys* and atherinopsinins is striking. Two characters (Chs 15, 36) are shared between *Basilichthys* and all atherinopsinins, and two more characters (Chs 37, 40) are shared among *Basilichthys*, *Atherinops*, *Atherinopsis*, and *Colpichthys* (Fig. 45). Despite *Basilichthys* sharing four derived characters with the above atherinopsin genera, a sister group relationship between *Basilichthys* and Atherinopsini is two steps longer than one of the most parsimonious hypothesis prefered herein (Fig. 2A). Crabtree (1987: fig. 2) presented a hypothesis of relationships based on character-state treated allozyme data in which Sorgentinini is sister to the *Atherinopsis* - *Leuresthes* clade. The latter hypothesis is 6 steps longer than the shortest tree found using the data set of Table 3 and is not supported in this study.

CHARACTERS

Jaws

Presence of a continuous, unfolded sheath of skin between the upper jaws and the forehead, or frenum (Ch. 37; Fig. 16), has traditionally been used as an indicator of the absence of premaxillary protrusion (Eigenmann, 1927; Schultz, 1948; De Buen, 1950, 1955). While presence of a frenum may be a good estimator of upper jaw mobility in atherinoids and atheriniform outgroups, it is certainly misleading in atherinopsids. The amount of premaxillary protrusion in *Basilichthys* is less than that of *Odontesthes* (De la Hoz & Vial, 1994). Similarly, *Atherinopsis*, *Atherinops*, and *Colpichthys* have obviously reduced protractibility of the upper jaw when compared to *Leuresthes*. *Basilichthys*, *Atherinops*, *Atherinopsis*, and *Colpichthys* all have a frenum, but have significantly more upper jaw mobility when compared to *Labidesthes* or long-jawed species of *Chirostoma* which lack such a frenum. Presence or absence of a frenum should not be used to make absolute statements of upper jaw mobility, but instead, of relative amounts of displacement. Fowler (1903) stated clearly the degree of protractibility when he defined the subfamily Atherinopsinae: "Premaxillaries not *freely* protractile, the skin continuous mesially with forehead." (my italics)

Coupled with absence of a frenum in *Leuresthes* and *Odontesthes*, is presence of long and slender ascending processes of the premaxillae (Figs 4, 17). The long and slender premaxillary ascending process was regarded as a derived feature by White (1985), whereas Chernoff (1986b) considered it a plesiomorphic feature for atherinopsids. White further argued for the greater proximity of the ascending process to the symphysis in *Leuresthes* relative to *Odontesthes* as evidence supporting the independent origin of these states. White's hypothesis of character polarity, however, includes at least three different features that are functionally associated to upper jaw protrusion: frenum, length, and width of ascending process of premaxilla. The amount of upper jaw mobility is better correlated to length, not width, of the ascending process of the premaxilla. Preserved specimens of *Colpichthys* have a greater amount of premaxillary protrusion than *Chirostoma labarcae*, for example, despite the presence of a frenum and the broad ascending process in the former. A long premaxillary ascending process is indeed a plesiomorphic feature within atherinopsids (Chernoff,

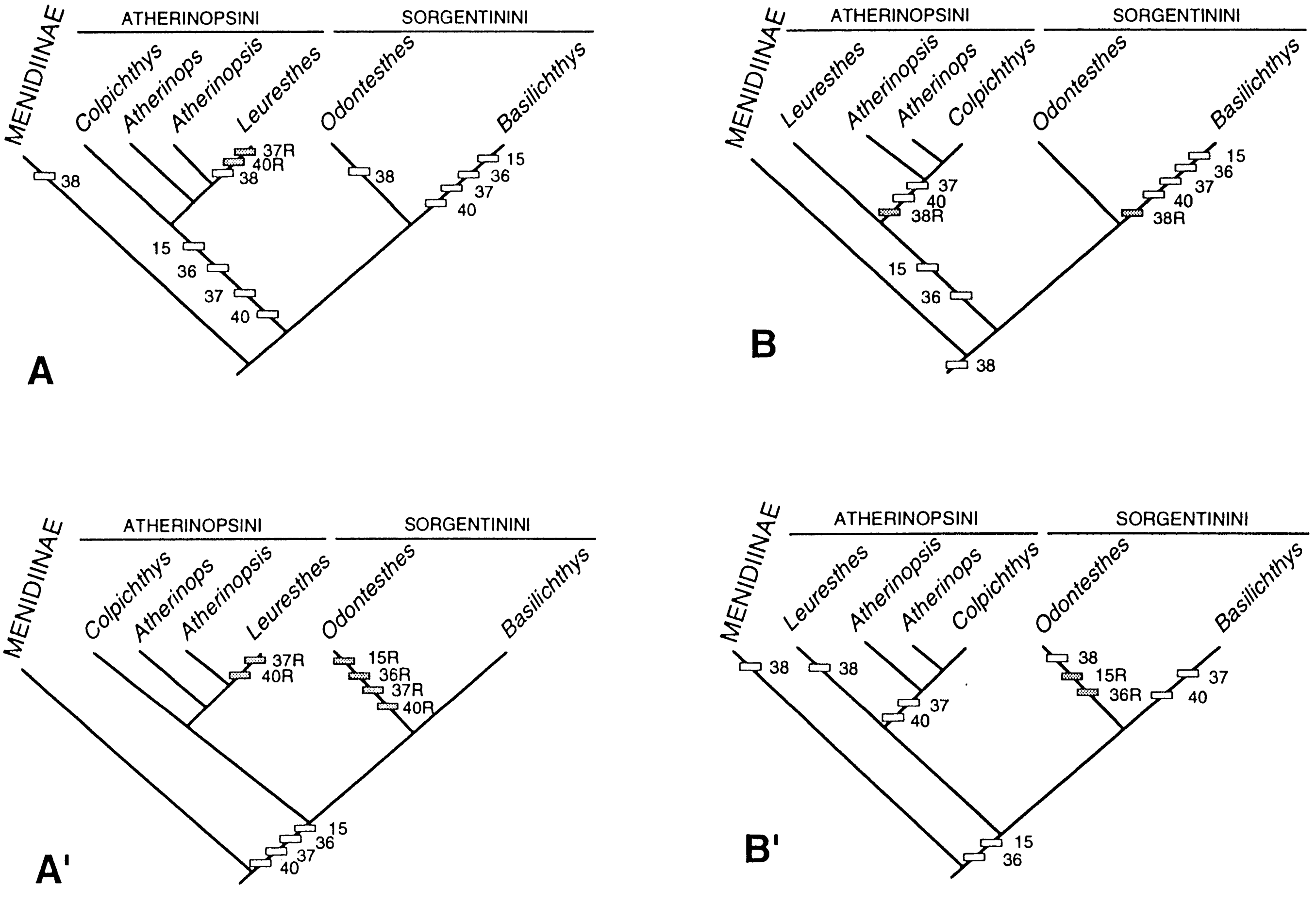

Fig. 45. Alternative optimization of characters on both equally parsimonious cladograms of atherinopsid relationships; A, A', *Colpichthys* is sister to *Atherinops*, *Atherinopsis*, and *Leuresthes*; B, B', *Leuresthes* is sister to *Atherinopsis*, *Atherinops*, and *Colpichthys*.

1986b). A premaxillary ascending process with a slender base and presence of a frenum, however, are both regarded as derived features in this study. Neither these derived characters nor their functional expression can be unambiguously optimized because of the conflict in atherinopsinin relationships (Fig. 45). Presence of a frenum (Ch. 37) is either ambiguously optimized in atherinopsines (Fig. 45A, 45A') or independently derived in *Basilichthys* and atherinopsinins except for *Leuresthes* (Fig. 45B). Similarly, a slender premaxillary ascending process (Ch. 38) is either independently derived in menidiines, *Leuresthes*, and *Odontesthes* (Fig. 45A), or ambiguously optimized in atherinopsids (Fig. 45B, 45B'). In summary, I agree with Chernoff (1986b) regarding a long ascending process as plesiomorphic for atherinopsids, and I agree with White (1985) that a slender ascending premaxillary process is derived. All atherinopsids have some degree of upper jaw mobility, the amount of which is restricted either by a frenum or a shorter premaxillary ascending process, or both.

Temporal sensory canals

The sensory-canal bones of the temporal region are named according to the bones with which they are associated (i.e., pterotic, postemporal, supracleithral). Extrascapular bones are canal-bearing bones not associated with other bones, imbedded in the skin usually between the pterotic-canal and the postemporal-canal bones. As defined above, mugilids have three extrascapulars (Stiassny, 1993: fig. 7D), cyprinodontiforms and beloniforms have no temporal canals, some atherinoids have temporal and postemporal canals (melanotaeniines, atherinids [Fig. 10B], and *Dentatherina*), atherinopsids have postemporal canals, but only atherinopsines and *Melanorhinus* have extrascapulars.

Extrascapular bones of atherinopsids are formed by a medial transversally-oriented canal and a lateral horizontally-oriented canal. These bony canals are either fused into a single three-pored bone, or are present as two separate bones in *Melanorhinus* (Stiassny, 1993: fig 7C) and some sorgentinins (Figs 11, 32; White, 1985). Stiassny (1993) mentioned the presence of extrascapulars in *Iso*, but I have been unable to find any such ossifications in the material at hand and Said (1983) did not mention them in the osteological description of the genus.

The postemporal canal of atherinopsids is different in menidiines and in atherinopsines. Menidiines have a postemporal canal similar to the extrascapular described above (three-pored postemporal canal), whereas atherinopsines have a postemporal canal with one pore at either end (two-pored postemporal canal). The postemporal canal of menidiines has the same form and spatial orientation as the three-pored extrascapular bone of atherinopsines. Stiassny (1993) considered the sensory-canal bones of *Melanorhinus* as extrascapulars, but when compared to other menidiines it is clearly the postemporal-canal bone that is actually detached from the postemporal. Such "detachments" do occur occasionally in other taxa, as seen in some cleared and stained specimens of *Membras martinica* (UMMZ 199183) and *Odontesthes hatcheri* (CAS 12699), in which the canal bones are partly or fully disassociated from the postemporal on one or both sides of the head. If the canal-bearing bones of menidiines and atherinopsines are compared based on their morphology and relative positioning, independent of the bones they are attached to, the three-pored postemporal canal of menidiines corresponds anatomically to the extrascapular(s) of atherinopsines, not the two-pore postemporal canal of atherinopsines.

According to Johnson (1993: 17) the postemporal canal of percoids "...typically develops as an integral part of the posttemporal (i.e., it does not ossify separately and later fuse)". Given the postemporal canal sometimes ossifies separately and does not fuse to the underlying postemporal bone, the extrascapular and postemporal bones seem to be different by definition rather than by non-homology. If this hypothesis is correct, the extrascapulars of atherinopsines and *Melanorhinus* are homologous to the postemporal canal of menidiines. The three-pored temporal canals of atherinopsids are anatomically similar to extrascapular two of mugilids, but whether these three-pored temporal bones are homologous is less clear because the position of the pores and the shape of the bones are not equivalent (Fig. 10A, 10D). The homology among the postemporal canal of atherinopsines, extrascapular three of mugilids, and the posterior extrascapular of *Elassoma* as implied by Johnson & Patterson (1993: fig 14) is an interesting hypothesis that requires a better understanding of the development of these bones, and corroboration of *Elassoma* - mugilid - atherinomorph relationships.

Presence of two extrascapular bones was hypothesized as diagnostic of sorgentinins by White (1985). Separation of the horizontal and vertical elements of the extrascapulars is variable in sorgentinins such that both states may be present on the same individual, therefore failing the conjunction test of homology (Patterson, 1982). Both elements are consistently fused together in atherinopsinins. Assuming the extrascapulars of atherinopsines and the postemporal canal bone of menidiines are homologous (see above), and considering the presence of separate elements in *Melanorhinus* and some specimens of *Membras martinica* (UMMZ 199183), two separate extrascapular elements appear to be the plesiomorphic condition and the presence of fused elements in atherinopsinins would be a derived condition.

Axial skeleton

Atherinopsinins have between 10 and 15 vertebrae with so called "precaudal haemal arches", i.e., haemal arches anterior to the first vertebra that bears a haemal spine. "Precaudal haemal arches" are ventrally directed parapophyses of the vertebra with a haemal bridge separating dorsoventrally the haemal canal from the swimbladder. The paired projections ventral to the haemal bridge, or haemal hypophyses, seem to correspond to the ventral ends of the haemal parapophyses rather than being homologous to haemal spines as proposed by White (1985: 6). The possible homology of these haemal arches raises a number of issues the very least of which is the coding of Characters 86 and 95. The most fundamental issue raised is the arbitrary and contradictory definitions of what constitutes a precaudal or a caudal vertebra. "The first caudal vertebra...", as defined by Hubbs & Lagler (1958: 24), "...is the first vertebra bearing a definite hemal spine." The earliest usage I found of this definition is that of Ford (1937). Romer on the other hand, defined caudal vertebrae for fishes "...by the presence of hemal arches in the tail" (Romer & Parsons, 1986:183). Normally these two definitions coincide on the same vertebra as in sorgentinins and menidiines, such that the first vertebra with a haemal arch also has the first haemal spine (Figs 35-38). It is in the case of atherinopsinins (Fig. 39), most atherinoids, and many other teleosts, however, that the definitions are in conflict with each other (Ford, 1937; Clothier, 1950; Patten, 1978). An arbitrary choice between definitions affects the coding of some characters and ultimately the phylogenetic analysis. Choice of definitions must come from an assessment of similarity among the component parts of this vertebral "puzzle", which must be based on sound morphological arguments, and include developmental and comparative studies. "Precaudal haemal arches" are present in mugilids, atherinoids except for notocheirids, *Melanorhinus*, some species of *Atherinella*, and atherinopsinins. Ontogenetic information is unavailable at this time to make a convincing argument as to whether "precaudal haemal arches" should be considered modified precaudal vertebrae or modified caudal vertebrae. Defining caudal vertebrae sensu Romer (presence of haemal arches) for Characters 86 and 95, contrary to the more general definition used by ichthyologists today (presence of haemal spines), results from my understanding that all haemal arches are serial homologs, irrespective of the position of the first haemal spine, which is an ontogenetically independent element (Mabee, 1993: fig. 10).

CONCLUSIONS

The phylogenetic hypothesis of relationships among atherinopsine genera proposed by White (1985) is reevaluated. Anatomical data of White (1985), Chernoff (1986b), and Dyer (1993), and enzymatic data of Crabtree (1987) are combined into a single data matrix of 123 characters and 25 taxa. Taxonomic results proposed by White (1985) are unchanged in this study (Table 2). Phylogenetic relationships among atherinopsinin genera, however, are resolved in two equally parsimonious hypotheses (Figs 2, 42). *Colpichthys* is the sister to *Atherinops*, *Atherinopsis*, and *Leuresthes*, the latter two each others closest relatives (Figs 2A, 42A). The alternative hypothesis mirrors the above topology with *Leuresthes* as sister to *Atherinopsis*, *Atherinops*, and *Colpichthys* (Figs 2B, 42B). In the hypothesis proposed by White (1985) *Colpichthys* and *Atherinops*, and *Leuresthes* and *Atherinopsis*, are sister taxa. Crabtree (1978) presented an alternative to White's hypothesis in which Sorgentinini is sister to the *Leuresthes* - *Atherinopsis* clade. White's hypothesis is one step longer than those presented in this study and Crabtree's is seven steps longer.

Atherinopsinae is diagnosed by eight characters, Atherinopsini by seven characters, and Sorgentinini by eight characters (Fig. 1). Atherinopsini has four genera: *Colpichthys*, with two species (*C. regis*, *C. hubbsi*), is diagnosed by nine characters; *Atherinops affinis* is diagnosed by three characters; *Atherinopsis californiensis* is diagnosed by seven characters; and *Leuresthes*, with two species (*L. tenuis*, *L. sardina*), is diagnosed by five characters. Sorgentinini has two genera: *Odontesthes*, with about 25 species, is diagnosed by seven characters, and *Basilichthys*, with five species, is diagnosed by 22 characters.

Two species groups are recognized in *Basilichthys*. The *Basilichthys microlepidotus* species group comprises the nominal species *B. microlepidotus* and *B. australis* from Chile. The *Basilichthys semotilus* species group comprises *B. semotilus* and *B. archaeus* from Peru, and an undescribed species from Río Loa in Chile. The undescribed species is tentatively proposed as sister to *B. semotilus* and *B. archaeus.*

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APPENDIX 1

Material examined: Institutional abbreviations follow Leviton *et al.* (1985) except for MNHN-M (Museo Nacional Historia Natural de Montevideo, Uruguay) and ZVC-P (Zoología de Vertebrados - Peces, Facultad de Humanidades y Ciencias, Universidad Nacional, Montevideo, Uruguay). The number of specimens studied are in brackets, 'st.' indicates stained-and-dissected specimens, and the number of cleared-and-stained specimens are in parenthesis. Genera and species are listed alphabetically within each major grouping. Brief locality data is added for atherinopsines only.

Mugilidae: *Agonostomus monticola* UMMZ 178460(5), UMMZ 199463[16+(3)], ANSP 122356(2), FMNH 4623; *Crenimugil crenilabis* ANSP 114275(1); *Joturus pichardi* ANSP 99859(1); *Liza argentea* ANSP 135485(4); *Mugil curema* UMMZ 209709(3), ANSP 128030(3); *Mugil dussumieri* ANSP 61891(1); *Mugil trichodon* ANSP 145654(5).

Beloniformes

Adrianichthyoidei: *Horaichthys setnai* UMMZ 201181(1), ANSP 157315(4); *Oryzias javanicus* UMMZ 146566(10), FMNH 68669(5); *Oryzias latipes* UMMZ 146592(10), UMMZ 218498, FMNH 58732(5); *Oryzias melastigma* UMMZ 232000(3).

Exocoetoidei: *Arrhamphus brevis* UMMZ 100333[3 st.], FMNH 47553[3]; *Chriodorus atherinoides* UMMZ 102192[9+1st.], UMMZ 143079(4); *Cololabis saira* UMMZ 71135[2 st.], FMNH 63758(1), ANSP 88978(1); *Cypselurus melanurus* ANSP 50519(3); *Cypselurus starksi* UMMZ 212929(1); *Dermogenys pusilla* UMMZ 195917(4); *Fodiator acutus* UMMZ 190985[2 st.], ANSP 88928(1); *Hemiramphus balao* ANSP 111444(1); *Hirundichthys affinis* ANSP 14973(1); *Hyporhamphus neglectus* ANSP 48851(2); *Hyporhamphus unifasciatus* ANSP 118641(5); *Parexocoetus brachypterus* ANSP 144887(1); *Scomberesox saurus* FMNH 48552(2); *Strongylura marina* ANSP 116170(5); *Xenentodon cancila* ANSP 123993(2); *Xenentodon sp.* UMMZ 218510(2); *Zenarchopterus dispar* ANSP 79674(2).

Cyprinodontiformes

Cyprinodontoidei: *Adinia xenica* UMMZ 158860(5); *Alfaro cultratus* ANSP 104371(4); *Anableps dowei* ANSP 91678(2); *Aphyosemion australe* ANSP 141548(4); *Aplocheilichthys spilauchen* ANSP 38679-88(2); *Chapalichthys pardalis* UMMZ 202427(4); *Cyprinodon variegatus* ANSP 95086(5); *Fundulus diaphanus* ANSP 90980(4); *Fundulus heteroclitus* ANSP 116576(5); *Fundulus notatus* UMMZ 209055(5); *Lucania goodei* ANSP 140561(5); *Orestias agassii* FMNH 77376(2); *Profundulus guatemalensis* UMMZ 218513(2); *Profundulus labialis* ANSP 64776(4); *Profundulus hildebrandi* UMMZ 157634(5).

Aplocheiloidei: *Aphyosemion gulare* ANSP 141552(5); *Epiplatys spilauchen* UMMZ 187902(2); *Pterolebias sp.* ANSP 141546(4); *Rivulus agile* FMNH 85368(5); *Rivulus bondi* UMMZ 141915(10); *Rivulus deltaphilus* FMNH 70375(4); *Rivulus harti* FMNH 50098(2); *Rivulus hildebrandi* ANSP 151286(3); *Rivulus marmoratus* ANSP 103453(2); *Rivulus tenuis* FMNH 82194(4).

Atheriniformes

Notocheiridae: *Notocheirus hubbsi* UMMZ 231951(3); *Iso rhothophilus* UMMZ 217631(1), UMMZ 212579(2).

Atherionidae: *Atherion elymus* UMMZ 204128(1).

Melanotaeniidae

Bedotiinae: *Bedotia geayi* UMMZ 217630(3), UMMZ 218508(4); *Bedotia sp.* UMMZ 218515(2), FMNH 99280(3); *Rheocles alaotrensis* UMMZ 217679(1), FMNH 99281(1).

Melanotaeniinae: *Melanotaenia nigrans* UMMZ 203847(3); *Melanotaenia rubrostriata* UMMZ 203849(3).

Pseudomugilinae: *Pseudomugil signifer* UMMZ 217684(1), I-081(3); *Pseudomugil tenellus* UMMZ 203852(5); *Telmatherina ladigesi* FMNH 152041(2).

Atherinidae

Atherininae: *Atherina boyeri* UMMZ 185092(1); *Atherina sp.* FMNH 77485(2); *Atherinason hepsetoides* UMMZ 212576; *Atherinosoma microstoma* UMMZ 212562(3), UMMZ 212581.

Atherinomorinae: *Atherinomorus eendrachtensis* UMMZ 196221, UMMZ 203854(3); *Atherinomorus lacunosus* FMNH 21105(2), FMNH 63916(2), FMNH 21198(2); *Atherinomorus stipes* UMMZ 199482, UMMZ 174207(2); *Hypoatherina bleekeri* FMNH 52131(1), FMNH 57459(1); *Hypoatherina tsurugae* UMMZ 142801[1 st.]; *Stenatherina ovalaua* UMMZ 212578(1); *Stenatherina regina* FMNH 40475(2), FMNH 23504(2); *Stenatherina temmincki* FMNH 44136(2).

Craterocephalinae: *Craterocephalus fluviatilis* UMMZ 212564(2); *Craterocephalus pauciradiatus* UMMZ 214554[5];

Atherinopsidae

Menidiinae

Menidiini: *Chirostoma arge* UMMZ 197622(6); *Chirostoma chapalae* UMMZ 197612(4); *Chirostoma consocium* UMMZ 179720(1); *Chirostoma estor* UMMZ 197650(2); *Chirostoma humboldtianum* UMMZ 97663(1); *Chirostoma jordani* UMMZ 197602(5); *Chirostoma labarcae* UMMZ 193463(4); *Chirostoma lucius* UMMZ 179717(1); *Chirostoma mezquital* UMMZ 211095(3); *Chirostoma promelas* UMMZ 193465(1); *Chirostoma sphyraena* UMMZ 186203(1); *Labidesthes sicculus* UMMZ 231999(1), UMMZ 222857(3); *Menidia colei* UMMZ 196562(5); *Menidia beryllina* UMMZ 203149(5); *Menidia menidia* UMMZ 136589(3); *Poblana alchichica* UMMZ 192371(4).

Membradini: *Atherinella alvarezi* UMMZ 196439(6); *Atherinella argentea* UMMZ 202408(4); *Atherinella brasiliensis* GCRL V73:10997; *Atherinella crystallina* UMMZ 171990(3); *Atherinella guatemalensis* UMMZ 173523(5); *Atherinella sallei* UMMZ 184767(3); *Atherinella schultzi* UMMZ 184709(6), UMMZ 191736(6); *Melanorhinus microps* UMMZ 198779(1); *Membras gilberti* UMMZ 202405(1), *Membras martinica* UMMZ 199183(1).

Atherinopsinae

Atherinopsini: *Atherinops affinis* UMMZ 72212[33+(2)], Newport Beach, California; UMMZ 176309(5), La Jolla, San Diego, California; UMMZ 141158(3), Morrow Bay, San Luis Obispo, California; UMMZ 232001(4), Catalina Harbor, California; *Atherinopsis californiensis* UMMZ 190946(3), Brighton Beach, Terminal Island, Los Angeles, California; UMMZ 68147[33+(3)], Elkhorn Slough, California; *Colpichthys regis* UMMZ 161601[1], UMMZ 190400[3+(1)], Gulf of California, Sonora, Mexico; *Colpichthys hubbsi* LACM W78-11[4 st.], Sonora, Mexico; *Leuresthes tenuis* UMMZ 65910[2+(1)], San Pedro, California; *Leuresthes sardina* FMNH 62412[22+(2)], Gulf of California, nr San Felipe, Baja California Norte, Mexico.

Sorgentinini: *Basilichthys sp.* UMMZ 215515[11+(1)], Río Loa, Chile; UMMZ 215520[86+(4)], Río Loa, Chile; *B. archaeus* UMMZ 217958[6+(1)], Río Ocoña, Arequipa, Peru; UMMZ 217990[3+(1)], Río Vitor, Arequipa, Peru; UMMZ 218077[13+(2)], Río Cotahuasi, Arequipa, Peru; *B. australis* UMMZ 215505[13+(3)], Río Itata, Ñuble, Chile; UMMZ 215506[1+(1)], Estero Mela, Ñuble, Chile; UMMZ 215507[5+(2)], Río Cobquecura, Ñuble, Chile; *B. microlepidotus* CAS 42587[43+(3)], Río Elqui, La Serena, Elqui, Chile; UMMZ, 215487[8+(2)], Estero Catapilco, Petorca, Chile; UMMZ 215499[22+(2)], Río Limarí, Limarí, Chile; UMMZ 215502[4+(1)], Río Quilimarí, Choapa, Chile; *B.*

semotilus UMMZ 217959[61+(5)], Río Ilabaya, Río Locumba dr., Tacna, Peru; UMMZ 218050[310+(3)], Río San Juan, Río Jequetepeque dr., Cajamarca, Peru; UMMZ 218074[27+(3)], Río Santa, Ancash, Peru; *Odontesthes argentinensis* UMMZ 231948(2), Montevideo, Uruguay; UMMZ 232009[1 st.], Golfo Nuevo, Chubut, Argentina; UMMZ 218820[1 st.], Golfo Nuevo, Chubut, Argentina; UMMZ 218821[1 st.], Pto. Madryn, Chubut, Argentina; *O. bonariensis* UMMZ 218609[10+(2)], Laguna Sauce Grande, Buenos Aires, Argentina; UMMZ 218824[21+(1)], Río Rapel, Cachapoal, Chile; *O. Cauque brevianalis* UMMZ 215459(35+(4)], Estero Catapilco, Petorca, Chile; UMMZ 215468[112+(13)], Estero Los Perales, nr Río Itata, Nuble, Chile; *O. Austromenidia gracilis* UMMZ 215529[6+(1)], Isla Robinson Crusoe, Juan Fernández Archipelago, Chile; *O. hatcheri* UMMZ 218450[72+(2)], Lago Cochrane, Capitán Prat, Chile; UMMZ 218804[8 st.], Río Chubut inferior, Chubut, Argentina; CAS 12699[8+(2)], Lago Frías, Nahuel-Huapi, Río Negro, Argentina; *O. humensis* UMMZ 221327[9+(1)], Lagoa Mangueira, R.S., Brazil; MNHN-M 2671[6+(1)], Río San Salvador, Río Uruguay dr., Soriano, Uruguay; *O. incisa* UMMZ 95499[3+(1)], Necochea, Buenos Aires, Argentina; UMMZ 218799[5+(1)], Mar del Plata, Buenos Aires, Argentina; UMMZ 218816[4 st.], UMMZ 218817[1 st.], UMMZ 218818[1 st.], UMMZ 218819[1 st.], Golfo Nuevo, Chubut, Argentina; USNM 163378[5 st.], Mar del Plata, Argentina; *O. nigricans* UMMZ 218798[4+(1)], Straits of Magellan, Tierra del Fuego, Chile; UMMZ 218802[1 st.], Pto. Madryn, Chubut, Argentina; UMMZ 218979[17+(3)], Camilla Creek, East Falkland Island; *O. perugiae* UMMZ 221328[9+(1)], Lagoa Emboaba, R.S., Brazil; MNHN-M 2670[5+(1)], Río San Salvador, Soriano, Uruguay; MZUSP 15446[3 st.], Lagoa dos Quadros, R.S., Brazil; *O. platensis* UMMZ 232008[1 st.], Golfo Nuevo, Chubut, Argentina; UMMZ 218815(1), ?Rawson, Chubut, Argentina; *O. Austromenidia regia* 215521[11+(1)], Valdivia, Valdivia, Chile; UMMZ 218455[11+(1)], Castro, Isla Grande Chiloé, Chile; UMMZ 215530[3+(1)], Valparaíso, Chile; CAS-SU 37431[9+(1)], Islas Chincha, Pisco, Peru; *O. retropinnis* UMMZ 231950[3+(1)], Uruguay; UMMZ 218796[28+(2)], Los Talas, nr La Plata, Buenos Aires, Argentina; ZVC-P 1159[3+(1)], Arroyo Cuaró Grande, Artigas, Uruguay; *O. Austromenidia smitti* UMMZ 218448[15+(1)], Punta Arenas, Magallanes, Chile; UMMZ 218980[19+(3)], Camilla Creek, East Falkland Island.

APPENDIX 2

List of synapomorphies: Characters preceded by a plus (+) are diagnostic. Characters considered as additional support to a clade are preceded by a dash (-) if unambiguously optimized on one of the two cladograms, and those preceded by an asterisk (*) are ambiguously polarized features on both trees.

ATHERINOPSIDAE

+Ch. 18: postorbital sphenotic process wide.
+Ch. 19: dermosphenotic not articulated to postorbital process.
+Ch. 20: dermosphenotic sensory canal enclosed.
+Ch. 29: pterotic wing present.
+Ch. 30: exoccipital with wing or processes.
+Ch. 36: postemporal with anterior process.
+Ch. 39: premaxilla with narrow anterior joint.
+Ch. 44: premaxillary alveolar arm broadly dilated.
+Ch. 45: premaxilla-dentary coronoid ligament very short.
+Ch. 46: maxilla-anguloarticular coronoid ligament present.
+Ch. 47: premaxilla-maxilla ligament long to mid-region of alveolar arm.
+Ch. 55: ethmomaxillary ligament with palatine attachment.
+Ch. 61: vertical shaft of preopercular canal enclosed by bone.
+Ch. 67: opercular dorsal border discontinuous with dorsal process.
+Ch. 76: Baudelot's ligament attached to cleithrum, parapophysis of vertebrae 1, and epineural 1.
+Ch. 77: pectoral struts present.
+Ch. 78: pectoral-fin spur fused to second ray.
+Ch. 79: ventral postcleitrum expanded, placed between pleural ribs 1 and 2, and two dorsal rami of about equal size.
+Ch. 84: interdorsals without a ventral shaft.
+Ch. 88: pleural ribs posterior to first anal-fin pterygiophore.
-Ch. 25: secondary trigeminofacial arch present.
-Ch. 57: palatine posteroventral spine extended to quadrate.
*Ch. 4: anterior vomerine shelf.
*Ch. 48: labial ligament folded lateral to premaxilla.
*Ch. 54: palatine dorsal process present.
*Ch. 85: six or more interdorsal pterygiophores.
*Ch. 95: first caudal vertebra dorsal to anterior half of anal fin.

MENIDIINAE

+Ch. 3: vomer with single, median dorsal lamina.
+Ch. 25: trigeminofacial arch with posterior enclosure of jugular vein.
+Ch. 53: A1 mandibular branch present.
+Ch. 73: tooth patches fused with ceratobranchial 4.
+Ch. 75: anterior border of cleithrum dorsomedial wing curved ventrally, extended to scapular foramen at most.
+Ch. 97: two suborbital rows of scales.
+Ch.106: Chernoff (1986b): vagus nerve foramen with posterior wall; urohyal pedicel with wide dorsal surface; infrapharyngobranchial 2 with deep medial groove and tooth plate short & wide; parapophysis of vertebra 1 enlarged; epineural 1 short, attached to posterior dorsomedial wing of cleithrum; pelvic bone with ventral cradle for fin rays.
-Ch. 38: premaxillary ascending process with narrow base.
-Ch. 57: palatine spine extended to quadrate.
*Ch. 35: postemporal sensory canal with three pores.
*Ch. 82: origin of the first dorsal fin posterior to anus.

MENIDIINI

+Ch. 22: dermosphenotic median flange absent.
+Ch. 59: endopterygoid teeth absent.
+Ch. : Chernoff (1986b): fused upper hypural plate.
-Ch. 50: three rows of teeth on oral jaws.

MEMBRADINI

+Ch. 60: hyomandibular nerve divided inside of hyomandibula.
+Ch. 70: infrapharyngobranchial 1 absent.
+Ch. : Chernoff (1986b): rostral sensory system; dorsal process of maxilla expanded and elongate; step-shaped mesethmoid (see Ch. 9); thick and short epineural 1.

ATHERINOPSINAE

+Ch. 6: ethmoid cartilage folded ventral of vomer midline.
+Ch. 11: nasal ventral process overlaps lacrimal subnasal shelf.
+Ch. 12: nasal sensory canal detached anteriorly.
+Ch. 23: postocular shelf on dorsal half of dermosphenotic.
+Ch. 26: basisphenoid belophragm short.
+Ch. 34: Baudelot's ligament ossified at basioccipital.
+Ch. 54: palatine dorsal process pointed and folded over ethmoid block.
+Ch. 89: haemal funnel present.
-Ch. 1: vomerine median process with dorsal ridge.
-Ch. 81: median process of pelvic bone reduced or absent.
*Ch. 15: ventral condyle of lateral ethmoid ossified.
*Ch. 31: pterotic - exoccipital wings contiguous.
*Ch. 35: extrascapular sensory canal with three pores and postemporal sensory canal with two pores.
*Ch. 61: vertical and horizontal shaft of preopercular sensory canal enclosed by bone.

ATHERINOPSINI

+Ch. 3: vomer with two well developed dorsal laminae.
+Ch. 21: dermosphenotic with three sensory-canal pores.
+Ch. 28: supraoccipital crest "trifid".
+Ch. 70: infrapharyngobranchial 1 cartilaginous.
+Ch. 71: cranial process of infrapharyngobranchial 2 with small condylar surface and at right angle with that of infrapharyngobranchial 3.
+Ch. 72: uncinate process of epibranchial 3 long and attached laterally.
+Ch. 90: haemal-hypophysis funnel.
-Ch. 50: three rows of teeth or less on oral jaws.
-Ch. 84: interdorsal series discontinuous.
-Ch. 99: large scales present on cleithrum shaft.
-Ch.109: Aspartate aminotransferase (M-Aat-A).
*Ch. 36: postemporal anterior process wide.
*Ch. 37: presence of an upper jaw frenum.
*Ch.112: Esterase (Est-1).

COLPICHTHYS

+Ch. 60: presence of a hyomandibular nerve foramen.
+Ch. 75: ventral extension of anterior border of cleithrum dorsomedial wing not reaching scapular foramen.
+Ch. : Todd (1976): teeth with asymmetrical cusps; White (1985): notch in the dorsal process of maxilla, external row of gill rakers on anterior portion of fourth ceratobranchial expanded medially in a plate-like form, infrapharyngobranchial teeth hair-like; Crabtree (1989): female with ovipositor and eggs lacking filaments; few gill rakers (<20 lower limb) on the first branchial arch.
-Ch. 47: maxilla-premaxilla distal ligament attached to anteroventral corner of premaxillary alveolar arm.
-Ch. 84: a continuous series of interdorsal bones.
-Ch. 85: six or more interdorsal bones.
-Ch.101: no scales on the anal fin.
-Ch.110: Aspartate aminotransferase (S-Aat-A).
-Ch.113: Glucose-6-phosphate isomerase (Gpi-A).
-Ch.121: Phosphoglucomutase (Pgm-A).

ATHERINOPS

+Ch. 97: two rows of subocular scales.
+Ch.123: Superoxide dismutase (Sod-A).
+Ch. : White (1985): Frills of skin between the maxilla and premaxilla.
-Ch. 99: lack of scales on the cleithrum shaft.
*Ch. 74: absence of a urohyal ventral plate.
*Ch. 82: origin of the first dorsal fin over anus.

ATHERINOPSIS

+Ch. 20: dermosphenotic canal not enclosed by bone.
+Ch. 32: pterotic and epioccipital wing bases contiguous under temporal fossa epaxial musculature.
+Ch. 64: dorsal process of opercle not blade-like.
+Ch.102: scales small (>12 dorsal scales).
+Ch.121: Phosphoglucomutase (Pgm-A).
+Ch.123: Superoxide dismutase (Sod-A).
+Ch. : White (1985): modification of the ventral process of the maxilla for the attachment of premaxillary and rostral-cartilage ligaments,
*Ch. 74: absence of a urohyal ventral plate.

LEURESTHES

+Ch. 53: mandibular branch of A1 muscle tendon anterior to lacrimal branch.
+Ch. 60: hyomandibular nerve divided inside of hyomandibula.
+Ch. 80: pelvic median plate extending to anterior tip.
+Ch.100: scales present between anterior rays of second dorsal fin.
+Ch. : Moffat & Thomson (1975): unique beach-spawning habits.
-Ch. 1: lack of a vomerine dorsomedial ridge.
-Ch. 12: reduced anterior detachment of nasal sensory canal.
-Ch. 37: no upper jaw frenum.
-Ch. 38: premaxillary ascending process with narrow base.
-Ch. 40: well developed dorsal process of the maxilla.
-Ch. 81: pelvic medial process well developed.
-Ch.115: Glutamate dehydrogenase (Gtdh-A).
*Ch. 82: origin of first dorsal fin over anus.

SORGENTININI

+Ch. 10: ethmomaxillary ligament attached to ethmoid cartilage.
+Ch. 33: basioccipital fenestration present.
+Ch. 56: palatorostral ligament present.

+Ch. 59: endopterygoid tooth patch absent.
+Ch. 86: precaudal vertebrae over 50% of total vertebrae.
+Ch. 91: haemal-arch funnel.
+Ch.107: Adenylate kinase (Ak-A).
+Ch.108: Aminopeptidase (Ap-A).

ODONTESTHES
+Ch. 9: mesethmoid absent.
+Ch. 24: trigeminal foramen enclosed by prootic, sphenotic, and pleurosphenoid.
+Ch. 41: maxillary ventral process about equal length as dorsal process.
+Ch. 53: mandibular branch of A1 muscle tendon present, anterior to lacrimal branch.
+Ch. 65: opercle fenestrated internally.
+Ch. 66: presence of fenestrated medial lamina between posterior and ventral struts.
+Ch. 94: anterior haemal spines short.
-Ch. 12: nasal sensory canal clearly detached from nasal bone.
-Ch. 25: secondary trigeminofacial arch present.
-Ch. 38: premaxillary ascending process with narrow base.
-Ch.101: scales present between anterior rays of anal fin.

BASILICHTHYS
+Ch. 3: vomer with two parasagittal dorsal laminae.
+Ch. 5: vomer slightly concave ventrally.
+Ch. 7: vomer with single, median tooth patch.
+Ch. 13: lacrimal condyle of lateral ethmoid does not reach the ventral edge of the lateral ridge.
+Ch. 22: dermosphenotic medial flange absent.
+Ch. 32: pterotic and epiotic wings contiguous.
+Ch. 42: ventral process of maxilla with condyle.
+Ch. 46: maxillo-anguloarticular ligament absent.
+Ch. 48: labial ligament with lateral fold reduced.
+Ch. 51: dentary coronoid flat at level with anguloarticular coronoid.
+Ch. 52: dentary gnathic spine absent.
+Ch. 54: palatine dorsal process tall, spoon shaped.
+Ch. 55: ethmomaxillary ligament not attached to palatine.
+Ch. 62: preopercular pores 1 & 2 with bony enclosure.
+Ch. 64: opercular dorsal process not blade-like.
+Ch. 68: opercular posterodorsal border concave.
+Ch. 83: anterior spine of first dorsal fin shorter than spine of second dorsal fin.
+Ch. 86: precaudal vertebrae over 57% of total vertebrae.
+Ch. 95: first caudal vertebrae over posterior half of anal fin.
+Ch. 96: dorsal head scales with reversed imbrication.
+Ch. 97: four suborbital scale rows.
+Ch. 98: interopercular scales on posterior half only.
-Ch. 25: secondary trigeminofacial arch absent.
-Ch. 37: presence of an upper jaw frenum.
-Ch. 40: dorsal process of maxilla short.
-Ch. 47: premaxilla-maxilla ligament anteroventral region of alveolar arm.
-Ch. 57: palatine spine not contacting quadrate.
*Ch. 8: single median vomerine tooth patch.
*Ch. 28: supraoccipital crest bifid.
*Ch. 36: postemporal anterior process wide.
*Ch. 91: haemal arches with flaring expansions only.
*Ch.102: body scales small.

SEMOTILUS species group
+Ch. 2: vomerine dorsomedial spine.
+Ch. 48: lateral fold of labial ligament greatly reduced.
+Ch. 63: four pores on horizontal shaft of preopercle.
+Ch. 96: scales of interorbital region only with reversed imbrication.
*Ch. 26: basisphenoid with anterior elongation to interorbital cartilage.
*Ch. 58: ectopterygoid absent.

APPENDIX 3

Ambiguous characters: Ambiguity due to alternative equally parsimonious reconstructions of a character's evolution may lead to loss of diagnostic information if only the unique and unambiguous traits are considered as informative of relationships. Some of this phylogenetic information can be retrieved, in the form of additional supporting characters, if the type of ambiguity affecting each character is identified.

Three classes of character ambiguities have been identified that allow, given the assumptions, for the recovery of characters as evidence of monophyly:
1) character is ambiguous because the relatively primitive state is present in a highly derived sister taxon to one of two ingroup sister taxa (Fig. 46A). The auxiliary assumption is that the ingroup sister-taxon with the plesiomorphic condition is derived by some mode of paedomorphic development;
2) despite presence of the derived character state in the ingroup, that character state is ambiguous because of other character-state polymorphism, absence of data, or both, in one or more outgroups (Fig. 46B). The auxiliary assumption is that the plesiomorphic condition is present at the outgroup nodes; and
3) a non-additive multistate character is ambiguous because the character states present in each of two ingroup sister taxa are different and derived relative to the plesiomorphic state present in outgroups (Fig. 46C). The auxiliary assumption is that both states are derived independently from the primitive condition present in their common ancestor.

Different modes of optimization are chosen for each individual character according to the type of ambiguity identified after the phylogenetic analysis. Rather than choosing a single optimization criterion for all characters prior to the analysis, an *a posteriori* approach is considered a more appropriate method for additional-character support of monophyly. In the first and second types of ambiguity, characters are optimized to the node of greater generality with subsequent reversals (ACCTRAN in PAUP), whereas in the third type of ambiguity the derived character states are optimized to nodes of lesser generality by assuming the primitive state at the preceding node (DELTRAN in PAUP). The number of ad hoc assumptions decreases when suites of characters of the same class of ambiguity are present at one node (Appendix II: Atherinopsinae).

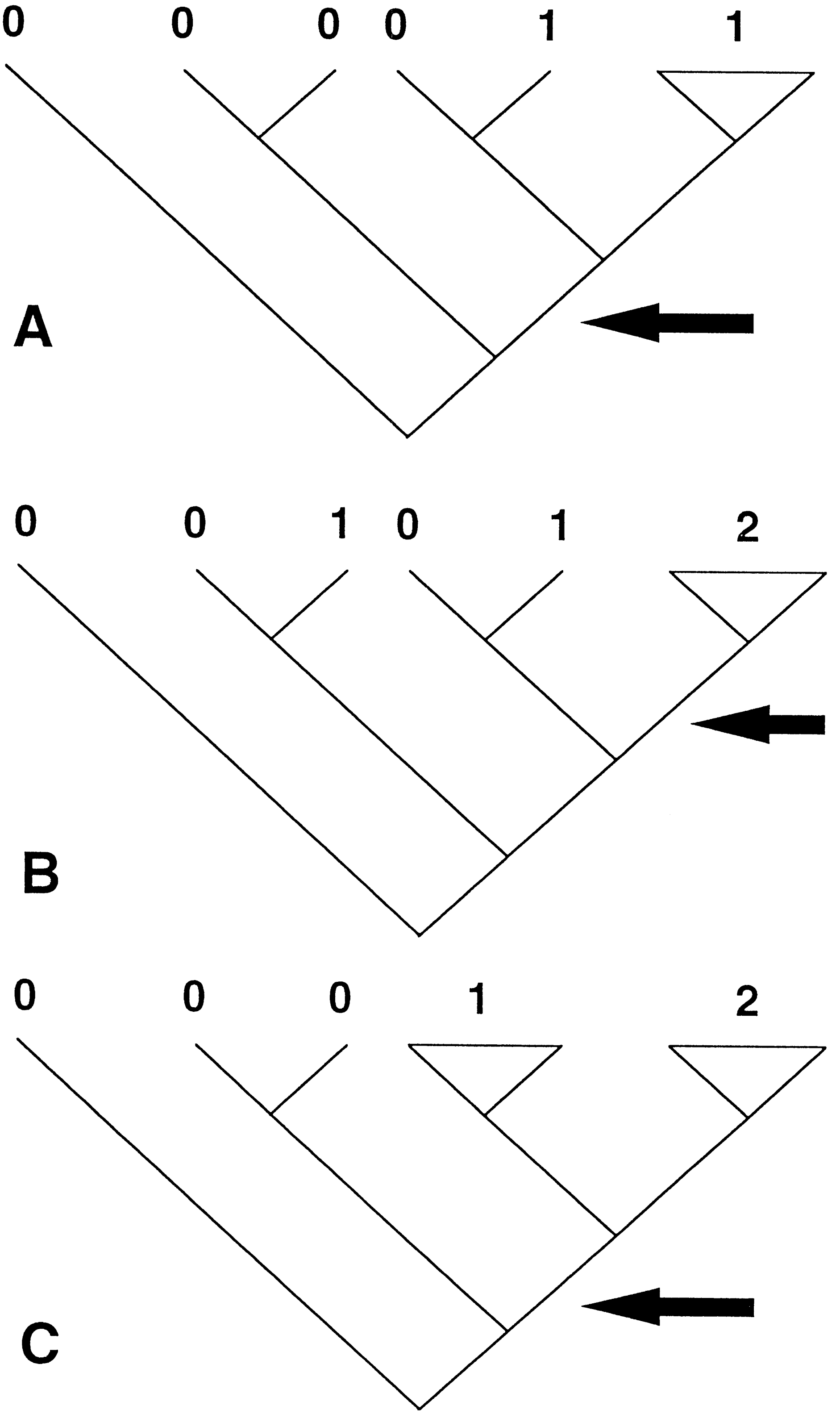

Fig. 46. Three classes of character-state distributions that result in ambiguous optimizations when mapped on a cladogram; A, Type 1 ambiguity, because the relatively primitive state is present in a highly derived sister taxon to one of two ingroup sister taxa; B, Type 2 ambiguity, because of character-state polymorphism, absence of data, or both, in one or more outgroups; C, Type 3 ambiguity, because the character states present in each of two ingroup sister taxa are different and derived relative to the plesiomorphic state of a non-additive multistate character, present in outgroups. Arrows indicate node of suggested *a posteriori* optimization.