BIOCELL
2006, 30(1): 69-88

ISSN 0327 - 9545
PRINTED IN ARGENTINA

Symposium: BIOLOGY AND CULTURE OF SILVERSIDES (PEJERREYES)

Systematic revision of the South American silversides (Teleostei, Atheriniformes)

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Key words: Atherinopsinae, *Odontesthes*, Phylogeny, Taxonomy, Morphology,

The taxonomic and systematic history of the South American silversides has changed significantly since Campos (1984) review. As a result of phylogenetic studies of the subfamilies Menidiinae (Chernoff, 1986b), Atherinopsinae (White, 1985; Crabtree, 1987; Dyer 1997, 1998) and of the order Atheriniformes (Saeed *et al*., 1994; Dyer and Chernoff, 1996) the taxonomy and classification of silversides has changed notoriously (Table I). Two systematic studies with different methodologies and divergent results in many ways coincided in that the subfamilies Menidiinae and Atherinopsinae, traditionally considered as atherinids, were to form part of the family Atherinopsidae (Saeed *et al*., 1994; Dyer and Chernoff, 1996).

The purpose of this paper is to review the present state of the systematics (taxonomy, relationships and distribution) of the South American silversides in the context of phylogenetic revisions of Atheriniformes and Atherinopsinae. All systematic results presented herein are based on published material (Dyer and Chernoff, 1996; Dyer, 1993, 1997, 1998, 2000, 2003a,b; Dyer and Gosztonyi, 1999; Malabarba and Dyer, 2002). In addition to some diagnostic features of the taxa involved (genera, tribes, subfamilies, and families), an identification key and some identification and diagnostic problems, are presented.

Atheriniformes

Atheriniformes is phylogenetically diagnosed by ten characters (Dyer and Chernoff, 1996) and is sister to the superorder Cyprinodontea (Fig. 1), formed by the orders Beloniformes and Cyprinodontiformes.[1] These three orders form part of the series Atherinomorpha (Fig. 1). Six families and 49 genera are recognized in Atheriniformes (Dyer and Chernoff, 1996; Table 1). More recent studies of relationships among families of Atheriniformes involve only the melanotaeniids, pseudomugilids, and telmatherinids (Aarn and Ivantsoff, 1997; Aarn *et al*., 1998). One of the main conclusions of Saeed *et al*. (1994) and Dyer and Chernoff (1996) is that subfamilies and genera traditionally considered as a part of Atherinidae, now form part of other families such as: Atherinopsidae

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Received on April 21, 2005. Accepted on May 11, 2005.

[1] Phylogenetic relationships among families are based on a data matrix of 83 morphological characters and 31 taxa (Dyer and Chernoff, 1996).

TABLE 1.

Sequential classification of families and subfamiles of Atheriniformes, genera of Atherinopsidae, and species of Sorgentinini. The order of genera and species is alphabetical or in phylogenetic sequence when indicated by an asterisk (*). (gr-esp.= species group)

Series Atherinomorpha Greenwood, Rosen, Weitzman, Myers
- Order Atheriniformes Rosen
  - Family Atherinopsidae Fowler
    - Subfamily Atherinopsinae Fowler
      - Tribe Atherinopsini Fowler
        - Genus *Atherinops* Steindachner
        - Genus *Atherinopsis* Girard
        - Genus *Colpichthys* Hubbs
        - Genus *Leuresthes* Jordan & Gilbert
      - Tribe Sorgentinini Pianta de Risso & Risso
        - Genus *Basilichthys* Girard
          - gr-esp. *microlepidotus*
            - *australis* Eigenmann
            - *microlepidotus* Jenyns
          - gr-esp. *semotilus*
            - *archaeus* Cope
            - *semotilus* Cope
        - Genus *Odontesthes* Evermann & Kendall*
          - *hatcheri* Eigenmann
          - *humensis* de Buen
            - *retropinnis* de Buen
            - Subgenus *Odontesthes*
              - *bicudo* Malabarba & Dyer
              - *ledae* Malabarba & Dyer
              - *mirinensis* Bemvenuti
              - *orientalis* de Buen
              - *perugiae* Evermann & Kendall
              - *piquava* Malabarba & Dyer
          - *bonariensis* Valenciennes
          - *argentinensis* Valenciennes
          - Subgenus *Cauque* Eigenmann *sedis mutabilis*
            - *brevianalis* Günther
            - *mauleanum* Steindachner
          - gr-esp. *incisa sedis mutabilis*
            - *incisa* Jenyns *sedis mutabilis*
            - *nigricans* Richardson *sedis mutabilis*
          - *platensis* Berg *sedis mutabilis*
          - Subgenus *Austromenidia* Hubbs* *sedis mutabilis*
            - *smitti* Lahille
            - *regia* Humboldt
            - *gracilis* Steindachner
    - Subfamily Menidiinae Schultz
      - Tribe Menidiini Schultz
        - Genus *Labidesthes* Cope
        - Genus *Menidia* Bonaparte [includes *Chirostoma* Swainson]
      - 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*
        - Subfamily Telmatherininae Munro *sedis mutabilis*
      - 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 *sedis mutabilis*
          - Subfamily Atherininae Günther *sedis mutabilis*
          - Subfamily Craterocephalinae Dyer & Chernoff *sedis mutabilis*
- Superorder Cyprinodontea Dyer & Chernoff
  - Order Cyprinodontiformes Berg

(Menidiinae and Atherinopsinae), Atherionidae (*Atherion*), and Phallostethidae (*Dentatherina*). Atherinidae now includes only the subfamilies Atherininae, Atherinomorinae, and Craterocephalinae (Fig. 1), and is represented in America by three atherinomorine species found in the Caribbean (Dyer, 2003a): *Hypoatherina harringtonensis, Atherinomorus stipes*, and *Alepidomus evermanni*. According to the phylogenetic hypothesis of Dyer and Chernoff (1996), Atherinopsidae is the sister group of the remaining atheriniform families (Fig. 1). The other atheriniform family present in American waters of the Southern Hemisphere is Notocheiridae, and is the sequential sister group of the remaining atheriniforms (Fig. 1).

Genera and species are organized by families, Notocheiridae and Atherinopsidae, and ordered hierarchically within each family. The systematic history is discussed briefly for each taxonomic group.

Notocheiridae Schultz

Schultz (1948) proposed *Notocheirus* and *Iso* as atherinid sister groups within Tropidostethinae. Because Tropidostethinae was preocuppied, Schultz (1950) corrected the name to Notocheirinae and designated *Notocheirus hubbsi* Clark (1937), as type species. This correction was followed by Fowler (1951) and is why Notocheiridae has priority over Isonidae of Rosen (1964). Isonidae has been the name most widely used for this group (Greenwood *et al*., 1966; Rosen and Parenti, 1981; Nelson, 1984). Saeed *et al*. (1994) proposed Notocheiridae and Isonidae for each of the genera, an unnecessary and unjustified position according to Dyer and Chernoff (1996). Notocheiridae, with the single species *Notocheirus hubbsi* is distributed from Valparaiso in the Pacific and Puerto Deseado in the Atlantic, to the southern tip of Tierra del Fuego. *Notocheirus hubbsi* is a rare species and scarce in collections because it inhabits the surf and has been collected only accidentally in intertidal pools in the South of Chile. Gosztonyi (1972) is the only person that has had the privilege to study a collection of 22 female specimens from a single locality. The presence in some specimens of odontodes (teeth on head bones related to laterosensory canals) is a signal of a potential new species (Dyer, 2000), for which more specimens need to be examined.

Atherinopsidae Fowler

Atherinopsidae is diagnosed by 20 characters that identify it as a monophyletic group and sister to the remaining families of Atheriniformes (Atherinoidei: Dyer

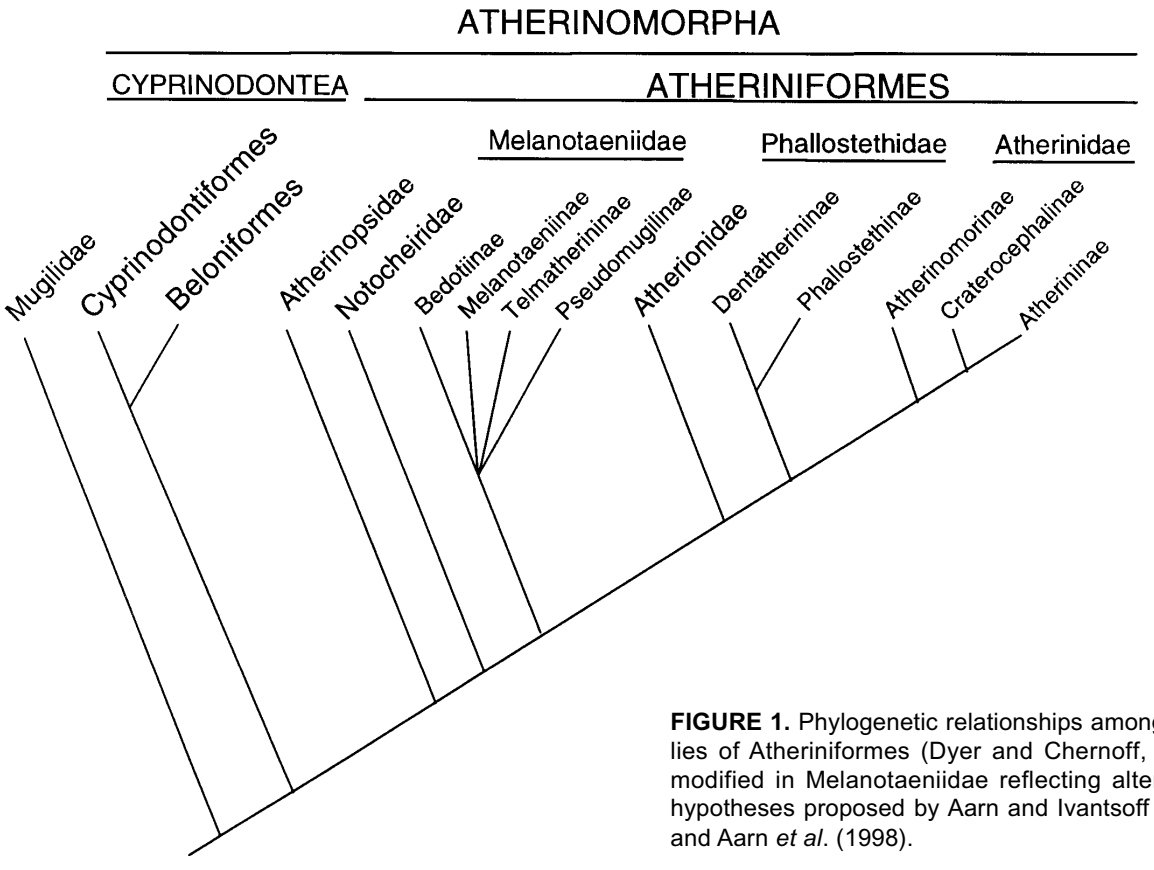

FIGURE 1. Phylogenetic relationships among families of Atheriniformes (Dyer and Chernoff, 1996), modified in Melanotaeniidae reflecting alternative hypotheses proposed by Aarn and Ivantsoff (1997) and Aarn *et al*. (1998).

and Chernoff, 1996). Composed of 13 genera and 104 species (Dyer, 2003b) grouped in the subfamilies Menidiinae y Atherinopsinae (Fig. 2), endemic to the continental and coastal marine waters of the Americas (Dyer, 1997). The sister group relationship between both subfamilies was proposed by White (1985) and Chernoff (1986b) in their systematic revisions of Atherinopsinae and Menidiinae, respectively, and corroborated by Dyer and Chernoff (1996).

Menidiinae Schultz

Menidiinae was proposed by Schultz (1948) to lodge all American atherinids that lack a haemal funnel, however its monophyly was confirmed much later by Chernoff (1986b). Menidiinae is significantly larger than Atherinopsinae, with 74 species distributed mostly in continental waters of North and Central America. Menidiinae is diagnosed by 13 characteres (Chernoff, 1986b; Dyer, 1997) and is composed of two tribes and five genera (Fig. 2): Menidiini (*Menidia* [inc. *Chirostoma*], *Labidesthes*) and Membradini (*Membras, Atherinella, Melanorhinus*), of which only *Atherinella* has representatives in the Southern Hemisphere (Chernoff, 1986b).

Membradini is diagnosed by 6 characters (Chernoff, 1986b; Dyer, 1997, 1998) and is composed of 43 species, 35 of which are grouped into four subgenera of *Atherinella*. The subgenus *Eurystole* is composed of 17 freshwater and marine species, the latter of which are found in the Atlantic (from Costa Rica to Central Brazil) and Pacific (from Gulf of California to northern Chile, including the Galapagos Islands) (Chernoff, 1986b). *Atherinella (Eurystole) nocturna* (Myers and Wade, 1942) is distributed along the coasts of Ecuador, Peru and northern Chile (Chernoff, 1986b; Kong and Bolados, 1987). The subgenus *Xenomelaniris* is composed of only three marine and estuarine species: *A. robbersi* en Lake Totumo, Colombia; *A. venezuelae* in Trinidad & Tobago and Venezuela; and *A. brasiliensis* in the Atlantic from Venezuela to Uruguay (Dyer, 2003b).

Atherinopsinae Fowler

Atherinopsinae was created by Fowler (1903) for all atherinids without premaxillary protrusion. Schultz (1948) redefined Atherinopsinae to include those species with distally dilated premaxillaries and a haemal funnel. White (1985) revised the group phylogeneti-

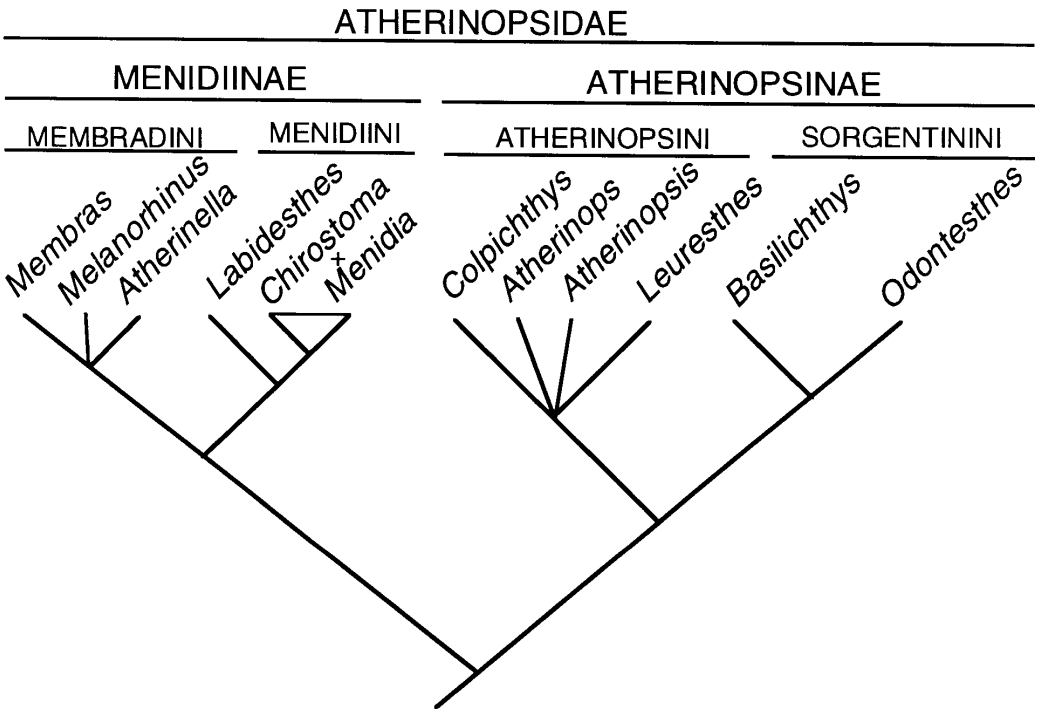

FIGURE 2. Phylogenetic relationships among genera of Atherinopsidae (Chernoff, 1986b; Dyer, 1997, 1998).

cally and determined it as a monophyletic group with eight diagnostic characters. Atherinopsinae is diagnosed by a different set of eight characters (Dyer 1997, 1998)[2] and is composed of six genera in two antitropical tribes: Atherinopsini in North America (*Atherinops, Atherinopsis, Colpichthys, Leuresthes*) and Sorgentinini in South America (*Basilichthys, Odontesthes*). Crabtree (1987) tested White's (1985) hypothesis using electrophoretic evidence, but had ambiguous results depending on the method of coding the data. Dyer (1997) analyzed the accumulated morphological evidence together with the enzymatic evidence and corroborated the monophyly of the tribes as did the monophyly of *Basilichthys* and *Odontesthes* (Figs. 2, 3).

Sorgentinini is diagnosed by eight characters and composed of two genera and at least 19 species (Dyer, 1997, 1998). White (1985) originally called this tribe Basilichthyini, not knowing the previous availability of Sorgentinini (see White, 1989).

Basilichthys Girard

Basilichthys is diagnosed by 22 characters and is composed of five species in two species groups (Dyer, 1997): the *microlepidotus* species group (*B. australis* and *B. microlepidotus*) and the *semotilus* species group (*B. archaeus*, *B. semotilus* and *B.* sp.). *Basilichthys* is found only in lakes and rivers of the western versant of the Andes from Reque River in Lambayeque (7° S), Peru, to rivers of Chiloé Island (43° S), Chile. *Basilichthys microlepidotus* records in Argentina (Evermann and Kendall, 1906; Aramburu and Ringuelet, 1965) are nomenclatorial mistakes attributed to the Patagonian silverside *Odontesthes hatcheri*.

The *microlepidotus* species group, though without a phylogenetically diagnostic character, has descriptive features that clearly identify it as a group (see key, Gajardo, 1987). It is distributed in Central Chile from Huasco River, III Región (28° - 29°S) to Chiloé Island, X Región (42° - 43°S) (Fig. 4).

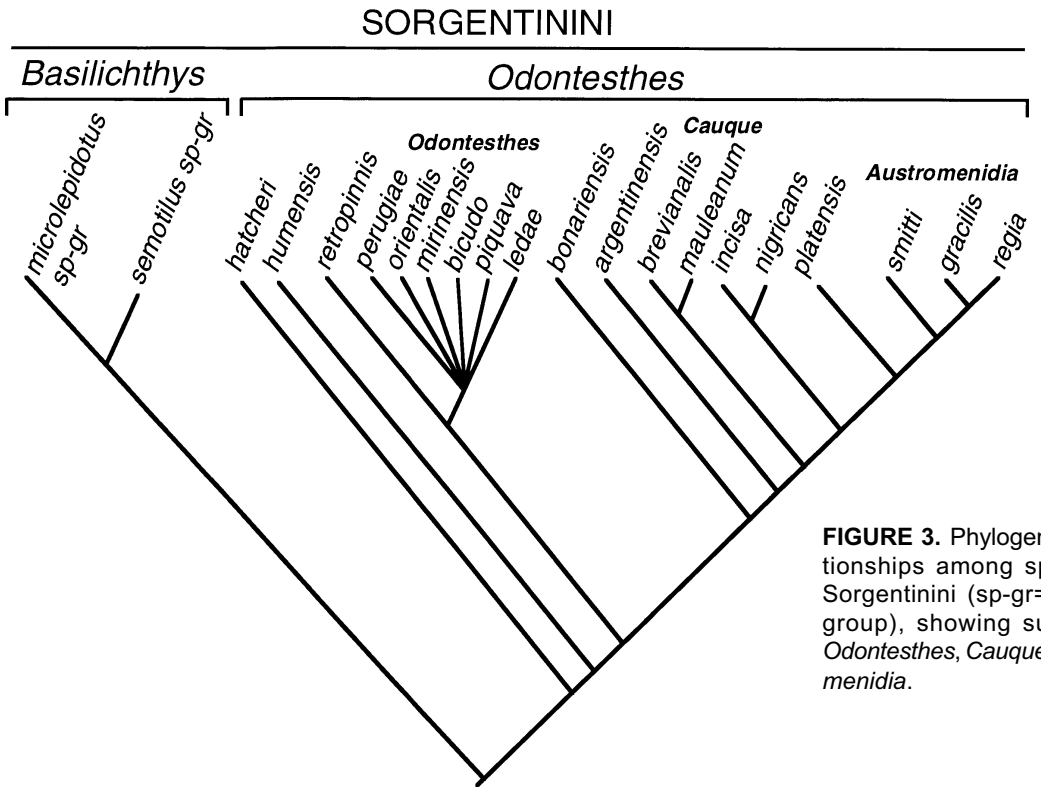

FIGURE 3. Phylogenetic relationships among species of Sorgentinini (sp-gr= species group), showing subgenera *Odontesthes*, *Cauque* y *Austromenidia*.

[2] The phylogenetic relationships among genera and species of Atherinopsinae are based on a data matrix of 25 taxa and 123 characters, analyzed using a cladistic methodology based on parsimony in PAUP (Swofford, 1993) and MacClade (Maddison and Maddison, 1992). Characters were polarized by multiple-outgroup comparison (Farris, 1982; Maddison *et al*., 1984; Clark and Curran, 1986).

The *semotilus* species group is diagnosed by four characters and is distributed from Reque River, Lambayeque (7°S), Perú, to the Loa River, Iquique (22°S), I Región, Chile (Fig. 4).

Odontesthes Evermann & Kendall

Odontesthes is diagnosed by seven characters of which three are unique to the family. It is the genus with most species (19 recognized species) and most ample distribution, in marine coastal waters and temperate freshwater drainages of South America (Fig. 4). Marine forms are distributed from the austral tip of Tierra del Fuego to Piura, Peru, including the Juan Fernandez Archipelago in the southeastern Pacific, and to Santos, Brazil, including the Falkland or Malvinas Islands in the southwestern Atlantic. Freshwater forms are extended from Patagonia to La Serena, IV Region, Chile, and to Rio Grande do Sul, southern Brazil.

Of the eleven available generic names that are junior synonyms of *Odontesthes*, only *Austromenidia* (Hubbs, 1918) and *Cauque* (Eigenmann, 1928) are recognized at present because, based on the hypothesis of relationships, they are the only clades with two or more species. Other generic names available such as *Austroatherina* (Marrero, 1950), *Kronia* (Miranda-Ribeiro, 1915), *Patagonina* (Eigenmann, 1928), *Tupa* and *Yaci* (de Buen, 1953) have a single species (monotypic) and there is no sense in recognizing them as such. Furthermore, if they were to be recognized as such, at least three new genera would have to be described for species such as *O. humensis*, *O. bonariensis* and *O. argentinensis*. This situation could change for *Kronia* if the morphological, ecological and molecular information (Brugger *et al*., 1990; Phonlor and Cousin, 1997; Bemvenuti, 1993; Beheregaray and Levy, 2000; Beheregaray and Sunnucks, 2001) were to form a pattern sufficient to propose an estuarine species and a marine species for what is now recognized as divergent populations of *O. argentinensis*.

Subgenus *Odontesthes* Evermann & Kendall

The subgenus *Odontesthes* includes the type species *O. perugiae* and *O. orientalis*, both inhabitants of the Uruguay and La Plata rivers and their tributaries, and another four species in the Mirim and dos Patos lagoons (*O. mirinensis*; Bemvenuti, 1995), and Tramandaí River system (*O. bicudo*, *O. ledae*, *O. piquava*; Malabarba and Dyer, 2002). A molecular phylogeny based on microsatellite markers and mitochondrial DNA proposes that the species of the Mirim-Patos-Tramandaí system conform a monophyletic group, however not the three endemic species from the Tramandaí River system (Beheregaray *et al*., 2002). Three new species are in the process of being described

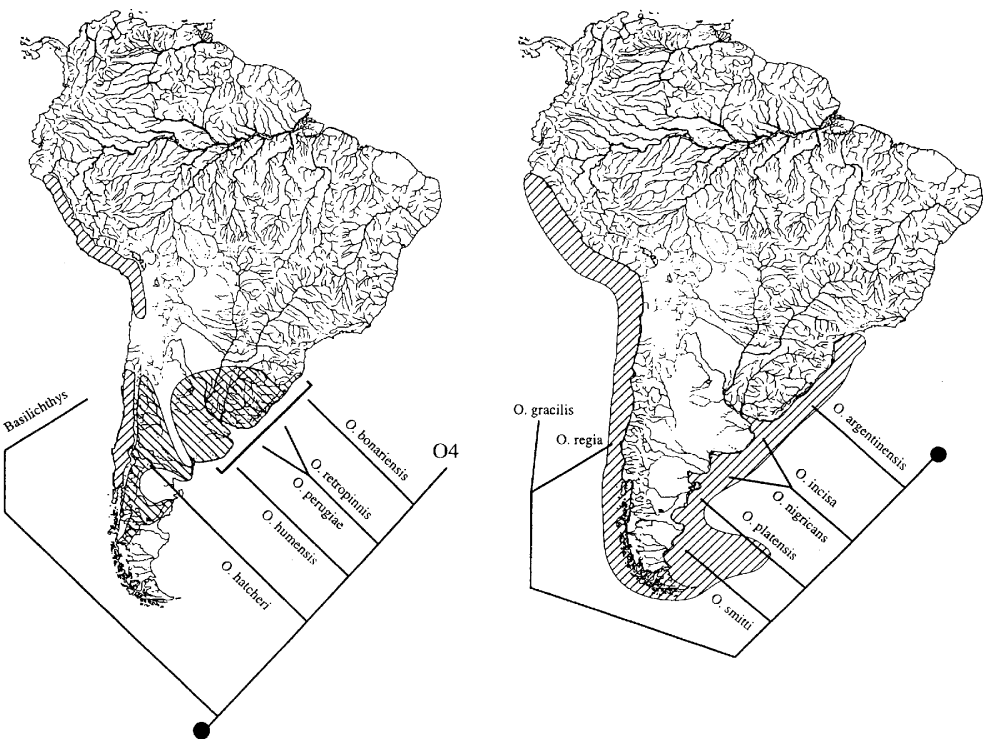

FIGURE 4. Distribution map of marine and freshwater species of sorgentinins and superimposed cladogram of species relationships. Root of tree and node 04 represented by black-filled circle. Subgenus *Cauque* is not included in this diagram of relationships.

from the northern part of the dos Patos Lagoon, RS, Brazil (Malabarba, pers. com.) and a phylogenetic analysis of the subgenus is required.

Subgenus *Austromenidia* Hubbs

Austromenidia is diagnosed by five characters and is composed of three marine species: in the Pacific from Piura, Peru, to Aysen, XI Region (*O. regia*), and the Juan Fernandez Archipelago (*O. gracilis*), and in the Atlantic from Mar del Plata, Argentina, to the Straits of Magellan reaching up to Puerto Natales, including the Falkland or Malvinas Islands (*O. smitti*). *Austromenidia* was described by Hubbs (1918) and characterized by species that had a combination of upper jaw protrusion, small scales, and an anterior position of the first dorsal fin. It was distinguished in this way from *Basilichthys* that has no upper jaw protrusion, and from *Odontesthes* and *Kronia* that have large scales and a posterior position of the first dorsal fin. *Odontesthes hatcheri, O. nigricans,* and the subgenus *Cauque* also fit into this definition of Hubbs, and were included in *Austromenidia* by Schultz (1948). However, based on the hypothesis of relationships presented in Figure 3, *O. hatcheri* could not be included in the subgenus *Austromenidia,* and the species of the subgenus *Cauque* and *O. nigricans* are potential candidates. The characters supporting the relationships among the species of *Cauque*, *O. nigricans* and *O. incisa, O. platensis* and *Austromenidia* are in conflict among themselves and more evidence is required to confirm or propose a new set of relationships (Dyer and Gosztonyi, 1999). It is for this reason that the species now included in *Austromenidia* are only those for which a substantial amount of evidence is available to justify the monophyly of *Austromenidia*, that is *O. regia, O. gracilis* and *O. smitti* (Dyer and Gosztonyi, 1999). This does not preclude the possibility that other species be included as long as a solid base of characters supports the monophyly of the group.

Subgenus *Cauque* Eigenmann

Cauque is diagnosed by seven characters, is endemic of South-Central Chile, and is present in rivers and estuaries from La Serena to Chiloé (*O. brevianalis*), and in lakes and deep rivers from Maule River to

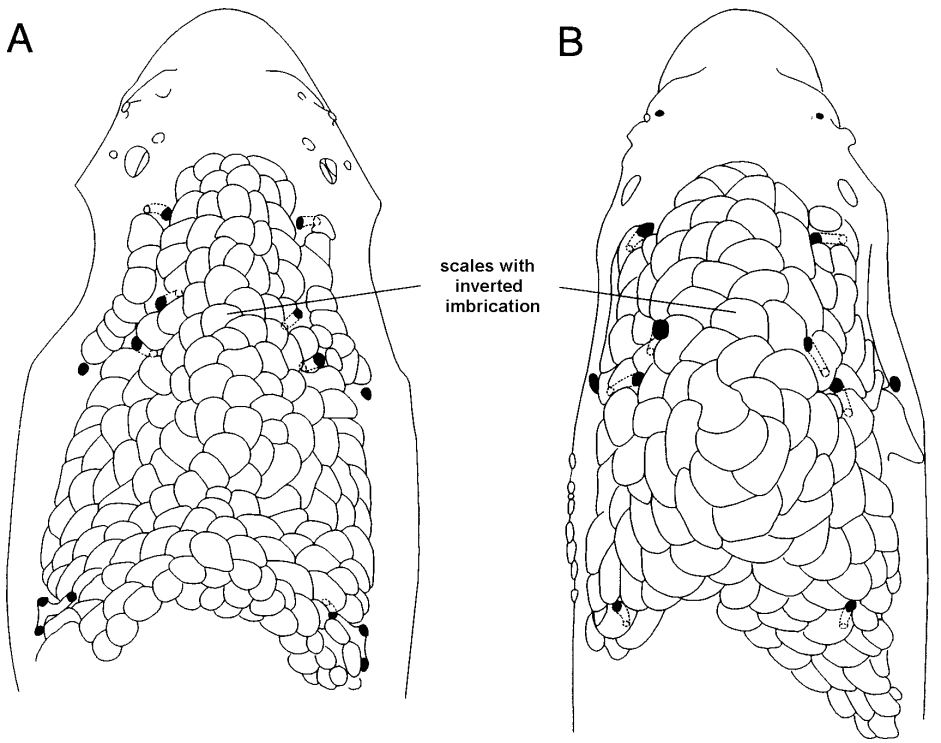

FIGURE 5. Dorsal view of the head of *Basilichthys*; A, *B. micolepidotus* ; B, *B. semotilus*.

Llanquihue Lake (*O. mauleanum*). The identity and relationships of the species require an exhaustive revision. Tentatively only two species are recognized: *O. brevianalis*, a predominantly estuarine species and in the lower courses of the rivers; and *O. mauleanum*, a predominantly lacustrine species and in deep rivers. *Odontesthes wiebrichi* is considered as a possible hybrid between *O. brevianalis* and *O. regia* because in addition to having intermediate meristic counts between both species, it is collected only in the Valdivia River mouth (Corral), together with the above mentioned species. The type specimens of *Odontesthes itatanum* have meristic counts of scales and vertebrae much higher than the other species, for which there is some evidence that it is a valid species. More specimens from the Itata River are required to verify and compare them to the types.

Other species

Odontesthes hatcheri is present in lakes and rivers of Patagonia, including the Argentine precordilleran drainages of San Juan and Mendoza, as far south as Santa Cruz River. It is found in rivers of southern Chile that extend into Argentina, from Puelo River to Baker River. This species is characterized by having a ventral mouth, molariform pharyngeal teeth, small scales with a black posterior margin, a haemal funnel without expansions, and 21-27 gill rakers on the lower limb of the first arch. This species hybridizes with *O. bonariensis* (see *Odontesthes bonariensis*).

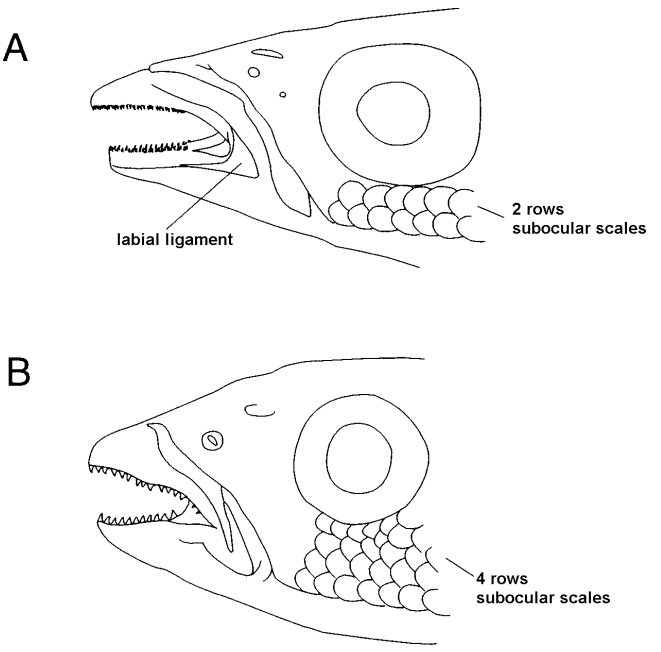

FIGURE 6. Lateral view of the snout region; A, *Odontesthes perugiae*; B, *Basilichthys semotilus*.

Odontesthes humensis is present in lakes and large bodies of water of the drainages of the La Plata and Uruguay rivers, dos Patos and Mirim lagoons. The main difference between *O. humensis* and *O. guazu* is in the pectoral fin extending or not to the base of the pelvic fin (de Buen, 1953), a condition quite variable in other species of silversides. This species is characterized by having a ventral mouth, 20 to 24 short and thick gill rakers on the lower limb of the first arch, and molariform pharyngeal teeth that provide it with a benthic diet, mainly mollusks (Bemvenuti, 2004). This species hybridizes with *O. bonariensis* (see *Odontesthes bonariensis*).

Odontesthes retropinnis is present in lakes and slow moving rivers of the La Plata and Uruguay rivers, and Mirim lagoon drainages. This species is characterized by having small mandibular teeth and 45 to 60 gill rakers of the lower limb, the highest number in all of South American silversides. The absence of expansions of the haemal funnel (also in *O. hatcheri*) is the feature de Buen (1953) used to create the genus *Yaci*.

Odontesthes bonariensis has its origins in lakes and lagoons of the Province of Buenos Aires, Argentina, and Rio Grande do Sul, Brazil. Despite there are no records of *O. bonariensis* being native to Uruguay, the populations of this species in dos Quadros and dos Patos lagoons in Brazil are presumed to be native because there are no records of introductions. This is a euryhaline species, with 30 to 40 gill rakers on the lower branch. Specimens of this species have the largest registered size (52 cm LS) than any other atherinopsid or atheriniform. The aquaculture of this species begun in Chascomús Lake, Argentina, in 1904 (Evermann and Kendall, 1906; Valette, 1939; Berasain *et al*. 2004), in dos Quadros Lagoon, RS, Brazil since 1943 (Kleerekoper, 1945), in Japan since 1966 (Ohashi, 2004), and in Italy since 1974 (Tortonese, 1985). This species was introduced during the 1940's into Chile (Riegel, 1960) and into Bolivia in the late 1940's entering Lake Titicaca in 1955 or 1956 (Calsina-Cota, pers.com.).

Studies on the reproductive biology of this species have determined not only the ages of sexual differentiation but also evidence of temperature dependent sex determination (Strüssmann and Patiño, 1995; Strüssmann *et al*., 1996a, b, c, 1997b). Also, an efficient way of inducing triploidy has been developed, but its use for aquaculture purposes is still to be determined (Strüssmann *et*

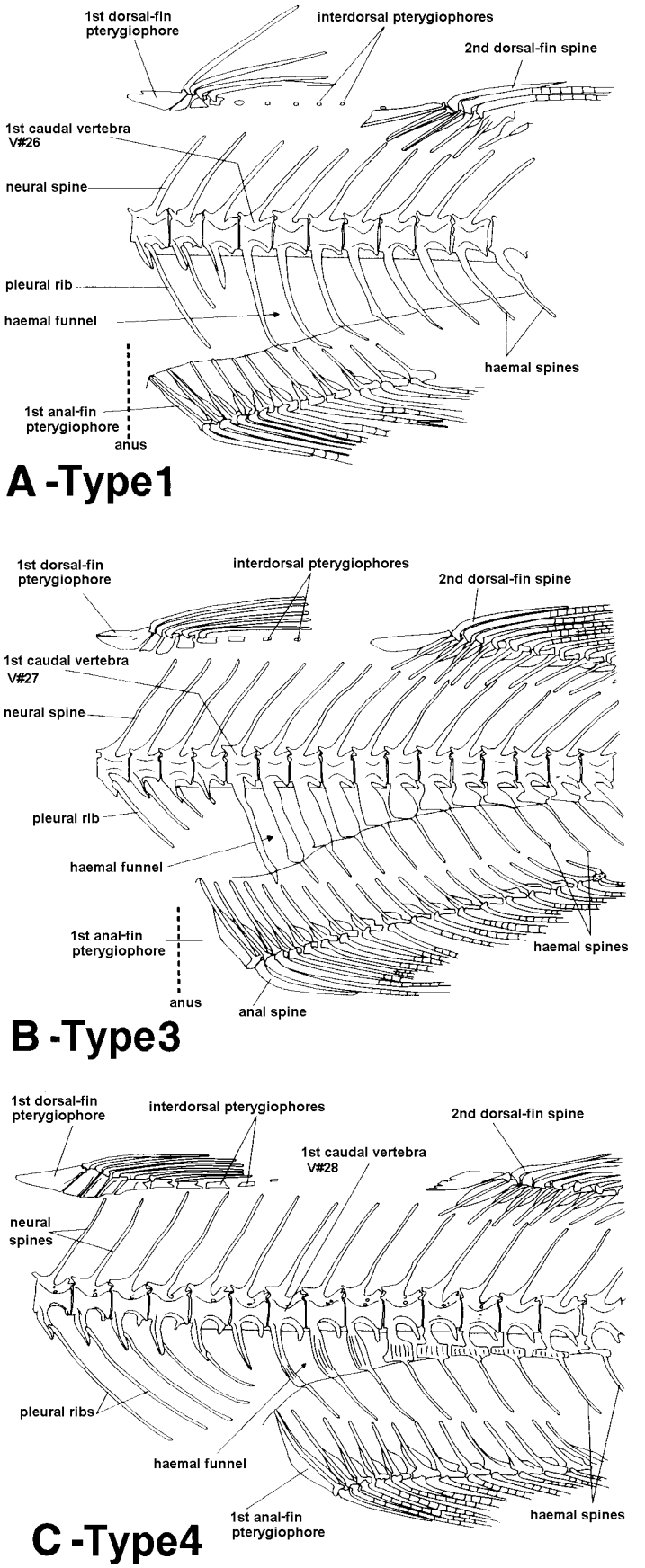

FIGURE 7. Lateral view of median fins and axial skeleton; A, *Odontesthes retropinnis*; B, *Odontesthes bonariensis*; C, *Odontesthes regia*.

al., 1993). Hybrids of this species with *O. hatcheri* are found in some lakes of the Argentine Patagonia (ej., Pellegrini Lagoon), partly due to the artificial insemination practices carried out by aquaculturists for stocking purposes (M. Amalfi, 1990, C. Strüssmann, 2004 com. pers)[3]. The same would be happening with *O. humensis* in the southern part of the dos Patos Lagoon, Brazil (Bemvenuti, 2004) , possibly related to the aquaculture station at Pelotas. In Japan, where the aquaculture of *O. bonariensis* and *O. hatcheri* is well developed, both species have hybridized spontaneously and genetic markers have been developed for their identification and differentiation (Yoshizaki *et al.*, 1997; Strüssmann *et al.*, 1997a).

Odontesthes argentinensis is considered at present as a widely distributed western Atlantic coastal species, in marine and estuarine environments from the Province of Sao Paulo, Brazil, to south of Chubut, Argentina. It is distinguished by having crenulate predorsal scales and 26 to 30 gill rakers on the lower branch (see key here and in Malabarba and Dyer, 2002). Numerous studies of this species in southern Brazil (Bemvenuti, 2004) have compared the estuarine and the marine groups in terms of egg morphology (Phonlor and Cousin, 1997), morphometrics (Bemvenuti, 1993; Cuello and García, 2004), electrophoresis (Beheregaray and Levy, 2000) and DNA (Beheregaray and Sunnucks, 2001). Nevertheless, the differences found are not conclusive to propose two species as did de Buen (1953) with *Kronia rex* and *K. alba*.

Odontesthes incisa is a western Atlantic coastal marine species, distributed from Rio Grande do Sul, Brazil, to Santa Cruz, Argentina. It is characteristically a small species (known as "cornalito") with large crenate[4] scales on all of body and canine-type teeth on both mandibular jaws. The osteology of this species was described in detail by Pianta de Risso and Risso (1953) in a journal of limited distribution and placed in a new genus and subfamily.

Odontesthes nigricans is a southwestern Atlantic species, with estuarial incursions for reproduction, distributed from the Province of Buenos Aires to Cape Horn and Falklands or Malvinas Islands. It is distinguished for having small and crenate scales, less than 20 gill rakers on the lower branch, and the first dorsal fin placed anteriorly over the base of the pelvic fin. In two studies

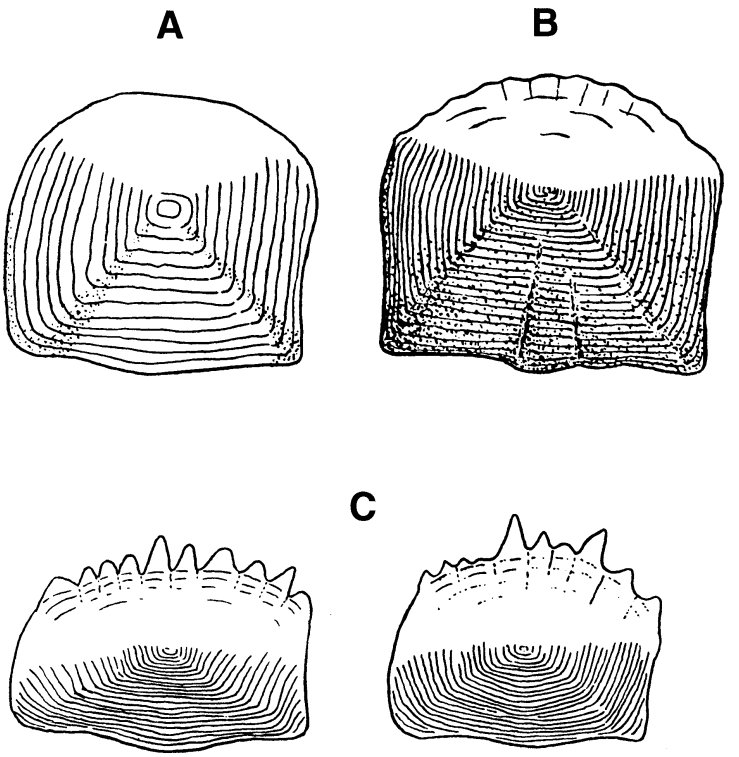

FIGURE 8. Scales posterior border up; A, *Odontesthes humensis*, smooth; B, *O. argentinensis*, crenulate; C, *O. incisa*, crenate. Figures modified from de Buen (1953).

of the axial skeleton of marine silversides (Piacentino and Torno, 1987; Piacentino, 1990), this species was described as having a haemal funnel of the type that is diagnostic of the subgenus *Austromenidia*. Radiographs of the type specimens of *O. nigricans* and *O. alburnus* clearly show an absence of a haemal funnel for this species.

Odontesthes platensis is a western Atlantic coastal species, distributed from La Plata River to the south of Chubut, Argentina. Known as "panzón" or big belly, this is a species that is not frequent in collections, though apparently very abundant towards the beginning of the 20th century (García, 1998).

Biogeography

Placing the hypothesis of evolutionary relationships of the South American atherinopsines over the distribution map of the species (Fig. 4), two biogeographic hypotheses can be proposed: a) the elevation of the Andes during the middle to late Miocene was the vicariant process that separated *Basilichthys* (to the West) and *Odontesthes* (to the East), this coinciding with the earliest fossil remains of *Basilichthys* found in Chile (Rubilar, 1994) and *Odontesthes* (Cione, pers.com.)[5] ; and b) Sorgentinini is primitively a freshwater group, because the basal species of both *Basilichthys* and *Odontesthes* are primarily in freshwater and, consequently the marine silversides of *Odontesthes* are derived, not primitive as was the traditional assumption (Lahille, 1929a,b; White, 1986, among others).

Contrary to the assumptions of White (1985, 1986) the biogeographic analysis of Sorgentinini indicates that this group is primitively freshwater. *Basilichthys* and the basal species of *Odontesthes* are freshwater (Dyer, 1998; Fig. 4), being marine a derived condition within the group (Dyer, 1998). The use of freshwater as a character is ambiguous because the sister group of Sorgentinini (Atherinopsini) is marine and the primitive condition of Menidiinae is ambiguous.

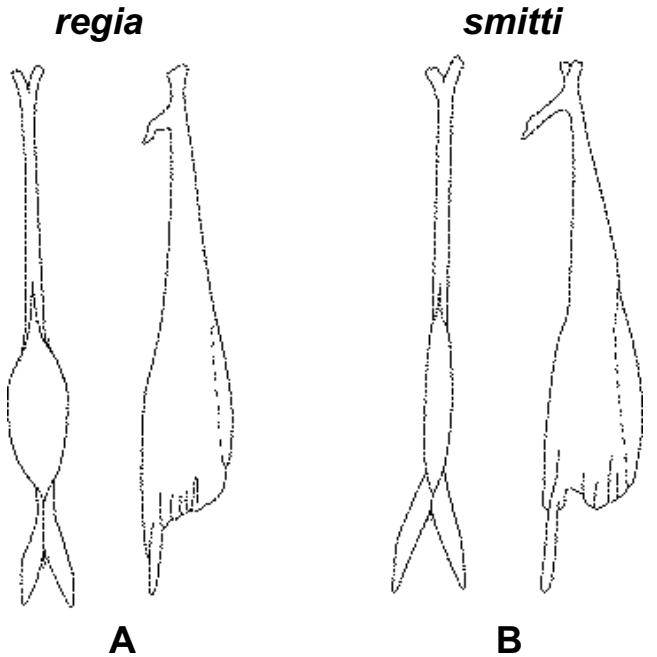

FIGURE 9. Ventral and lateral views of the urohyal; A, *O. regia*; B, *O. smitti*.

[3] Lic. Marina Amalfi, Cinco Saltos, Prov. Río Negro, Argentina.
[4] Scale nomenclature follows that of Roberts (1993).
[5] Alberto Cione, Div. Paleontologia, Museo La Plata, Argentina.

Artificial identification key for South American silverside species of the southern cone (*based only characters present in adult specimens*)

1a. Presence of first dorsal fin (with the exception of some specimens of the *Basilichthys semotilus* species group); body scales cycloid, rounded, without spines; maximum body height posterior to pectoral fin; base of pectoral fin does not surpass the dorsal margin of the lateral band..... Family Atherinopsidae..... 2

1b. Absence of the first dorsal fin; body scales elongated dorsoventrally with 3 to 5 spines; maximum body height at pectoral fin level; base of pectoral fin dorsal to lateral band..... ..... Family Notocheiridae ..... *Notocheirus hubbsi*

2a. Presence of postemporal bone only; preopercular sensory canal open, without a bony tube; presence of a series of canals and concavities in the skin anterior to the frontal bones and between the nasals (Rostral sensory system); anal fin with 24 or more rays .... Subfamily Menidiinae 3

2b. Presence of extrascapular and postemporal bones; horizontal branch of the preopercular sensory canal in a bony tube (except *Odontesthes mirinensis*); absence of a rostral sensory system; anal fin with 15 to 21 rays .... Subfamily Atherinopsinae 4

3a. Rostral sensory system enclosed forming membrane tubes with pores; 53 to 57 scales on lateral line above lateral band ..... *Atherinella (Eurystole) nocturna*

3b. Rostral sensory system with 4 anterior and 2 posterior fosas; 35 to 40 scales on lateral line over lateral band ..... *Atherinella (Xenomelaniris) brasiliensis*

4a. Presence of a frenum on the upper jaw (restricted premaxillary protrusion); dorsal scales on the head with inverted imbrication (anterior margin free, Fig. 5); four rows of suborbital scales (Fig. 6); labial ligament reduced .... *Basilichthys* 5

4b. Absence of a frenum on the upper jaw (premaxillary freely protractile); dorsal scales of the head with normal imbrication (posterior margin free); two or three rows of suborbital scales; labial ligament expanded (Fig. 6A) .... *Odontesthes* 6

5a. All dorsal head scales with inverted imbrication (Fig. 5A); horizontal branch of the preopercular sensory canal with five pores .... *Basilichthys semotilus* species group

5b. Dorsal head scales of interorbital region only with inverted imbrication (Fig. 5B); horizontal branch of preopercular sensory canal with four pores .... *Basilichthys microlepidotus* species group

6a. First dorsal fin over or posterior to anus (Fig. 7); scales large with less than 11 rows of dorsal scales between lateral bands[6] (except *O. platensis*) 7

6b. First dorsal fin over the pelvic fins; scales small, with more than 12 rows of dorsal scales between lateral bands 13

7a. Origin of first dorsal fin over or posterior to anus (Fig. 7A) 8

7b. Origin of first dorsal fin anterior to anus and posterior to pelvic fin (Fig. 7B) 11

8a. Scales absent along shaft of cleithrum; two rows of suborbital scales (Fig. 6A); two rows of teeth on jaws; origin of first dorsal fin closer to the anal fin origin than to the anus (Fig. 7A); scales smooth (Fig. 8A) 9

8b. Scales present along shaft of cleithrum; three or four rows of suborbital scales (Fig. 6B); one or three rows of teeth on jaws; origin of first dorsal fin closer to anus than to origin of anal fin (Fig. 7B); presence of crenate scales (Fig. 8B) 10

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[6] The dorsal scales were counted at the level of the pectoral fin's distal half, from side to side over the dorsum, beginning and ending on the row of scales that form half-part of the lateral band. This meristic is considered to represent scale size.

9a. Teeth on jaws of normal size and with inner row of same size or larger than outer row (Fig. 6A); vomer with three tooth patches or none; less than 40 gill rakers on lower branch (22-24 *orientalis & perugiae*; 26-30 *mirinensis, bicudo, ledae, piquava*) ..... Subgenus *Odontesthes*

9b. Teeth on jaws small with inner row of teeth shorter than outer row; vomer without teeth; more than 45 gill rakers on lower branch (12-14 + 46-50) ..... *O. retropinnis*

10a. Predorsal scales crenulate (Fig. 8B); presence of pelvic membrane between inner rays; jaw teeth approximately of same size, those of outer row larger than inner row; haemal funnel well developed (Fig. 7B); 26 to 28 gill rakers on lower branch ..... *O. argentinensis*

10b. Predorsal scales and of lateral band crenate (Fig. 8C); pelvic membrane absent between inner rays; jaw teeth of different sizes, some canine-type, without differences between inner and outer rows; absence of haemal funnel; 22 to 26 gill rakers on lower branch ..... *O. incisa*

11a. Less than 20 gill rakers (13-19) on lower branch; vomerine teeth absent or in three patches; lower jaw never prognathous 12

11b. More than 30 gill rakers (32-38) on lower branch; vomerine teeth present as a single median patch; lower jaw prognathous in large specimens ..... *O. bonariensis*

12a. Scales absent along shaft of cleithrum; scales present only on posterior half of interoperculum; presence of rows of scales between rays of anal fin; upper jaw prognathous and premaxillary protrusion directed ventrally; pharyngeal teeth molariform; vomerine teeth absent; absence of teeth on endopterygoid; scales large, with less than 10 rows of dorsal scales between lateral bands ..... *O. humensis*

12b. Scales present along shaft of cleithrum; scales present along entire interoperculum; absence of rows of scales between rays of anal fin; jaws equal; pharyngeal jaws without molariform teeth; vomer with 3 patches of teeth; presence of teeth on the endopterygoids; scales small, with more than 12 rows of dorsal scales between lateral bands ..... *O. platensis*

13a. Origin of first dorsal fin over anterior half of pelvic fin; absence of a haemal funnel; less than 20 gill rakers on lower branch; final-ray origin of second dorsal fin notably anterior to final-ray origin of anal fin; scales crenate ..... *O. nigricans*

13b. Origin of first dorsal fin over posterior half of pelvic fin; presence of haemal funnel; more than 21 gill rakers on lower branch (except the subgenus *Cauque*); final-ray origin of second dorsal fin over the final-ray origin of anal fin; scales crenate or smooth 14

14a. Jaws equal and protrusion directed anteriorly; absence of scale rows between anal-fin rays; pharyngeal teeth not molariform; teeth present on endopterygoid; haemal funnel type 4 (Fig. 7C) ..... Subgenus *Austromenidia* 15

14b. Upper jaw prognathous and upper jaw protrusion directed ventrally; presence of scale rows between anal-fin rays; presence of molariform pharyngeal teeth; endopterygoid teeth absent; haemal funnel of type 1 or 3 (Fig. 7A,B) 17

15a. Urohyal ventral plate reduced (Fig. 9B) ..... *O. smitti*

15b. Urohyal ventral plate expanded in an oval shape (Fig. 9A) 16

16a. Four rows of suborbital scales; presence of vomerine teeth ..... *O. regia*

16b. Three rows of suborbital scales; absence of vomerine teeth ..... *O. gracilis*

17a. Scales with posterior margin smooth (Fig. 8A); more than 21 gill rakers on lower branch (21-27); haemal funnel without modified haemal arches (type 1, Fig. 7A) ..... *O. hatcheri*

17b. Scales crenate (Fig. 8C); less than 20 gill rakers on lower branch (12-19); haemal funnel with expansions of haemal arches of type 3 (Fig. 7B) ..... Subgenus *Cauque* 18

18a. Scales noticeably crenate along side of body ..... *O. mauleanum*

18b. Scales noticeably crenate only on caudal peduncle ..... *O. brevianalis*

APPENDIX 1.

List of atherinopsine species present in South America.

Museum acronyms follow Leviton *et al*. (1985).

Family Notocheiridae Schultz, 1948
Genus *Notocheirus* Clark, 1937
Type species: *Notocheirus hubbsi* Clark, 1937 {CAS-SU 5525}
Type locality: Valparaiso Bay, Chile.
Family Atherinopsidae Fowler, 1903
Subfamily Menidiinae Schultz, 1948
Tribe Membradini Chernoff, 1986
Genus *Atherinella* Steindachner, 1875
Type species: *Atherinella panamensis* Steindachner, 1875:477 {NMW 76439}
=*Eurystole* Jordan & Evermann *en* Jordan, 1895: 418
Type species: *Atherinella eriarcha* Jordan & Gilbert, 1882: 348
=*Thyrina* Jordan & Culver *en* Jordan, 1895: 419 (preoccupied)
Type species: *Thryrina evermanni* Jordan & Culver *en* Jordan, 1895:419
=*Melaniris* Meek, 1902: 117
Type species: *Melaniris balsana* Meek, 1902:117
=*Xenatherina* Regan, 1907: 64
Type species: *Menidia lisa* Meek, 1904:182
=*Thyrinops* Hubbs, 1918: 306
Type species: *Atherinichthys pachylepis* Günther, 1864:25
=*Archomenidia* Jordan & Hubbs, 1919: 54
Type species: *Atherinichthys sallei* Regan, 1903: 60
=*Nectarges* Myers & Wade, 1942: 126
Type species: *Nectarges nepenthe* Myers & Wade, 1942: 130
=*Euryarges* Myers & Wade, 1942: 128
Type species: *Nectarges nesiotes* Myers & Wade, 1942: 128
=*Coleotropis* Myers & Wade, 1942: 136
Type species: *Menidia starksi* Meek & Hildebrand, 1923: 267
=*Xenomelaniris* Schultz, 1948: 13, 33
Type species: *Atherina brasiliensis* Quoy & Gaimard, 1825: 332
=*Atherthyrina* Fowler, 1958: 16
Type species: *Thyrina evermanni* Jordan & Culver *en* Jordan, 1895: 419
=*Allomastax* Chernoff, 1986a: 243
Type species: *Melaniris sardina* Meek, 1907: 114

***Atherinella (Eurystole) nocturna* (Myers & Wade, 1942)**
Eurystole nocturna Myers & Wade, 1942 {USNM 88712}
Type locality: Guayaquil, Ecuador, probably opposite Estero Guayas.
***Atherinella (Xenomelaniris) brasiliensis* (Quoy & Gaimard, 1825)**
Atherina brasiliensis Quoy & Gaimard, 1825: 332 {MNHN A.4374}
Type locality: Rio de Janeiro Bay, Brazil.

Subfamily Atherinopsinae Fowler, 1903
Tribe Sorgentinini Pianta de Risso & Risso, 1953
Genus *Basilichthys* Girard, 1855
Type species: *Atherina microlepidota* Jenyns, 1841
=*Protistius* Cope, 1874: 66
Type species: *Protistius semotilus* Cope, 1874
=*Gastropterus* Cope, 1878: 700

Type species: *Gastropterus archaeus* Cope, 1878
=*Pisciregia* Abbott, 1899: 342
Type species: *Pisciregia beardsleei* Abbott, 1899

Species group *microlepidotus* de especies *microlepidotus*
***Basilichthys microlepidotus* (Jenyns, 1841)**
Atherina microlepidota Jenyns, 1841: 78 {BMIII 403}
Type locality: Valparaiso, Chile.
***Basilichthys australis* Eigenmann, 1928**
Basilichthys australis Eigenmann, 1928: 59
{CAS-SU 11678, 44699, 44703, 45179, 45180, 45182-45184, 45188-45190, 45192}
Type locality: from Maipo River to Rahue River, Chile.

Species group *semotilus*
Basilichthys semotilus* (Cope, 1874) de especies *semotilus
Basilichthys semotilus (Cope, 1874): 66 {ANSP 14404}
Type locality: Peruvian Andes, at 4.000 m altitude.
=*B. beardsleei* (Abott, 1899): 342 {CAS-SU 11961}
Type locality: Callao, Lima, Peru.
***Basilichthys archaeus* (Cope, 1878)**
Basilichthys archaeus (Cope, 1878):700 {ANSP 22002, 22003}
Type locality: Arequipa, Peru, at 2.500 m altitude.
***Basilichthys* sp.**
Locality: Loa and Codpa rivers, Chile.

Genus *Odontesthes* Evermann & Kendall, 1906
Type species: *Odontesthes perugiae* Evermann & Kendall, 1906: 94
=*Kronia* Miranda-Ribeiro, 1915: 9
Type species: *Kronia iguapensis* Miranda-Ribeiro, 1915: 10
=*Pseudothyrina* Miranda-Ribeiro, 1915: 11
Type species: *Pseudothyrina jheringi* Miranda-Ribeiro, 1915: 11
=*Austromenidia* Hubbs, 1918: 307
Type species: *Basilichthys regillus* Abbott, 1899: 339
=*Cauque* Eigenmann, 1928: 56
Type species: *Chirostoma mauleanum* Steindachner, 1896: 231
=*Patagonia* Eigenmann, 1928: 56 (typographic error of *Patagonina*)
=*Patagonina* Eigenmann, 1928: 56
Type species: *Menidia hatcheri* Eigenmann, 1909
=*Austroatherina* Marrero, 1950: 113
Type species: *Atherina incisa* Jenyns, 1841 (available by subsequent designation)
=*Bachmannia* Nani *in* Szidat & Nani, 1951: 336 (preoccupied in Siluriformes)
Type species: *Basilichthys smitti* Lahille, 1929a
=*Sorgentinia* Pianta de Risso & Risso, 1953: 13
Type species: *Atherina incisa* Jenyns, 1841
=*Tupa* De Buen, 1953: 48
Type species: *Atherinichthys platensis* Berg, 1895
=*Yaci* De Buen, 1953: 51
Type species: *Yaci retropinnis* De Buen, 1953

***Odontesthes hatcheri* (Eigenmann, 1909)**
Menidia hatcheri Eigenmann, 1909: 281 {types lost}
Type locality: Pueyrredón Lake, Santa Cruz, Argentina.
=?*Basilichthys cuyanus* Burmeister, 1861: 534 {types lost}
Type locality: Guanacache Lagoon, San Juan, Argentina.
=*Basilichthys andinus* Lahille, 1929b: 324 {types lost}
Type locality: Traful Lake, Rio Negro, Argentina.

=*Basilichthys patagonicus* Marrero, 1950: 67 {types lost}
Type locality: Limay River, Rio Negro, Argentina.

***Odontesthes humensis* de Buen, 1953**
Odontesthes humensis de Buen, 1953:34 {MNHN-M 1807}
Type locality: Negro River, Uruguay.
=*Odontesthes guazu* de Buen, 1953: 40 {MNHN-M 1805}
Type locality: Uruguay River, Uruguay.

***Odontesthes retropinnis* (de Buen, 1953)**
Yaci retropinnis de Buen 1953:52 {MNHN-M 1809}
Type locality: Negro River, Uruguay.

***Odontesthes bonariensis* (Valenciennes, 1835)**
Atherina bonariensis Valenciennes *in* Cuvier & Valenciennes, 1835:469 {MNHN-P A.4407}
Type locality: Buenos Aires, Argentina.
=*Atherina lichtensteinii* Valenciennes *in* Cuvier & Valenciennes, 1835:476 {ZMB 1883}
Type locality: Montevideo, Uruguay.
=*Basilichthys chascomunensis* Lahille, 1929b:305 {types lost}
Type locality: Buenos Aires, Argentina.
=*Basilichthys puntanus* Lahille, 1929b:305 {types lost}
Type locality: San Luis, Argentina.

***Odontesthes argentinensis* (Valenciennes, 1835)**
Atherina argentinensis Valenciennes *in* Cuvier & Valenciennes, 1835:472 {MNHN-P A.4362, A.4363}
Type locality: Montevideo, Uruguay.
=?*Atherina lessoni* Valenciennes *in* Cuvier & Valenciennes, 1835:471 {types lost}
Type locality: Santa Catarina, Brazil.
=*Kronia iguapensis* Miranda Ribeiro, 1915:10 {MNRJ 1351}
Type locality: Iguape, São Paulo, Brazil.
=*Pseudothyrina iheringi* Miranda Ribeiro, 1915:10 {MNRJ 2369}
Type locality: Rio Grande do Sul, Brazil.
=*Basilichthys bonariensis charruanus* Lahille, 1929b:319 {MACN 5178?}
Type locality: Patagonian coast, Mar del Plata, Buenos Aires, Argentina.
=*Basilichthys bonariensis propinquus* Lahille, 1929b:320 {types lost}
Type locality: Buenos Aires, Argentina.
=*Menidia thomasii* Meinken, 1931:377 {?KHMM}
Type locality: Uruguay.
=*Kronia rex* de Buen, 1953:64 {MHNM 1803}
Type locality: La Paloma, Rocha, Uruguay.
=*Kronia alba* de Buen, 1953:59 {MHNM 1801}
Type locality: Rocha Lagoon, Rocha, Uruguay.

Subgenus *Odontesthes* Evermann & Kendall, 1906
***Odontesthes perugiae* Evermann & Kendall, 1906**
Odontesthes perugiae Evermann & Kendall, 1906:94 {USNM 55572}
Type locality: Argentina.
=*Basilichthys microather* Marrero, 1950:75 {types lost}
Type locality: La Plata River, Argentina.

***Odontesthes orientalis* de Buen, 1950**
Odontesthes orientalis de Buen, 1950:149 {MNHN-M 1808}
Type locality: Negro River, Uruguay.
***Odontesthes mirinensis* Bemvenuti, 1995**
Odontesthes mirinensis Bemvenuti, 1995:885 {MCP 17696}
Type locality: Mirim Lagoon, RS, Brazil.

Odontesthes piquava **Malabarba & Dyer, 2002**

Odontesthes piquava Malabarba & Dyer, 2002:261 {MCP 26152}

Type locality: da Pinguela Lagoon, Tramandaí (29º49'S; 50º10'14"W), RS, Brazil.

Odontesthes bicudo **Malabarba & Dyer, 2002**

Odontesthes bicudo Malabarba & Dyer, 2002: 264 {MCP 26153}

Type locality: Emboaba Lagoon, Osório (29º57'57"S; 50º13'45"W), RS, Brazil.

Odontesthes ledae **Malabarba & Dyer, 2002**

Odontesthes ledae Malabarba & Dyer, 2002: 266{MCP 26151}

Type locality: Fortaleza Lagoon, Cidreira (30º09'33" S; 50º13'44" W), RS, Brazil.

Subgenus *Cauque* Eigenmann, 1928

Odontesthes mauleanum **(Steindachner, 1896)**

Atherinichthys mauleanum Steindachner, 1896:231 {NMW 62506, 62507, 16979}

Type locality: Maule River, VII Region, Chile.

=*Atherinichthys itatanum* Steindachner, 1896:232 {NMW 62608}

Type locality: Itata River, VIII Region, Chile.

=*Cauque molinae* Fowler, 1940:183 {ANSP 69147}

Type locality: Malleco River at Angol, IX Region, Chile.

Odontesthes brevianalis **(Günther, 1880)**

Atherinichthys brevianalis Günther, 1880:25 {MNHN 1890-119}

Type locality: Valparaiso, V Region, Chile.

=*Cauque wiebrichi* Eigenmann, 1928:58 {CAS 49902}

Type locality: Valdivia, X Region, Chile.

=*Odontesthes (Cauque) debueni* Fischer, 1962 {ZMH 1698}

Type locality: Estero Lenga, Concepcion, VIII Region, Chile.

Odontesthes nigricans **(Richardson, 1848)**

Atherina nigricans Richardson, 1848:77 {BMNH 1848.3.10:29}

Type locality: Malvinas or Falkland Islands.

=*Atherinichthys alburnus* Günther, 1861:404 {BMNH 1859.10.12:30.33}

Type locality: Straits of Magellan, Chile.

=?*Menidia patagoniensis* Eigenmann, 1909:280 {types lost}

Type locality: ?Punta Arenas, Straits of Magellan, Chile.

=?*Basilichthys nigricans macropterus* Lahille, 1929b:332 {types lost}

Type locality: Malvinas Islands and Río Gallegos, Straits of Magellan, Argentina.

=*Basilichthys malvinensis* Marrero, 1950:121 {types lost}

Type locality: Southwest Atlantic, in Argentina from Península Valdés to Los Estados Island and Malvinas Islands.

Odontesthes incisa **(Jenyns, 1841)**

Atherina incisa Jenyns, 1841:79 {BMIII 405}

Type locality: 39º S; 61º W, several miles from continent; opposite Punta Sauce, Buenos Aires, Argentina.

=*Menidia uruguayensis* Devincenzi, 1924:205 {MNHN-M 1804}

Type locality: La Plata River, Montevideo, Uruguay.

Odontesthes platensis **(Berg, 1895)**

Atherinichthys platensis Berg, 1895:27 {MACN 5162, 5195}

Type locality: Mar del Plata, Argentina.

Subgenus *Austromenidia* Hubbs, 1918

Odontesthes regia **(Humboldt, 1821)**

Atherina regia Humboldt *in* Humboldt & Valenciennes, 1821: 187 {types lost}

Type locality: Callao, Peru.

=*Atherina laticlavia* Valenciennes *in* Cuvier & Valenciennes, 1835: 473 {MNHN-P 2980}

Type locality: Valparaiso, Chile.

=*Chirostoma affine* Steindachner, 1898: 313 {ZMB 15674}
Type locality: Iquique, Chile.
=*Basilichthys jordani* Abbott, 1899: 341 {CAS-SU 6070}
Type locality: Callao, Peru.
=*Basilichthys octavius* Abbott, 1899: 340 {CAS-SU 6069}
Type locality: Callao, Peru.
=*Basilichthys regillus* Abbott, 1899: 339 {CAS-SU 6071}
Type locality: Callao, Peru.

***Odontesthes gracilis* (Steindachner, 1898)**
Chirostoma gracile Steindachner, 1898: 314 {ZMB 15675}
Type locality: Cumberland Bay, Robinson Crusoe Island, Juan Fernandez Archipelago, Chile.

***Odontesthes smitti* (Lahille, 1929a)**
Basilichthys smitti Lahille, 1929a: 84 {types lost}
Type locality: «Fin de Barrancas», Gulf of San Matías, SE Atlantic, Argentina.
=*Atherina jacksoniana* Quoy & Gaimard, 1825: 333 {MNHN 3096, A.2895}
Type locality: original card: Port Jackson, NSW, Australia)
?=*Menidia patagoniensis* Eigenmann, 1909: 280 {types lost}
Type locality: Straits of Magellan (?Punta Arenas), Chile.
=*Basilichthys smitti var. australis* Lahille, 1929a: 84 {types lost}
Type locality: Río Gallegos, Argentina, and Puerto Natales, Chile.
=*Basilichthys madrynensis* Lahille, 1929b: 326 {types lost}
Type locality: Port Madryn, Golfo Nuevo, Chubut, Argentina.

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