Phylogenetic revision of the South American subgenus *Austromenidia* Hubbs, 1918 (Teleostei, Atherinopsidae, *Odontesthes*) and a study of meristic variation

Revisión filogenética del subgénero *Austromenidia* Hubbs, 1918 (Teleostei, Atherinopsidae, *Odontesthes*) y un estudio de variación merística

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Abstract.- *Austromenidia* was created by Hubbs to group species that distinguished themselves from *Odontesthes* proper in having small scales and a first dorsal fin well in advance of the anal fin, and from *Basilichthys* in having upper jaw protrusion. *Austromenidia* was first placed as a junior synonym of *Odontesthes* by de Buen and later by White in the first phylogenetic hypothesis of Atherinopsinae. A phylogenetic study of South American silversides corroborated the genus *Odontesthes* as a well diagnosed monophyletic group, and recognized two subgenera: *Cauque* and *Austromenidia*. The subgenus *Austromenidia* is diagnosed by five characters of which two are unique within Atherinopsidae: an enlarged and rounded lacrimal condyle of the lateral ethmoid, and haemal-arch expansions of the haemal funnel with anteroposterior projections. Though *O. platensis* is the sister species to the subgenus, other species such as *O. nigricans* and the subgenus *Cauque* are potential alternatives as indicated in the resulting classification. The subgenus *Austromenidia* is composed of the marine species *O. regia* Humboldt, *O. gracilis* Steindachner, and *O. smitti* Lahille, the latter as sister of the former two species. *Odontesthes smitti* is diagnosed by a reduced or folded ventral plate of the urohyal and is distributed along the southeastern coasts of the Argentine Patagonia from Mar del Plata (ab. 39°S) to southern Tierra del Fuego, Falkland or Malvinas Islands, and incursions into the southeastern Pacific through the Strait of Magellan extending north to Puerto Natales (51°S), Chile. *Odontesthes regia* is diagnosed by the posterior extension of the haemal-arch funnel to the posterior end of the anal fin, and is distributed along the southeastern Pacific shores of Perú and Chile, from Piura (ab. 5°S) to the Archipelago of Los Chonos, Aysén (ab. 46°S). *Odontesthes gracilis* is diagnosed by relatively small-sized teeth, three suborbital rows of scales, no vomerine teeth, and a maximum-recorded size is of 120 mm SL. It is an endemic species of the Juan Fernández Archipelago (ab. 33°S, 79°W), off Chile. Because of the great latitudinal range of distribution of *O. regia* and *O. smitti*, a study of meristic variation is presented. Because of the broad overlap of ranges of variation these characteristics are unsuitable as diagnostic traits, but certainly useful as descriptive features. Whereas vertebral numbers increase with latitude, following Jordan's rule, gill rakers of the lower branch increase in number mainly with size. Whereas anal-fin rays increase only slightly with latitude, dorsal-fin ray numbers do not.

Keywords: Atheriniformes, silverside fishes.

Resumen.- *Austromenidia* fue creado por Hubbs para agrupar a especies que se distinguían de *Odontesthes* por poseer escamas pequeñas y la primera aleta dorsal muy adelantada de la anal, y de *Basilichthys* en tener protrusión de la mandíbula superior. *Austromenidia* fue puesto en la sinonimia de *Odontesthes* primero por de Buen y luego por White en la primera revisión filogenética de la subfamilia Atherinopsinae. Dyer realizó un estudio filogenético de los pejerreyes sudamericanos, corroboró al género *Odontesthes* como un grupo monofilético y reconoció dos subgéneros: *Cauque* y *Austromenidia*. El subgénero *Austromenidia* es diagnosticado por cinco caracteres, de los cuales dos son únicos en la familia Atherinopsidae: el cóndilo lacrimal del etmoides lateral es grande y redondeado, y las expansiones hemales del embudo hemal tienen proyecciones anteroposteriores. Aunque *O. platensis* es el grupo hermano del subgénero, otras especies como *O. nigricans* y el subgénero *Cauque* son alternativas potenciales. Estas alternativas de relaciones están reflejadas en la clasificación. El subgénero *Austromenidia* está compuesta por las especies marinas *O. regia* Humboldt, *O. gracilis* Steindachner y *O. smitti* Lahille, siendo esta última la especie hermana del clado *O. regia* - *O. gracilis*. *Odontesthes smitti* es

diagnosticado por una reducida placa ventral del urohial. Se encuentra distribuida por la costa argentina del Atlántico suroccidental, desde Mar del Plata (aprox. 39°S) hasta el canal de Beagle en Tierra del Fuego, en las islas Malvinas, y adentrándose al Pacífico suroriental por el estrecho de Magallanes hasta el Seno de Última Esperanza, Puerto Natales (51°S), Chile. *Odontesthes regia* está diagnosticado por la extensión posterior del embudo hemal que se extiende hasta el extremo posterior de la aleta anal. Se encuentra distribuida por las costas del Pacífico suroriental de Perú y Chile, desde Piura (5°S) hasta el archipiélago de Los Chonos, Aysén (46°S). *Odontesthes gracilis* está diagnosticado por dientes relativamente pequeños, tres corridas de escamas suborbitales, ausencia de dientes vomerinos, y de un tamaño máximo de 120 mm de longitud estándar. Es una especie endémica del archipiélago de Juan Fernández (aprox. 33°S, 79°W), Chile. Debido al gran espectro latitudinal de distribución de las especies *O. regia* y *O. smitti*, se presenta un estudio de la variabilidad merística registrada. Debido a la amplia sobreposición de los rangos de variación, estas características no sirven como caracteres diagnósticos de estas especies, pero ciertamente son buenos descriptores de ellas. Mientras el número de vértebras aumenta con la latitud, siguiendo la regla de Jordan, el número de branquispinas de la rama inferior aumenta principalmente con el tamaño. Mientras el número de rayos de la aleta anal aumenta levemente con la latitud, el número de rayos de las aletas dorsales no aumenta del todo.

Palabras Claves: Atheriniformes, pejerreyes marinos.

Introduction

Austromenidia was erected by Hubbs (1918), and characterized by species having a combination of upper jaw protrusion, small scales, and a first dorsal fin well in advance of the anal fin. In this way, *Austromenidia* was distinguished from species of *Basilichthys* Girard, which have no protrusion, and from species of *Odontesthes* Evermann & Kendall and *Kronia* Miranda Ribeiro, which have large scales and a spinous dorsal fin over the anus. Because of the lack of unique diagnostic features, *Austromenidia* was placed in synonymy of *Odontesthes* by de Buen (1950, 1955), Mann (1954) and many subsequent authors. Campos (1984) resurrected *Austromenidia* from synonymy of *Odontesthes* without providing additional diagnostic evidence.

White (1985) provided the first phylogenetic hypothesis among atherinopsine genera and proposed *Odontesthes* as a monophyletic group, including *Austromenidia* as a junior synonym. In his hypothesis, *Odontesthes* is the sister group of *Basilichthys* (White 1985) and both constitute the tribe Sorgentinini (White 1989). *Odontesthes* is the most diverse atherinopsine genus, composed of between 17 and 25 recognized species, distributed in marine and freshwater habitats across temperate South America (Dyer 1998). A phylogenetic hypothesis among species of *Odontesthes* was proposed by Dyer (1993, 1998), a taxonomic result of which is that *Cauque* Eigenmann and *Austromenidia* were recognized as subgenera, and the latter composed of three species: *O. regia* Humboldt, *O. gracilis* Steindachner, and *O. smitti* Lahille.

In a revision of the marine pejerreyes of Argentina, García (1987) discussed the striking similarity between the Pacific species *O. regia* and the Atlantic species *O. smitti* and suggested their possible synonymy. Further complicating the taxonomy is *Atherina jacksoniana* Quoy & Gaimard (1825), based on five specimens from Port Jackson (now Sydney), N.S.W., Australia, that were not destroyed in the wreck of the *"Uranie"* at the Falkland or Malvinas Islands. Whitley (1943:137) argued convincingly that this species is a South American atherinopsine, possibly close to *O. laticlavia* (=*O. regia*) according to C.L. Hubbs, rather than an Old World atherine. Schultz (1948) also discussed the issue of *O. jacksoniana*, tentatively referred this species to *Austromenidia*, and was not specific as to which species name it must replace. The seniority of *O. jacksoniana* poses a potential nomenclatorial problem because it predates all atherinopsine names, but it has never been used to describe a sorgentinine.

Most of the available species names in the subgenus *Austromenidia* were described last century, reflecting new collecting localities along the temperate south American coastline. The proliferation of new species names was due to a lack of comparative material, typological species concepts, or the use of traditional external meristics and body proportions as taxonomic characters.

Meristic characters often used in taxonomy are affected by physical properties of the environment such as temperature, salinity, or oxygen concentration (Hubbs 1922, Barlow 1961, Fowler 1970, Chernoff 1982, Lindsey 1988, Blaxter 1992). The number of species described from different latitudes along the coasts of Chile and Perú (*O. affinis*, *O. laticlavia*, and *O. regia*), and Argentina (*O. smitti*, *O. smitti* var. *australis*, and *O. madrynensis*) possibly reflects an environmental effect on meristics (Fig. 1).

The purpose of this study is a phylogenetic revision of the subgenus *Austromenidia*, including a diagnosis and description of the species based on their internal anatomy and meristics. A comparative study of the

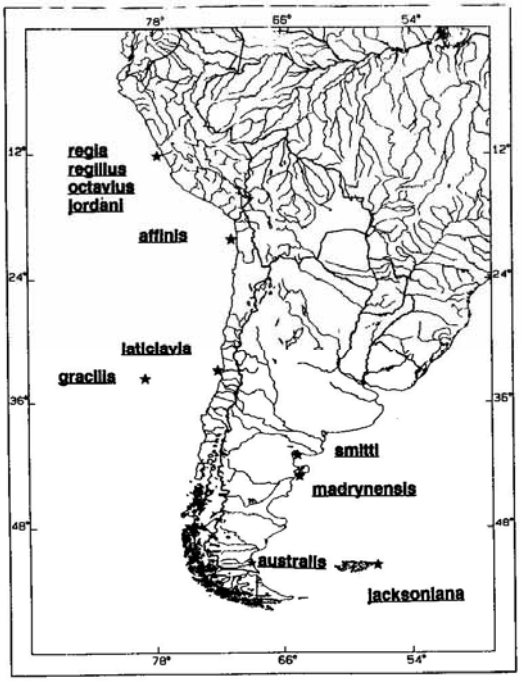

Figure 1
Type localities of nominal species of the subgenus *Austromenidia*.
Localidades tipo de las especies nominales del subgénero *Austromenidia*.

latitudinal variation in meristics between the Atlantic and Pacific species is discussed.

Taxonomic history of the subgenus *Austromenidia*

The first sorgentinin species to be described was *Atherina regia* Humboldt, 1821, from the Pacific coast of South America near Callao, Lima, Perú (Fig. 1). Abbott (1899) described four new species from this same locality, three of which correspond to the subgenus *Austromenidia*: *O. jordani*, *O. octavius* and *O. regillus* (Fig. 1). The latter species was designated as the type species of *Austromenidia* by Hubbs (1918). Valenciennes (1835) described *O. laticlavia*, from Valparaíso, Chile, a southern Pacific form considered by some authors as a species (Fowler 1951,Pequeño 1989) or as a subspecies of *O. regia* (Mann 1954, de Buen 1955, Bahamonde & Pequeño 1975). Steindachner (1898) described *O. affinis* from Iquique, Chile, a port roughly half way between Valparaíso and Callao (Fig. 1). The other nominal species mentioned above have been regarded in the literature as synonyms of *O. regia*.

Steindachner (1898) described *O. gracilis*, an endemic species from the Juan Fernández Archipelago (Fig. 1). This species was placed erroneously in *Basilichthys* by various authors (Fowler 1945, 1951, Mann 1954, de Buen 1955, Sepúlveda & Pequeño 1985), and properly placed by Campos (1984) in *Austromenidia* as originally suggested by Jordan & Hubbs (1919).

Lahille (1929a) described the Atlantic species *O. smitti* based on specimens from Golfo San Matías, Prov. Río Negro, Argentina, and a southern form as *O. smitti* var. *australis* from Puerto Gallegos and Seno Última Esperanza (Fig. 1). In his monograph on south American pejerreyes, Lahille (1929b) described *O. madrynensis* from Golfo Nuevo, Prov. Chubut, Argentina (Fig. 1). Subsequently, only *O. smitti* has been used for this Atlantic species (Ringuelet & Aramburu 1960, López 1964, Menni *et al.* 1984, García 1987). Eigenmann (1909) very briefly described *O. patagoniensis* in a key, based on three small specimens probably from Punta Arenas, Chile. The types are missing and the description is insufficient to clearly determine whether the specimens corresponded to *O. smitti* or *O. nigricans*, both common species in the Straits of Magellan.

A taxonomic problem is caused by *Atherina jacksoniana* Quoy & Gaimard, 1825, a species described as part of the Australian fauna. Radiographs of the type material, notes and counts made on the type specimens by Chernoff (*pers. comm.*), data and discussions presented by Whitley (1943) and Schultz (1948) have led me to conclude that *O. jacksoniana* is indeed *O. smitti*, most probably from the Falkland Islands (Fig. 1). This raises the question of seniority of the two synonyms. In strict application of the principle of priority in the International Code of Zoological Nomenclature, Article 23(a) (I.C.Z.N. 1985: 47), there is no doubt that *O. jacksoniana* is the senior synonym to *O. smitti*. Based on the purpose of the principle of priority (Art. 23b), however, and the latest proposal by the I.C.Z.N. (Savage 1990) we are in favor of maintaining the current usage of *O. smitti* over *O. jacksoniana* and shall do so for the present paper. This case will be referred to the International Commission for a final ruling.

Materials and Methods

A total of 437 specimens were examined (Appendix 1). Radiographs were made of 244 specimens, 11 specimens were cleared and double stained using the technique of Taylor & Van Dyke (1985), and 182 alcohol specimens were dissected and alizarin stained. Meristics were counted as in Chernoff (1986:88), except that the first vertebra was included in the count of total vertebrae (TV). Caudal vertebrae (CV) were distinguished from precaudal vertebrae (PCV) as having a haemal arch (see Dyer 1997). Counts taken from radiographs were made using a Wild dissecting microscope over a light box. Figures were all produced using computer graphics programs. Anatomical figures were made from drawings on a Wild stereomicroscope with an attached *camera lucida*, or scanned from their original sources and modified. Maps with locality data were produced using FISHMAP, version 1.6.3 (Buckup 1993). Graphs were made using SYGRAPH (Wilkinson 1988). Institutional abbreviations are those of Leviton *et al.* (1985) or otherwise noted. The methodology of character and phylogenetic analyses are discussed in Dyer (1997, 1998). Character numbers (Ch.) and their coding for the phylogenetic analysis data matrix are summarized in Appendix 2.

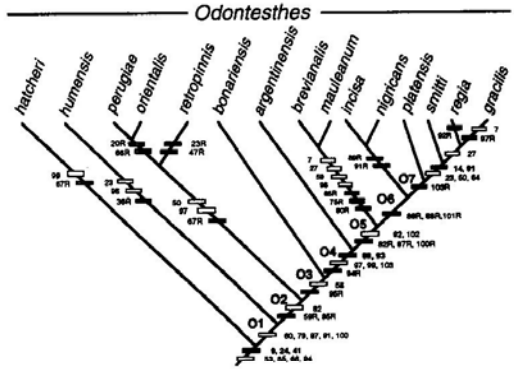

Figure 2

Phylogenetic relationships among species of *Odontesthes*. All diagnostic characters are unambiguously derived at that node. Unique characters within atherinopsids are in bold and opposite black bars, reversed characters (with an "R") are opposite grey bars, and homoplasious characters independently derived elsewhere are opposite white bars. For character numbers mentioned in text see Appendix 2. Other character numbers see Dyer (1997, 1998).

Relaciones filogenéticas entre especies de *Odontesthes*. Todos los caracteres son derivados en ese nodo. Caracteres únicos dentro de la familia Atherinopsidae están en negrilla y frente a barras negras; caracteres revertidos (con una "R") están frente a barras grises; y caracteres homoplásticos están frente a barras blancas. Para caracteres mencionados en el texto ver Apéndice 2. Otros caracteres no mencionados ver Dyer (1997, 1998).

Results

Relationships

Relationships among *Odontesthes* species and species groups are fully resolved (Fig. 2) and the classification reflecting that pattern is in Table 1 (Dyer 1998). The subgenus *Austromenidia* includes species *O. regia* (Humboldt), *O. gracilis* (Steindachner), and *O. smitti* (Lahille). This clade is diagnosed by five characters, of which the enlarged and rounded lacrimal condyle of the lateral ethmoid (Fig. 3; Ch. 14) and the anteroposterior projections of the haemal-arch expansions (Fig. 4; Ch. 91) are unique.

The above species were included together with *O. hatcheri*, *O. nigricans*, and the subgenus *Cauque* in a more inclusive *Austromenidia* by Schultz (1948). Though it is tempting to include all species of subgenus *Cauque*, *O. nigricans*, and *O. platensis* into an expanded subgenus *Austromenidia* (Fig. 5A: Node O5), we have decided to restrict the use of *Austromenidia* to the species group for which there is good evidence of monophyly, namely, *O. smitti*, *O. regia*, and *O. gracilis*. The placement of *O. platensis* as sister group to *Austromenidia* is only tenuously supported and could change with only an additional character or two. This is indicated in the classification (Table 1) by *sedis mutabilis*. An alternative hypothesis of relationships within Node O5 of Figure 5 that is one step longer, places *O. incisa* as sister to *O. nigricans*, subgenus *Cauque*, *O. platensis*, and subgenus *Austromenidia* (Fig. 5B).

Odontesthes smitti is sister to the species pair *O. regia* and *O. gracilis* (Fig. 5), the latter relationship being diagnosed by the presence of a rounded anterior end of the parasphenoid ventral ridge (Fig. 6; Ch. 27).

Systematics

Subfamily Atherinopsinae Fowler, 1903
Tribe Sorgentinini Pianta de Risso & Risso, 1953
Genus *Odontesthes* Evermann & Kendall, 1906
Subgenus *Austromenidia* Hubbs, 1918
Type Species= *Basilichthys regillus* Abbott, 1899

Table 1
Sequenced classification of Sorgentinini, Atherinopsinae. Order of genera or species is chronological unless noted by an asterisk
(*= included taxa are phylogenetically sequenced)
Clasificación secuencial de Sorgentinini, Atherinopsinae. El orden de los géneros o especies es cronológico si no es señalado por un asterisco. (*= taxa filogenéticamente secuenciados)

Series Atherinomorpha Greenwood, Rosen, Weitzman, Myers, 1966
Order Atheriniformes Rosen, 1964
Suborder Atherinoidei
Family Atherinopsidae Fowler, 1903
Subfamily Menidiinae Schultz, 1948
Subfamily Atherinopsinae Fowler, 1903
Tribe Atherinopsini Fowler, 1903
Tribe Sorgentinini Pianta de Risso & Risso, 1953
Genus *Basilichthys* Girard, 1854
microlepidotus species group
B. microlepidotus (Jenyns, 1842)
B. australis Eigenmann, 1927
semotilus species group
B. semotilus (Cope, 1874)
B. archaeus (Cope, 1878)
Genus *Odontesthes* Evermann & Kendall, 1906*
O. hatcheri (Eigenmann, 1909)
O. humensis de Buen, 1953
perugiae-retropinnis species group
O. retropinnis (de Buen, 1953)
perugiae species group
O. perugiae Evermann & Kendall, 1906
O. orientalis de Buen, 1950
O. mirinensis Bemvenuti, 1995
O. bonariensis (Valenciennes, 1835)
O. argentinensis (Valenciennes, 1835)
Subgenus *Cauque* Eigenmann, 1927 *sedis mutabilis*
O. brevianalis (Günther, 1880)
O. mauleanum (Steindachner, 1896)
nigricans-incisa species group
O. nigricans (Richardson, 1848) *sedis mutabilis*
O. incisa (Jenyns, 1842) *sedis mutabilis*
O. platensis (Berg, 1895) *sedis mutabilis*
Subgenus *Austromenidia* Hubbs, 1918 *sedis mutabilis**
O. smitti (Lahille, 1929)
O. regia (Humboldt, 1821)
O. gracilis (Steindachner, 1898)
Superorder Cyprinodontea Dyer & Chernoff
Order Cyprinodontiformes
Order Beloniformes

Diagnosis: Species of *Odontesthes* with an enlarged lacrimal condyle of the lateral ethmoid (Fig. 3; Ch. 14), postocular shelf along entire length of dermosphenotic (Fig. 7; Ch. 23), two rows of teeth on jaws (Ch. 50), opercular dorsal process rounded (Fig. 8; Ch. 64), and haemal-arch funnel with anteroposterior projections restricted to the ventral half of the haemal arches (Fig. 4; Ch. 91).

Additional descriptive features: Species of *Odontesthes* with an endopterygoid tooth patch (Ch. 59), hyomandibular nerve divided inside of hyomandibula (Dyer 1997: Ch. 60), opercular posterodorsal border straight (Fig. 8: Ch. 68) and posteroventral border concave (Fig. 8: Ch. 69), ventral postcleithrum between pleural ribs one and three (Ch. 79), origin of first dorsal fin anterior to anus, over tip of pelvic fin or slightly posterior (Ch. 82), five or fewer interdorsals (Ch. 85), first pleural rib long (Ch. 87), posterior pleural ribs anterior to first anal-fin pterygiophore (Fig. 4: Ch. 88), haemal-funnel floor bulged dorsally (Fig. 4: Ch. 93), anterior haemal spines long (Fig. 4: Ch. 94), first caudal vertebra anterior to anal-fin origin (Fig. 4: Ch. 95), cleithrum shaft with small scales overlapping posterior border (Dyer 1997; Ch. 99), scales absent between anterior rays of second dorsal and anal fins (Chs 100, 101), scales small (Ch. 102) and posteriorly smooth (Ch. 103). Vertebrae numerous, with a total of 50 to 60; gill rakers on lower branch 24 - 35; pectoral-fin tip anterior of pelvic-fin origin, and lateral band wide.

Distribution: Marine, with juveniles sometimes found in estuaries; from Tierra del Fuego to Piura, Perú - including the Juan Fernández Archipelago- in the southeastern Pacific, and to Mar del Plata, Buenos Aires, Argentina -including the Malvinas or Falkland Islands- in the southwestern Atlantic (Fig. 9).

Odontesthes smitti (Lahille 1929a)

Basilichthys smitti Lahille, 1929a:84 (types missing). Type locality: "Fin de Barrancas", Golfo San Matías, SE Atlantic, Argentina.

=*Atherina jacksoniana* Quoy & Gaimard, 1825: 333 (Syntypes MNHN-P A.2895, MNHN-P 3096). Type locality: unknown (original label, Port Jackson, NSW, Australia).

?=*Menidia patagoniensis* Eigenmann, 1909: 280 (types missing). Type locality: Straits of Magellan (?Punta Arenas), Chile.

=*Basilichthys madrynensis* Lahille, 1929b: 326 (types missing). Type locality: Puerto Madryn, Golfo Nuevo, Chubut, Argentina.

=*Basilichthys smitti var. australis* Lahille, 1929a: 84 (types missing). Type locality: Río Gallegos, Argentina, and Puerto Natales, Chile.

Diagnosis: Species of subgenus *Austromenidia* with ventral plate of urohyal reduced or folded (Fig. 10B; Ch. 74).

Additional descriptive features: Species of subgenus *Austromenidia* with three vomerine tooth patches (Dyer 1997: fig. 7; Ch. 8), parasphenoid ventral ridge tapered anteriorly (Fig. 6B; Ch. 27), opercular fenestration covering an enlarged surface area of the opercle (Fig. 8; Ch. 65), haemal funnel extended posteriorly to middle

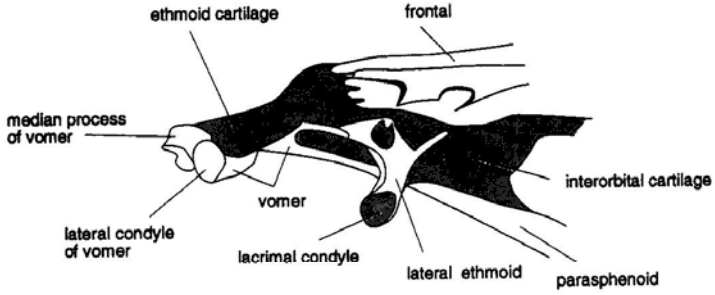

Figure 3
Lateral view of the ethmoid region of *Odontesthes gracilis* (UMMZ 215529).
Vista lateral de la región etmoidal de *Odontesthes gracilis* (UMMZ 215529).

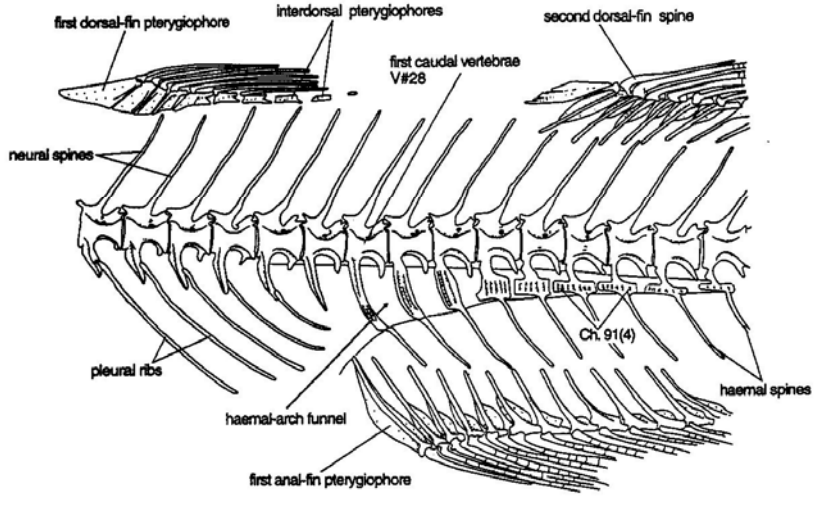

Figure 4
Lateral view of median fins and axial skeleton of *Odontesthes regia* (UMMZ 215521).
Vista lateral de las aletas impares y esqueleto axial de *Odontesthes regia* (UMMZ 215521).

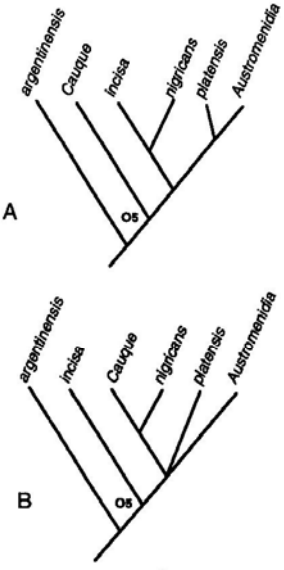

Figure 5

Alternative hypotheses of relationships among taxa of Node O5; A, Subgenus *Cauque* is sister to the other members of Node O5 (L=403); B, *Odontesthes incisa* is sister to the other members of Node O5 (L=404). *O. platensis* is sister to subgenus *Austromenidia*, to the *Cauque* - *O. nigricans* clade, or sister to *Cauque*, *O. nigricans*, and *Austromenidia*.

Hipótesis alternativas de relaciones entre taxa del Nodo 05; A, el subgénero *Cauque* es hermano de los otros miembros del Nodo 05 (L=403); B, la especie *Odontesthes incisa* es hermana de los otros miembros del Nodo 05 (L=404). La especie *O. platensis* es hermana del subgénero *Austromenidia*, del clado *Cauque* - *O. nigricans*, o hermana de *Cauque*, *O. nigricans*, y *Austromenidia*.

of anal fin (Fig. 4; Ch. 92), and four subocular rows of scales (Ch. 97). Two or more caudal vertebrae than precaudal vertebrae. Range of meristics from Table 2: first dorsal-fin rays, 5-9; second dorsal-fin rays, 10-14; anal-fin rays, 17-22; total number of vertebrae, 53-60; precaudal vertebrae, 25-30; caudal vertebrae, 26-32; total number of gill rakers, 26-43; gill rakers of upper branch, 7-11; gill rakers of lower branch, 19-35.

Distribution: Inshore marine of southwestern Atlantic along the coast of Argentina from Mar del Plata (38°S, 57°33'W) to the Beagle Channel in southern Tierra del

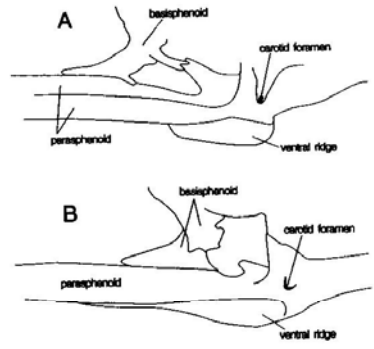

Figure 6

Lateral view of the parasphenoid ventral ridge; A, *Odontesthes gracilis* (UMMZ 215529); B, *Odontesthes humensis* (UMMZ 221327).

Vista lateral de la cresta ventral del parasfenoides; A, *Odontesthes gracilis* (UMMZ 215529); B, *Odontesthes humensis* (UMMZ 221327).

Fuego, possibly extending to Cape Horn (García 1987).This species is also found in the Malvinas or Falkland Islands, and in the western reaches of the Straits of Magellan north to Seno Última Esperanza, near Puerto Natales (51°40'S, 72°40'W), Chile (Fig. 9).

Comments: Lack of collections between Puerto Natales (ab. 52°S) and the Aysén region (ab. 46°S) has left a distributional gap that could be filled in by a southern range extension of *O. regia*, a northern range extension of *O. smitti* in the Pacific, or both. *Odontesthes regia* and *O. smitti* could be either allopatric or sympatric in this region. Verbal accounts on the presence of unidentified "pejerreyes" in Puerto Edén (49°07'S, 74°25'W) indicates an extension in the distribution of one or both species. Further collections are required to answer this question. The only information available regarding the biology of this species is in papers by Elías *et al.* (1984) and Gosztonyi *et al.* (1991) on age and growth. This is the most important species of the million dollar per year fishery resource in the area of Golfo Nuevo (Elías *et al.* 1984). It is also caught in great abundance in the winter months and early spring in the region of Mar del Plata (García 1987).

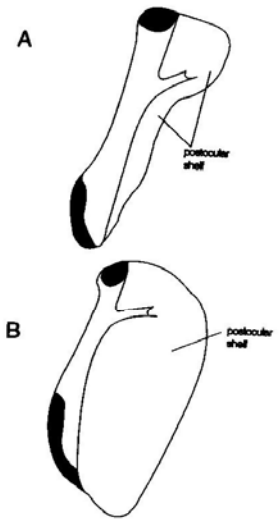

Figure 7
Posterior view of the dermosphenotic bone; A, *Odontesthes brevianalis* (UMMZ 215459); B, *Odontesthes incisa* (UMMZ 218799).
Vista posterior del dermoesfenótico; A, *Odontesthes brevianalis* (UMMZ 215459); B, *Odontesthes incisa* (UMMZ 218799).

Odontesthes regia (Humboldt 1821)

Atherina regia Humboldt *in* Humboldt & Valenciennes, 1821: 187 (Types missing). Type locality: Callao, Perú.

=*Atherina laticlavia* Valenciennes *in* Cuvier & Valenciennes, 1835: 473. (Syntypes MNHN-P 2980). Type locality: Valparaíso, Chile.

=*Chirostoma affine* Steindachner, 1898: 313. (Holotype ZMB 15674). Type locality: Iquique, Chile.

=*Basilichthys jordani* Abbott, 1899: 341. (Holotype CAS-SU 6070, Paratype CAS-SU 6073). Type locality: Callao, Perú.

=*Basilichthys octavius* Abbott, 1899: 340. (Holotype CAS-SU 6069). Type locality: Callao, Perú.

=*Basilichthys regillus* Abbott, 1899: 339. (Holotype CAS-SU 6071, Paratypes CAS-SU 6072, BMNH 1900.9.29). Type locality: Callao, Perú.

Diagnosis: Species of *Austromenidia* with haemal-arch funnel extended to posterior end of anal fin (Ch. 92)

Additional descriptive features: Species of *Austromenidia* with three vomerine tooth patches (Dyer 1997: fig.7; Ch. 8), parasphenoid ventral ridge rounded anteriorly (Fig. 6A; Ch. 27), endopterygoid with enlarged tooth patch (Ch. 59), and four suborbital rows of scales (Ch. 97). Range of meristics from Table 3: first dorsal-fin rays, 5-9; second dorsal-fin rays, 9-13; anal-fin rays, 15-20; total number of vertebrae, 50-56; precaudal vertebrae, 24-28; caudal vertebrae, 24-29; total number of gill rakers, 30-40; gill rakers of upper branch, 6-9; gill rakers of lower branch, 24-31.

Distribution: Inshore marine of southeastern Pacific from Piura (ab. 5°S), northern Perú, to the Archipelago of Los Chonos or Guaitecas, Aysén (ab. 46°S), XI Region, southern Chile (Fig. 9). Juveniles are sometimes found in estuaries.

Comments: Published reports of *O. smitti* in the southern Aysén region of Chile by Zama & Cárdenas (1984) and Zama (1988) conflict with reports of *Odontesthes* cf. *regia* in the archipelagos of Chiloé and Los Chonos by Navarro & Pequeño (1979). Collections made in the region of Aysén correspond to *O. regia*. Biological information of this species is about the development of eggs and larvae (Chirinos de Vildoso & Chuman 1964), growth and age determination (Villavicencio & Muck 1984), feeding (Silva & Stuardo 1985), and functional morphology (de la Hoz 1994, 1995, de la Hoz & Aldunate 1994, de la Hoz *et al.* 1994, de la Hoz & Vial 1988, 1994).

Odontesthes gracilis (Steindachner 1898)

Chirostoma gracile Steindachner, 1898: 314. Syntypes ZMB 15675. Type locality: Robinson Crusoe Island, Archipelago of Juan Fernández, Chile.

Diagnosis: Species of *Austromenidia* without vomerine teeth (Ch. 7), relatively small jaw teeth (see Ch. 50), and three suborbital scale rows (Ch. 97).

Additional descriptive features: Species of *Austromenidia* with parasphenoid ventral ridge rounded anteriorly (Fig. 6A; Ch. 27), and haemal funnel extended to middle of anal fin (Fig. 4; Ch. 92). Maximum recorded adult size is 120 mm SL. Range of meristics from Table 4: first dorsal-fin rays, 6-8; second dorsal fin rays, 11-12; anal-fin rays, 17-18; total number of vertebrae, 50-52; precaudal vertebrae, 24-26; caudal vertebrae, 26-27; total number of gill rakers, 32-36; gill rakers of upper branch, 7-8; gill rakers of lower branch, 25-28.

Distribution: Marine, endemic to the archipelago of Juan Fernández (33°S, 79°W), Chile (Fig. 9).

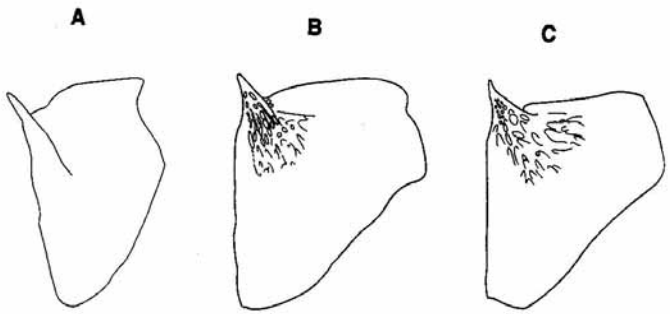

Figure 8

Lateral view of the opercle; A, *Chirostoma labarcae* (UMMZ 193463); B, *Odontesthes regia* (UMMZ 215521); C, *O. smitti* (UMMZ 218448).

Vista lateral del opérculo; A, *Chirostoma labarcae* (UMMZ 193463); B, *Odontesthes regia* (UMMZ 215521); C, *O. smitti* (UMMZ 218448).

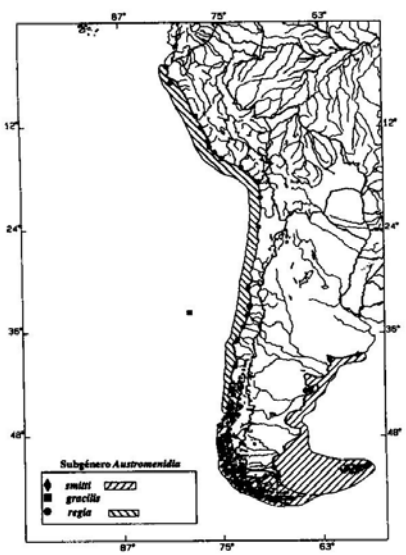

Figure 9

Distribution map of the species of the subgenus *Austromenidia*

Mapa de distribución de las especies del subgénero *Austromenidia*.

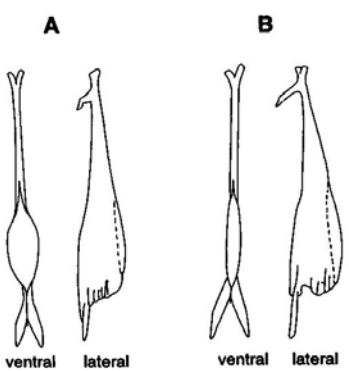

Figure 10

Lateral and ventral views of the urohyal; A, *Odontesthes regia* (UMMZ 215521); B, *O. smitti* (UMMZ 218448).

Vistas lateral y ventral del urohial; A, *Odontesthes regia* (UMMZ 215521); B, *O. smitti* (UMMZ 218448).

Comments: This species is endemic to the Archipelago of Juan Fernández, and has been collected only on Robinson Crusoe Island. Unlike many other fishes endemic to the Juan Fernández Archipelago (Sepúlveda 1987, Pequeño & Lamilla 1996) this species has not been found in the northern islands of San Félix (26°17'S, 80°05'W) and San Ambrosio (26°20'S, 79°58'W). Nothing is known about the biology of this species.

Meristic variation

Meristic characters have been used extensively for taxonomic and fisheries studies because they are relatively easy to count and because, unlike morphometric and color traits, they are usually considered to be fixed at early stages of vertebrate development (Johnson & Barnett 1975, Lindsey 1988). Lindsey (1988) reviewed the effects of temperature and other physical factors on meristic variation. In general, the number of meristic elements is inversely correlated with temperature. This inverse correlation with temperature is usually expressed by higher meristic counts at greater latitudes or a positive correlation with latitude. This pattern, known as Jordan's rule, mostly refers to vertebral counts (Jordan 1892). Species with wide latitudinal ranges are expected, therefore, to have larger ranges of meristic variation than species with narrower ranges of distribution. *Odontesthes regia* and *O. smitti* have wide distribution ranges (Fig. 9) and comparisons of their number of vertebrae, median-fin rays, and gill rakers on the first branchial arch, are presented. Whether the phenotypic trend of increase in number of elements with latitude is adaptive or purely environmental in these species, is unknown, though a genetic basis to this latitudinal variation has been determined for the Atlantic silverside, *Menidia menidia* (Billerbeck *et al.* 1997).

Vertebrae

The number of total vertebrae (TV) across the latitudinal range of *O. smitti* has an increase in mean value of about four vertebrae (Table 2: 55-59). *Odontesthes regia* has an mean increase of two TV across its latitudinal range (Table 3: 51-53). Both *O. regia* and *O. smitti* have a maximum variation of five vertebrae per locality (Fig. 11). There is no overlap between the TV means of *O. regia* and *O. smitti*, but the absolute ranges overlap quite widely (Fig. 11). Noteworthy is the broad overlap between populations of *O. regia* and *O. smitti* at 42° S (Fig. 11), however their means do not overlap (Table 2: loc 16; Table 3: loc 23). Both *O. regia* and *O. smitti* have an increase in the mean value of TV with latitude, but the greater values of *O. smitti* may be a reflection of the a more southerly distribution relative to *O. regia* (Fig. 11).

The number of precaudal vertebrae (PCV) across the latitudinal range of *O. smitti* has an increase in mean value of one vertebra (Table 2: 27-28), whereas *O. regia* has an increase in mean value of two PCV (Table 3: 25-27). *Odontesthes smitti* has a maximum variation of five vertebrae per locality, whereas *O. regia* has only three (Fig. 12). The absolute PCV ranges of variation between both species (Fig. 12) have a greater overlap than that of TV (Fig. 11). The mean ranges of PCV between species also overlap (Tables 2, 3), unlike that of the mean TV ranges.

The number of caudal vertebrae (CV) across the latitudinal range of *O. smitti* has a mean increase of three vertebrae (Table 2: 28-31), whereas *O. regia* has an increase of only one vertebra (Table 3: 26-27). *Odontesthes smitti* has a maximum variation of five vertebrae per locality, whereas *O. regia* has a maximum variation of four CV (Fig. 13). There is no overlap between the mean ranges of CV between *O. regia* and *O. smitti*, but the absolute ranges overlap quite broadly (Fig. 13).

The increase with latitude of mean values of PCV and CV is different in *O. smitti* and *O. regia*. In *O. smitti*, CV increase more with latitude than do PCV (Table 2), whereas in *O. regia* it is PCV that increase more than CV (Table 3). The northern populations of *O. smitti* have two or more CV than do PCV, a difference that increases with latitude because of the relative decrease of PCV. *Odontesthes regia* on the other hand, has roughly the same number of CV and PCV in the northern populations, and PCV increase slightly more than do CV with latitude. Therefore, southern populations of *O. smitti* have more CV than PCV, whereas southern populations of *O. regia* tend to have more PCV than CV.

Median-fin rays

The number of rays of the first-dorsal fin (D1) and the second-dorsal fin (D2) do not vary with latitude (Fig. 14). Anal-fin rays (Anal), however, have an increase in mean of only one ray across the latitudinal ranges of *O. regia* (Table 3: 17-18) and *O. smitti* (Tables 2: 19-20), with a maximum range of variation of five rays per locality (Fig. 15). The overlap in absolute ranges of anal-fin rays between *O. regia* and *O. smitti* is broad (Fig. 15), and the means at equivalent latitudes are very close (Table 2: loc 23; Table 3: loc 16).

Gill rakers

The mean number of total gill rakers (GRT) on the first branchial arch increase by only one or two rakers (Tables 2, 3) across the latitudinal range of both species. The absolute ranges of *O. regia* and *O. smitti* broadly overlap, as do their means (Fig. 16). *Odontesthes regia* has a maximum range of variation of seven GRT per

locality, whereas *O. smitti* has a maximum of sixteen GRT per locality (Fig. 16). The tremendous difference of variation per locality between both species is especially noticeable at latitudes 42°S and 47°S (Fig. 16) in which *O. smitti* has a noticeably larger range of variation than *O. regia*. *O. smitti* localities 22 and 23 are particular in this data set in that they include specimens smaller than 80mm SL (Table 2). The relationship between body size (SL) and number of gill rakers (GRT) is observed in Figure 17. Individuals of *O. smitti* larger than 86mm SL have more than 33 GRT, with a maximum of 43 GRT. The increase in GRT with body size is due to the increase in number of gill rakers on the lower branch only (GRL; Fig. 18). The number of gill rakers on the upper branch (GRU) is unchanged as body size increases (Fig. 18). Increase in the number of gill rakers with body size is a common occurrence in filter feeding fishes such as sardines and anchovies (Hildebrand 1946:80,96, Sáez 1988). Other meristics such as anal-fin rays and vertebral counts do not vary with body size (Fig. 19).

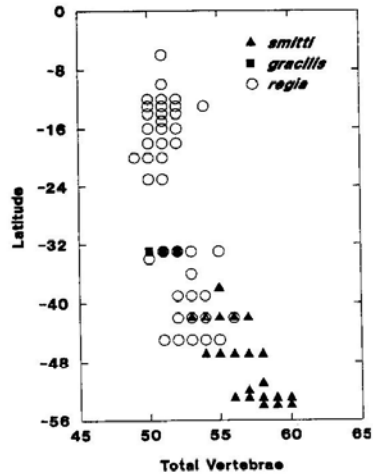

Figure 11

Variation in the number of total vertebrae (TV) with latitude South. Each circle represents at least one individual.

Variación en el número de vértebras totales (TV) con latitud Sur. Cada círculo representa a lo menos un individuo.

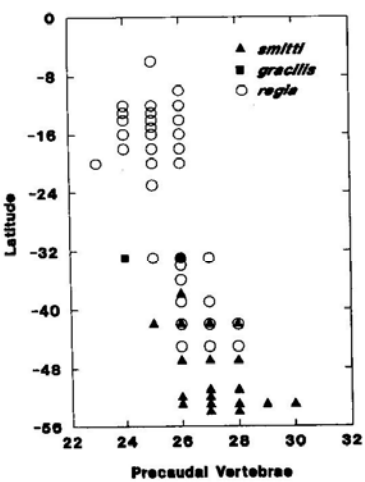

Figure 12

Variation in the number of precaudal vertebrae (PCV) with latitude South. Each circle represents at least one individual.

Variación en el número de vértebras precaudales (PCV) con latitud Sur. Cada círculo representa a lo menos un individuo.

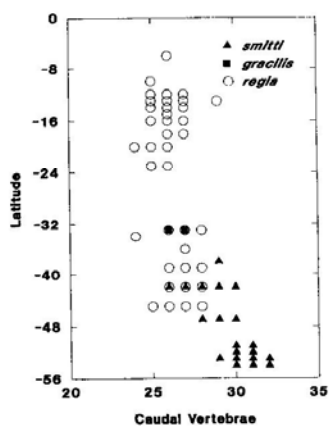

Figure 13

Variation in the number of caudal vertebrae (CV) with latitude South. Each circle represents at least one individual.

Variación en el número de vértebras caudales (CV) con latitud Sur. Cada círculo representa a lo menos un individuo.

Table 2

Meristics of *Odontesthes smitti* by locality. Meristics (min-max:avg/StD): TV, total vertebrae; PCV, precaudal vertebrae; CV, caudal vertebrae; Anal, anal-fin rays; D1, first dorsal-fin rays; D2, second dorsal-fin rays; GRU, gill rakers upper branch; GRL, gill rakers lower branch; GRT, gill rakers total; SL, standard length in mm; N, number of individuals. Localities: from 19 to 21 Chile, from 22 to 24 Argentina. 19, Dawson Island, southwestern Straits of Magellan; 20, Punta Arenas, Straits of Magellan; 21, Punta Catalina, eastern Straits of Magellan; 22, Puerto Deseado, Santa Cruz; 23, Puerto Madryn, Chubut; 24, Necochea, Buenos Aires; 25, Falklands or Malvinas.

Datos merísticos de *Odontesthes smitti* por localidad. Merísticos (min-max/DEst): TV, vértebras totales; PCV, vértebras precaudales; CV, vértebras caudales; Anal, rayos de aleta anal; D1, rayos de primera aleta dorsal; D2, rayos de segunda aleta dorsal; GRU, branquispinas de rama superior; GRL, branquispinas de rama inferior; GRT, branquispinas totales; SL, longitud estándar en mm; N, número de individuos. Localidades: de 19 a 21 Chile, de 22 a 24 Argentina. 19, isla Dawson, suroeste del estrecho de Magallanes; 20, Punta Arenas, estrecho de Magallanes; 21, punta Catalina, este del estrecho de Magallanes; 22, Puerto Deseado, Santa Cruz; 23, Puerto Madryn, Chubut; 24, Necochea, Buenos Aires; 25, Malvinas o Falklands.

Locality	TV	PCV	CV	Anal	D1	D2	GRU	GRL	GRT	SL (mm)	N
24 (38°S)	55-55:55	26-26:26	29-29:29	18-18:18	8-8:8	10-10:10	8-8:8	31-31:31	39-39:39	211-211	1
	0	0	0	0	0	0	0	0	0		
23 (42°S)	53-57:55	25-28:27	26-30:28	17-20:19	6-8:7	10-13:11	8-11:9.2	22-30:27	30-40:36	55.2-382	68
	0.77	0.68	0.78	0.81	0.56	0.65	0.76	1.52	1.95		
22 (47°S)	54-58:56	26-28:27	28-30:29	17-21:19	6-9:7	10-13:12	7-11:8.2	19-31:24	26-41:32	45-262	116
	0.77	0.54	0.69	0.89	0.80	0.64	0.98	2.84	4.21		
25 (51°S)	54-58:58	27-28:28	30-31:31	19-20:19	6-7:7	10-13:12	8-8:8	30-30:30	38-38:38	56-146	6
	0	0.5	0.5	0.47	0.37	0.96	0	0	0		
21 (52°S)	57-57:57	26-27:27	30-31:31	19-20:20	5-7:6	11-12:12	8-8:8	30-30:30	38-38:38	110-221	2
	0	0.5	0.5	1	1	0.5	0	0	0		
20 (53°S)	56-60:58	26-30:28	29-32:30	18-21:19	5-9:7	10-13:12	7-10:8.5	27-35:30	35-43:38	148-343	56
	1.14	0.89	0.74	0.70	0.89	0.64	0.63	1.24	1.4		
19 (54°S)	58-60:59	27-28:28	30-32:31	18-22:20	6-8:7	11-14:12	8-9:8.3	27-31:29	37-40:38	257-281	6
	0.75	0.47	0.58	1.29	0.69	0.94	0.47	1.25	1.07		
AVG	56.14	26.93	29.20	19.11	6.97	11.56	8.57	26.41	35.07		
StD	1.45	0.75	1.09	0.89	0.76	0.70	0.93	3.23	3.98		
				Range of means						Size range	Total
	(4) 55-59	(1) 27-28	(3) 28-31	(1) 19-20	(1)6-7	(1)11-12	(.9) 8.3-9.2	(7)24-30	(6)32-38	45-382	255
						Maximum variation per locality					
	5	5	5	5	5	4	5	13	16		

Conclusions

The subgenus *Austromenidia* is monophyletic, diagnosed by five characters of which two are unique: an enlarged lacrimal condyle and the anteroposterior projections of the haemal-arch funnel. The subgenus *Austromenidia* is composed of three marine species: *Odontesthes smitti*, *O. regia*, and *O. gracilis*. *Odontesthes smitti* is diagnosed by the presence of a reduced ventral plate of the urohyal, and distributed along the Atlantic coast of Argentina to Tierra del Fuego including the Malvinas or Falkland Islands and in the northwestern reaches of the Straits of Magellan. *Odontesthes smitti* is the sister species to the eastern Pacific *O. regia* - *O. gracilis* clade. *Odontesthes regia* is diagnosed by the haemal funnel extended posteriorly to over the middle of the anal fin, and distributed along the Pacific coast from northern Perú (ab. 5°S) to southern Chile (ab. 46°S). *Odontesthes gracilis* is diagnosed by the lack of vomerine teeth and relatively small jaw teeth, and is endemic to the Juan Fernández Archipelago.

Analysis of meristic features reveals a broad overlap of ranges of variation and are unsuitable as diagnostic traits, but their ranges and means are suitable as descriptive features of each species. *Odontesthes smitti* has two or more CV than PCV, a difference that increases with latitude. *Odontesthes regia* has roughly the same number of PCV and CV, with a slight increase of PCV relative to CV with latitude. The extent to which the meristic features overlap is in part due to the wide latitudinal range of distribution of *O. regia* and *O. smitti*. The range of variation of vertebral and gill raker means in *O. smitti* is greater than in *O. regia*, despite the smaller range in latitude. This may be a reflection of the more southerly distribution of the former species and the lower temperatures of the environment. Meristic characters that increase with latitude are vertebral counts, anal-fin rays, and gill rakers. Anal-fin ray numbers increase only slightly with latitude, whereas dorsal fin-ray numbers do not vary with latitude. Gill rakers of the lower branch varied with body size rather than latitude, unlike other meristics in this study.

Table 3

Meristics of *Odontesthes regia* by locality. Meristics: (min-max:avg/StD): TV, total vertebrae; PCV, precaudal vertebrae; CV, caudal vertebrae; Anal, anal-fin rays; D1, first dorsal-fin rays; D2, second dorsal-fin rays; GRU, gill rakers upper branch; GRL, gill rakers lower branch; GRT, gill rakers total; SL, standard length in mm; N, number of individuals. Localities: from Perú 1 - 8, from Chile 8 - 18 1, Lobos Afuera Island, Lambayeque; 2, Puerto Supe, Lima; 3, Callao, Lima; 4, Paracas, Pisco; 5, opposite Río Ica,; 6, Punta Lomas, Arequipa; 7, Quilca, Arequipa; 8, Arica; 9, Iquique; 10, Antofagasta; 11, Valparaíso; 13, Navidad, VI Región; 14, Talcahuano, Concepción; 15, Corral, Valdivia; 16, Castro, Chiloé; 17, Chacabuco, Aysén; 18, Quitralco, Aysén.

Datos merísticos de *Odontesthes regia* por localidad. Merísticos (min-max/DEst): TV, vértebras totales; PCV, vértebras precaudales; CV, vértebras caudales; Anal, rayos de aleta anal; D1, rayos de primera aleta dorsal; D2, rayos de segunda aleta dorsal; GRU, branquispinas de rama superior; GRL, branquispinas de rama inferior; GRT, branquispinas totales, SL, longitud estándar en mm; N, número de individuos. Localidades: de 1 a 7 Perú , de 8 a 18 Chile. 1, isla Lobos Afuera, Lambayeque; 2, Puerto Supe, Lima; 3, Callao, Lima; 4, Paracas, Pisco; 5, frente río Ica, Ica; 6, punta Lomas, Arequipa; 7, Quilca, Arequipa,; 8, Arica; 9, Iquique; 10, Antofagasta, 11, Valparaíso; 13, Navidad, VI Región; 14, Talcahuano, Concepción; 15, Corral, Valdivia; 16, Castro, Chiloé; 17, Chacabuco, Aysén; 18, Quitralco, Aysén.

Locality	TV	PCV	CV	Anal	D1	D2	GRU	GRL	GRT	SL (mm)	N
1 (6°S)	51-51:51	25-25:25	26-26:26	16-18:17	6-6:6	11-11:11	7-8:7.5	25-25:25	32-33:33	156-166	2
	0	0	0	1	0	0	0.5	0	0.5		
2 (10°S)	51-51:51	26-26:26	25-25:25	17-17:17	5-5:5	11-11:11	8-8:8	27-27:27	35-35:35	86-86	1
	0	0	0	0	0	0	0	0	0		
3 (12°S)	50-52:51	24-26:25	25-27:26	16-18:17	6-9:7	10-12:11	6-8:7.6	25-29:28	32-37:35	125-224	14
	0.73	0.52	0.59	0.64	0.77	0.64	0.62	1.15	1.51		
4 (13°S)	50-54:51	24-25:25	25-29:26	15-19:17	6-8:7	11-12:11	7-9:7.8	24-29:26	31-37:34	130-199	13
	1.14	0.36	1.14	0.91	0.68	0.42	0.58	1.42	1.75		
5 (14°S)	50-52:51	24-26:25	25-27:26	15-18:17	6-7:7	9-13:11	7-8:7.7	26-29:28	33-37:.35	114-145	12
	0.69	0.41	0.55	0.71	0.5	0.95	0.47	0.76	1.07		
6 (15°S)	51-51:51	25-25:25	26-26:26	16-16:16	7-7:7	11-11:11	7-7:7	26-26:26	33-33:33	157.5-158	1
	0	0	0	0	0	0	0	0	0		
7 (16°S)	50-52:51	24:26:25	25-27:26	16-19:18	6-7:7	9-12:11	7-8:7.9	25-29:27	32-37:35	134-172	22
	0.78	0.56	0.52	0.84	0.50	0.71	0.34	1.05	1.10		
8 (18°S)	50-52:51	24:26:25	26-27:26	16-18:17	6-8:7	10-13:11	6-9:7.9	24-29:27	30-37:35	129-225	17
	0.55	0.42	0.38	0.57	0.54	0.68	0.58	1.16	1.54		
9 (20°S)	49-51:50	23-26:25	24-26:25	16-18:17	6-7:7	11-12:11	8-9:8.4	26-29:27	34-38:36	129-160	5
	0.75	0.98	0.80	0.63	0.49	0.40	0.49	1.02	1.33		
10 (23°S)	50-51:50	25-25:25	25-26:25	16-18:17	5-8:7	10-12:11	8-8:8	25-28:27	33-36:35	109-150	5
	0.49	0	0.49	0.63	1.02	0.63	0	1.02	1.02		
11 (33°S)	51-55:53	25-27:26	26-28:27	18-18:18	6-8:7	10-11:11	7-7:7	25-30:27	32-37:34	107.5-149	4
	1.48	0.83	0.71	0	0.71	0.43	0	2.12	2.12		
13 (34°S)	50-50:50	26-26:26	24-24:24	16-16:16	6-6:6	9-9:9	7-7:7	26-26:26	33-33:33	156.5-157	1
	0	0	0	0	0	0	0	0	0		
14 (36°S)	53-53:53	26-26:26	27-27:27	17-17:17	6-6:6	11-11:11	8-8:8	27-27:27	35-35:35	111-111	1
	0	0	0	0	0	0	0	0	0		
15 (39°S)	52-54:53	26-27:26	26-28:27	16-20:18	6-8:7	11-13:12	7-9:8.1	25-30:27	33-39:35	147-248	14
	0.64	0.41	0.72	0.19	0.53	0.52	0.52	1.48	1.72		
16 (42°S)	52-56:53	26-28:27	26-28:27	16-19:18	6-8:7	10-12:11	7-9:8.3	26-30:28	33-39:36	158-229	13
	1.05	0.61	0.75	0.89	0.73	0.74	0.61	1.42	1.94		
17 (45°S)	51-54:53	26-27:27	25-28:27	17-19:18	6-8:7	10-12:11	7-9:8	26-29:28	34-38:36	183.5-207	14
	0.86	0.5	0.8	0.76	0.61	0.72	0.38	0.81	1.04		
18 (46°S)	52-55:54	26-28:27	25-27:26	17-18:18	6-8:7	10-12:11	8-9:8.4	27-31:28	35-40:37	193-217	10
	0.81	0.6	0.64	0.4	0.63	0.64	0.49	1.2	1.47		
AVG	51.69	25.57	26.12	17-47	6.77	11.17	7.92	27.26	35.18		
StD	1.41	0.95	1.81	0.87	0.67	0.73	0.57	1.32	1.65		
				Range of means						Size range	Total
	(2) 51-53	(2) 25-27	(1) 26-27	(1) 17-18	(1) 6-7	(1) 11-12	(.9) 7.5-8.4	(2) 26-28	(3) 34-37	86-248	149
				Maximum variation per locality							
	5	3	4	5	4	5	3	5	7		

Table 4

Meristics of *Odontesthes gracilis*. Meristics: (min-max:avg/StD): TV, total vertebrae; PCV, precaudal vertebrae; CV, caudal vertebrae; Anal, anal-fin rays; D1, first dorsal-fin rays; D2, second dorsal-fin rays; GRU, gill rakers upper branch; GRL, gill rakers lower branch; GRT, gill rakers total; SL, standard length in mm; N, number of individuals. Locality 12: Robinson Crusoe Island, Juan Fernández Archipelago (33°S, 78°W), Chile.

Datos merísticos de *Odontesthes gracilis*. Merísticos (min-max/DEst): TV, vértebras totales; PCV, vértebras precaudales; CV, vértebras caudales; Anal, rayos de aleta anal; D1, rayos de primera aleta dorsal; D2, rayos de segunda aleta dorsal; GRU, branquispinas de rama superior; GRL, branquispinas de rama inferior; GRT, branquispinas totales; SL, longitud estándar en mm; N, número de individuos. Localidad 12: isla Robinson Crusoe, archipiélago de Juan Fernández (33°S, 78°W), Chile.

Locality	TV	PCV	CV	Anal	D1	D2	GRU	GRL	GRT	SL(mm)	N
12	50-52: 51 0.75	24-26: 24 0.75	26-27: 26 0.47	17-18:18 0.37	5-7: 6 0.69	11-12:12 0.47	7-8: 7.5 0.5	25-28: 27 0.94	32-36: 34 1.21	62-109	6
				Maximum variation per locality							
	3	3	2	2	3	2	2	4	5		

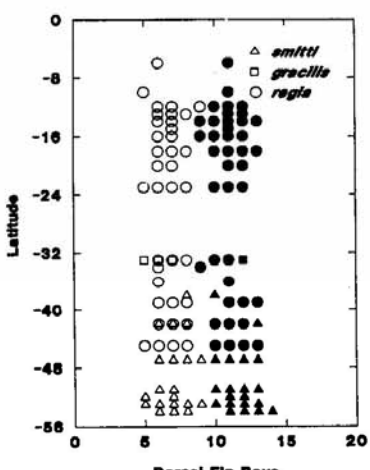

Figure 14

Variation in the number of dorsal-fin rays with latitude South. First dorsal fin in open symbols and second dorsal fin in closed symbols.

Variación en el número de rayos de las aletas dorsales con latitud Sur. Primera aleta dorsal en símbolos abiertos y segunda aleta dorsal en símbolos rellenos.

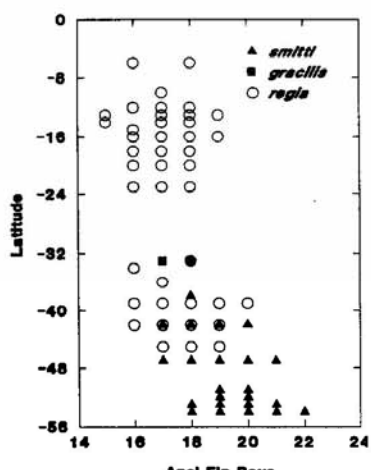

Figure 15

Variation in the number of anal-fin rays with latitude South. Each symbol represents at least one individual.

Variación en el número de rayos anales con latitud Sur. Cada símbolo representa a lo menos un individuo.

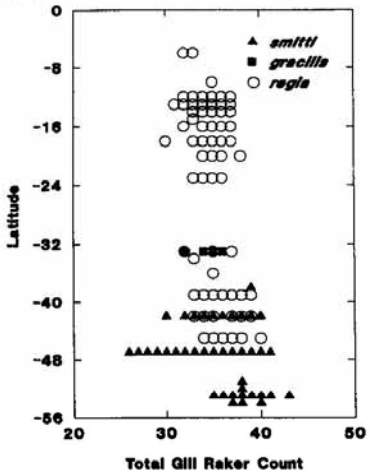

Figure 16

Variation in the total number of gill-rakers of the first branchial arch with latitude South. Each symbol represents at least one individual.

Variación en el número total de branquispinas del primer arco branquial con latitud Sur. Cada símbolo representa a lo menos un individuo

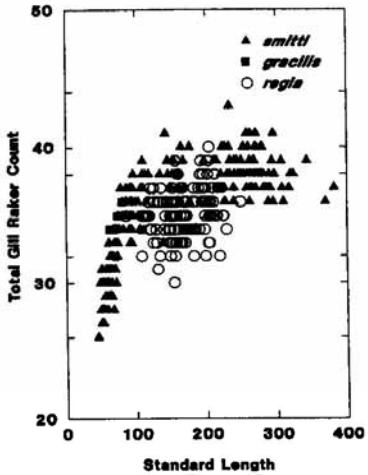

Figure 17

Variation in the total number of gill-rakers of the first branchial arch plotted against standard length. Each symbol represents at least one individual.

Variación en el número total de branquispinas del primer arco branquial con longitud estándar. Cada símbolo representa a lo menos un individuo.

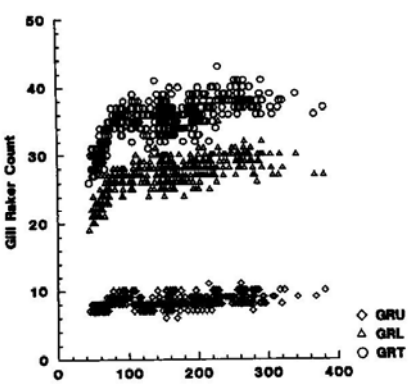

Figure 18

Variation in the total number of gill rakers (GRT), gill rakers of the lower branch (GRL) and upper branch (GRU), of the first branchial arch plotted against standard length. Each symbol represents at least one individual.

Variación en el número total de branquispinas (GRT), branquispinas de la rama inferior (GRL) y branquispinas de la rama superior (GRU) del primer arco branquial, versus longitud estándar. Cada símbolo representa a lo menos un individuo.

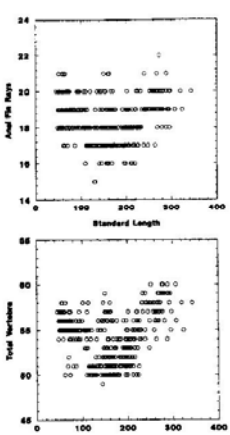

Figure 19

Variation in numbers of anal-fin rays and total vertebrae plotted against standard length. Each circle represents at least one individual.

Variación en número de rayos anales y total de vértebras versus longitud estándar. Cada círculo representa a lo menos un ejemplar.

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Appendix 1: *Material examined.*

Institutional abbreviations follow Leviton *et al.* (1985) except for CENPAT (Centro Nacional Patagónico, Puerto Madryn, Argentina), NRM (Swedish Museum of Natural History), and SOSC (Smithsonian Institution Oceanographic Sorting Center). In parenthesis, cleared and stained, or stained and dissected,. Uncatalogued material is abbreviated as 'uncat'. Specimen lots are listed alphabetically by institution. The number of specimens studied are in brackets. Left of the comma are the number cleared-and-stained specimens in parenthesis, and to the right of the comma the number of X-rayed specimens. Brief locality information is followed by province or state and country Outgroup taxa examined are listed in Dyer (1997).

Odontesthes

O. (Austromenidia) smitti

BMNH 1936.5.18:15[1], Stanley Harbour, Falklands; CENPAT 23[64], Pto. Madryn, Chubut, Argentina; CENPAT 28 [116], Pto. Deseado, Santa Cruz, Argentina; LACM uncat[2], Tierra del Fuego; MNHN A.2895[4], MNHN 3096[1], 'Port Jackson, Australia'; MNHN 1975-16[1], Straits of Magellan, Chile; MCZ 18133[3], MCZ 18134[10], MCZ 18135[5], MCZ 18136[1], MCZ 18137[11], Punta Arenas, Chile; NRM 11128[3], Pto. Gallegos, Santa Cruz, Argentina; NRM 11131[2], Seno Última Esperanza, Magallanes, Chile; NRM 11133[1], Pto. Madryn, Chubut, Argentina; UMMZ 75497[1], Necochea, Buenos Aires, Argentina; UMMZ 218448[(1),10], Punta Arenas, Chile; UMMZ 218980[(3)], UMMZ 218981[22], UMMZ 219994[6], Camilla Creek Estuary, Falkland or Malvinas; UMMZ 218459[4], Pto. Madryn, Chubut, Argentina; UMMZ 218797[1], Straits of Magellan, Tierra del Fuego, Chile; USNM 88716[2], USNM 88719[1], Port Stanley, Falklands or Malvinas; USNM 256719[15], Punta Arenas, Chile; USNM 305673[6], Dawson Island, Straits of Magellan, Chile; ZMH 7592[1], ZMH 7593, ZMH 7594[3], Punta Arenas, Chile.

O. (Austromenidia) gracilis

MCZ 90008[20], Juan Fernández Islands, Chile; NRM 10970[120], Robinson Crusoe Island, Juan Fernández Islands, Chile; UMMZ 215529[6], Cumberland Bay, Robinson Crusoe Island, Juan Fernández Islands, Chile; UMMZ 215529[(1),6], Cumberland Bay, Robinson Crusoe Island, Juan Fernández Islands, Chile; USNM 280280[43], Cumberland and Padre bays, Robinson Crusoe Island, Juan Fernández Islands, Chile.

O. (Austromenidia) regia

BMNH 1900.9.29.185[1], Perú; CAS 45176[3], Antofagasta, Chile; CAS 45380[8], mixed Valparaíso and Valdivia, Chile; CAS-SU 6069[1], Callao Bay, Lima, Perú; CAS-SU 6070[1], CAS-SU 6071[1], CAS-SU 6072[3], CAS-SU 6073(,1), Callao Bay, Lima, Perú; CAS-SU 37431[(1),9], Chincha Islands, Pisco, Perú ; LACM uncat[,20], LACM uncat[,5], LACM 44142-1, Valparaiso Harbor, Valparaíso, Chile; MCZ 18126[9], Paracas Bay, Pisco, Perú; MCZ 18142[2], Chile; MCZ 18187[4], Perú; SOSC LWK66-23[1], Navidad, Chile; SOSC LWK66-73[3], Iquique, Chile; SOSC LWK66-76[1], Punta Lomas, Arequipa, Perú; SOSC LWK66-83[12], opp. mouth Río Ica, Ica, Perú; SOSC LWK66-[1], Independencia Bay, Pisco, Perú; SOSC LWK66-97[2], Lobos de Afuera Island, Lambayeque, Perú; SOSC #300[1], Montemar, Valparaíso, Chile; UMMZ 215522[(5),9], Quintero Bay, Valparaíso, Chile; UMMZ 215521[(1),11], Valdivia market, Valdivia, Chile; UMMZ 215523[(3),10], Limarí River mouth, Limarí, Chile; UMMZ 215524[4], Maule River, Talca, Chile; UMMZ 215525[15], Arica, Chile; UMMZ 215526[(1),22], Quilca, Camaná, Perú; UMMZ 215527[2], Callao Bay, Lima, Perú; UMMZ 215528[1], UMMZ 215530[(1),3], Valparaíso, Chile; UMMZ 218453[10], Quitralco, Aysén, Chile; UMMZ 218455[(1),11], UMMZ 218456[2], Castro, Chiloé, Chile; UMMZ 218607[14], Puerto Chacabuco, Aysén, Chile, UMMZ 220600, Mejillones, Antofagasta, Chile; UMMZ 220601, Tocopilla, Antofagasta, Chile; USNM 77633[4], Paracas Bay, Pisco, Perú; USNM 77644[1], Callao Bay, Lima, Perú; USNM 128536[2], off Paita, Piura, Perú; USNM 176552[13], Quellón, Chiloé, Chile; ZMH 7595[1], Pto. Supe, Chancay, Perú; ZMH 7596[1], ZMH 7597[2], Callao, Lima, Perú; ZMH 7598[1], Talcahuano, Concepción, Chile; ZMH 7599[2], Arica, Chile; ZMH 7600[3], ZMH 7601[2], Iquique, Chile; ZMH 7602[2], Antofagasta, Chile; ZMH 7603[1], ZMH 7604[1], ZMH 7605[1], Corral, Valdivia, Chile.

Appendix 2: *Summary list of characters.*

The following list corresponds to the coding of characters mentioned in the text only. For a complete description of the characters and their polarization see Dyer (1997). Characters are grouped into traditional anatomical units and ordered within these groups from anterior to posterior and dorsal to ventral. The characters are sequentially numbered reflecting their anatomical position and that in the data matrix (Dyer 1997). The citations that follow some of the character headings indicate the original source or pertinent discussion for that character. The description of character states are as coded in the data matrix, as well as the consistency and retention (CI, RI) indices for that character. When both indices are identical only one figure is shown. Two sets of indices reflect the different values in each most parsimonious tree. Multistate characters are indicated as additive (add) or non-additive (n-add) according to their treatment in the phylogenetic analysis.

Neurocranium and associated sensory canal bones

1. *Number of vomerine tooth patches.* Vomerine teeth in atherinomorph outgroups are in a single U or V-shaped band along the anteroventral border of the bone. A derived condition is found in sorgentinins in which the vomerine teeth are present in a single median tooth patch or in three separate patches. Three separate patches, a median tooth patch and two patches under each lateral condyle, are found in *Odontesthes perugiae* (Dyer 1997: fig. 7), *O. argentinensis*, *O. platensis*, *O. smitti*, and *O. regia* . (0=vomerine teeth in a band; 1=single median vomerine tooth patch: 2=three vomerine tooth patches;

0.50, 0.60; add).

14. Lacrimal condyle shape. The plesiomorphic condition of the lateral ethmoid is to be articulated with the lacrimal along the lateral ridge and cartilaginous condyle of the preorbital wing. The ventral half of the lateral ridge is formed by a roughly oval cartilaginous condyle (Dyer 1993). A derived condition found in *O. smitti*, *O. regia*, and *O. gracilis* is for the lacrimal condyle to be distinctly enlarged and rounded (Fig. 3). (0=lacrimal condyle of lateral ethmoid oval in shape; 1=lacrimal condyle of lateral ethmoid enlarged and rounded in shape; 1.00)

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 in atherinopsines (Fig. 7A) except for *Basilichthys*. Another derived condition is found in *O. humensis*, *O. retropinnis*, *O. incisa*, *O. smitti*, *O. regia*, and *O. gracilis* in which the postocular shelf extends the entire length of the dermosphenotic (Fig. 7B). (0=medial flange narrow; 1=postocular shelf on dorsal half of dermosphenotic; 2=postocular shelf along entire length of dermosphenotic; 0.40, 0.63; add)

27 Parasphenoid ventral ridge. The parasphenoid has a laminar ridge along its ventral midline to which the adductor arcus palatini muscle is attached. In atherinopsines, the ventral ridge is mostly anterior to the dorsal processes of the parasphenoid, tapering anteriorly no further than the posteroventral end of the interorbital cartilage. A derived condition within *Odontesthes* is for the anterior end of the ventral ridge to be shorter, rounded, and clearly delineated as in *O. brevianalis*, *O. regia*, and *O. gracilis* (Fig. 6A), rather than extended anteriorly as in other species of *Odontesthes* (Fig. 6B). (0=anterior end of parasphenoid ventral ridge, smoothly tapered; 1=anterior end of parasphenoid ventral ridge, rounded; 0.50)

Jaws, suspensorium and associated ligaments.

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. Adult sorgentinins have three rows of teeth except for the *Basilichthys semotilus* species group and *Odontesthes hatcheri* that have more than three rows, and *O. perugiae*, *O. retropinnis*, *O. smitti*, *O. regia*, and *O. gracilis* that have two rows of teeth. An autapomorphic condition of *O. gracilis* is to have two rows of small teeth. (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)

59. Endopterygoid tooth patch. The presence of teeth on the ventrolateral surface of the endopterygoid is considered plesiomorphic in atheriniforms, though absent in Cyprinodontea. Size and position of tooth patches, however, is variable. In atherinopsines, teeth are present either as well developed or reduced tooth patches. Tooth patches are consistently absent in *Basilichthys*, *O. brevianalis*, *O. hatcheri*, and *O. humensis*. Large tooth patches are present in *O. regia*. (0=endopterygoid teeth present; 1=endopterygoid teeth absent; 0.20, 0.43)

60. Hyomandibular nerve. (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 [see Dyer 1997]; 0.40, 0.67; n-add)

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. 8A). 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*, *O. smitti*, *O. regia*, and *O. gracilis*, is a rounded dorsal process of the opercle lacking a lateral laminar flange (Fig. 8 B,C). (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. 8A). 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*. Fenestration is present on both medial and external faces of the opercle in *O. humensis*, *O. bonariensis*, *O. argentinensis*, *O. platensis*, *O. nigricans*, *O. smitti*, *O. gracilis*, and *O. regia* (Fig. 8 B,C). (0=no opercular fenestra; 1=opercular fenestra present on medial face; 2=opercular fenestra present on medial and external faces; 0.33, 0.78; add) *Odontesthes smitti* has the most developed opercular fenestration (Fig. 8C, García 1987), more so than *O. nigricans*..

68. Opercular posterodorsal border. The posterodorsal border of the opercle is concave in atherinomorph outgroups, menidiines (Fig. 8A), and *Basilichthys*. A straight posterodorsal border is a derived condition present in *Odontesthes bonariensis*, *O. argentinensis*, *O. platensis*, *O. nigricans*, *O. incisa*, *O. brevianalis*, *O. smitti*, *O. regia*, and *O. gracilis* (Fig. 8 B,C). (0=opercle posterodorsal border concave; 1=opercle posterodorsal border straight; 2=opercle posterodorsal border convex; 0.67, 0.77; add).

69. Opercular posteroventral border. The posteroventral border of the opercle is convex in atherinopsid outgroups (Fig. 8A). A derived condition present in *O. argentinensis*, *O. platensis*, *O. nigricans*, *O. incisa*, subgenus *Cauque*, *O. smitti*, *O. regia*, and *O. gracilis* is a concave or slightly concave posteroventral border (Fig. 8 B,C). (0=opercle posteroventral border convex; 1=opercle posteroventral border concave; 1.00).

Branchial basket

74. Urohyal ventral plate. (0=urohyal ventral plate present; 1=urohyal ventral plate absent [see Dyer 1997]; 0.50, 0.00)

The plesiomorphic condition of the ventral border of the urohyal is it widened in an oval-shaped plate (Fig. 10A). A derived condition found only in *Odontesthes smitti* is the ventral plate reduced, folded medially, and more elongate (Fig. 10B).

Pectoral girdle

79. *Ventral postcleithrum position.* (0=ventral postcleithrum anterior to pleural rib one [see Dyer & Chernoff 1996]; 1=ventral postcleithrum between pleural ribs one and two [see Dyer 1997]; 2=ventral postcleithrum between pleural ribs one and three; ?= polymorphic; 0.67, 0.91; add).

The position of the ventral postcleithrum in *O. brevianalis* and *O. gracilis* is variable in that it is placed between pleural ribs one and two or onaçe and three, and is coded as polymorphic in the data matrix (Dyer 1997).

Median fins

82. *Position of first dorsal fin.* (0=first dorsal fin well in advance of anus; 1=first dorsal-fin origin over or posterior to anus; 0.38).

85. *Number of interdorsal pterygiophores.* (0=six or fewer interdorsals; 1=more than six interdorsals; ?=polymorphic; 0.25, 0.63 / 0.20, 0.50).

Axial skeleton

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 vertebra three through 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 (Dyer 1997). Presence of two or more pleural-rib tips posterior to the dorsal tip of the first anal-fin pterygiophore is a derived feature of melanotaeniids (Dyer & Chernoff 1996) and atherinopsids except for *Membras*, *Melanorhinus*, *Odontesthes platensis*, *O. nigricans*, *O. incisa*, *O. smitti*, *O. regia*, and *O. gracilis* (Fig. 4). (0=pleural ribs anterior to dorsal tip of first anal-fin pterygiophore; 1=presence of two or more pleural ribs posterior to dorsal tip of first anal-fin pterygiophore; 0.50, 0.89).

91. *Haemal-arch funnel and expansions* (White 1985). The haemal arches in atheriniforms and outgroups have no expansions or modifications, except in *Atherina* and *Atherinason* (Schultz 1948). 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 (Dyer 1997: figs. 35-38). 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; sorgentinins except for the four species mentioned above, have flaring expansions of the haemal arches; *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; and *O. smitti*, *O. regia*, *O. gracilis* have anterior and posterior projections restricted to the base of the haemal arches in the posterior region of the haemal funnel (Fig. 4). The flaring of the haemal arches is most developed anteriorly except for the most anterior one (Fig. 4). (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; 0.40, 0.81; add).

92. *Posterior extension of the haemal-arch funnel.* In most species of sorgentinines, the haemal-arch funnel is extended posteriorly to the vertebra above the last anal-fin ray or beyond (Dyer 1997). A condition considered as derived is the posterior extension of the haemal-arch funnel only to a vertebra above mid-anal fin. This derived condition is found only in *Odontesthes platensis*, *O. smitti*, *O. gracilis*, and *O. brevianalis*. (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.* The condition considered plesiomorphic is for the haemal-arch funnel floor to be gradually tapered posteriorly, i.e., the floor of the funnel is slightly bulged ventrally (Dyer 1997). A condition regarded as derived is the abrupt tapering of the haemal funnel over anal pterygiophores one to three, forming a dorsal bulge of the funnel floor (Fig. 4). This derived condition is found in *Odontesthes argentinensis*, *O. platensis*, *O. brevianalis*, *O. smitti*, *O. regia*, and *O. gracilis*. (0=haemal-arch funnel floor gradually tapering posteriorly, bulged ventrally; 1=haemal-arch funnel floor abruptly tapering posteriorly, bulged dorsally; 1.0)

94. *Haemal-spine length.* (0=anterior haemal spines long; 1=anterior haemal spines short; 0.50, 0.75)

95. *Position of first caudal vertebrae.* (0=first caudal vertebrae anterior to anal-fin origin; 1=first caudal vertebrae over anterior half of anal fin; 2=first caudal vertebrae over posterior half of anal fin; ?=polymorphic; 0.50, 0.80; add)

Scales

97. *Number of suborbital scale rows.*- Three rows of scales below the middle of the orbit in adult specimens is considered the plesiomorphic condition in atheriniforms. In atherinopsines, this condition is found in Atherinopsini except *Atherinops*, in *Odontesthes hatcheri*, *O. humensis*, *O. bonariensis*, *O. incisa*, and *O. gracilis*. Four suborbital scale rows are found in *Basilichthys*, *Odontesthes argentinensis*, *O. platensis*, *O. nigricans*, *O. regia*, *O. smitti* and *O. brevianalis* (Dyer 1997: fig. 23 B,C). (0=three suborbital scale rows; 1=four suborbital scale rows; 2=two suborbital scale rows; 0.29, 0.58; n-add)

99. *Cleithrum scales.* No scales on the lateral shaft of the cleithrum is a plesiomorphic feature of atheriniforms. A

derived condition is the presence of large scales along the entire length of the cleithral lateral shaft (Dyer 1997: fig. 40A). This condition is present in atherinopsinins except for *Atherinops*, and in *Odontesthes* species except *O. humensis*, *O. bonariensis*, *O. retropinnis*, and *O. perugiae*. A derived condition is present in *Odontesthes nigricans*, *O. brevianalis*, *O. smitti*, *O. regia*, and *O. gracilis* in which smaller scales overlap the posterior border along the entire length of the cleithral lateral shaft (Dyer 1997: fig. 40B). (0=no scales on cleithrum shaft; 1=scales present along cleithrum shaft; 2=small scales only present along cleithrum shaft; 0.29, 0.67; add)

100. Scales on second dorsal fin. (0=no scales between rays on second dorsal fin; 1=scales present between anterior rays of second dorsal fin; 0.20, 0.43)

101. Scales on anal fin. (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 of atheriniformes. Small scales are the derived condition and in sorgentinins they are found in *Basilichthys*, *Odontesthes hatcheri*, *O. nigricans*, *O. platensis*, *O. brevianalis*, *O. smitti*, *O. regia* and *O. gracilis*. (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).