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 Atherinopsis in having upper jaw protrusion. Austromenidia was first placed as a junior synonym of Odontesthes by de Buen and later by White in the true phylogenetic context of the Atherinidae. A phylogenetic study of South American silversides demonstrated the genus Odontesthes as a well diagnosed monophyletic group, and recognized two subgenera: Caupo and Austromenidia. The subgenus Austromenidia is diagnosed by five characters which are unique within Atherinopsideae: an enlarged and rounded lateral musculature of the lateral line, and lateral-arch expansions of the neural fin with ante-mortem projections. Though O. plana is of the same size as the subgenus, other species such as O. regia and O. australis are potential alternatives as indicated in the resulting classification. The subgenus Austromenidia is composed of the marine species O. regia (Bolivian), O. armata (Somali), and O. plana (Perú, Chile), and is distributed along the southwestern coasts of the Argentine Peninsula from Mui de Pata (km 38.3) to southern Tierra del Fuego, Patagonia, and Malvinas Islands, and intrudes into the southeastern Pacific through the Strait of Magellan extending north to Punta Norte (33°S), Chile. Odontesthes regia is diagnosed by the posterior extension of the lateral-arch finned to the posterior end of the anal fin, and is distributed along the southeastern Pacific shores of Peru and Chile, from Pata (km 36.1) to the Archipelago de Las Canarias, Aysén (km 48.4). Odontesthes armata is diagnosed by relatively small teeth, three subadult rows of scales, no commissure teeth, and a maximum recorded size of 120 mm SL. It is an endemic species of the Juan Fernández Archipelago (km 37.3, 79°W), off Chile. Because of the great intraspecific range of distribution of O. regia and O. australis, 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 larvae nape increase with latitude, following, however's rule, all scales of the lower branch increase in number rapidly with age. Whereas adult fins may increase only slightly with latitude, dorsal-fin ray numbers may not.

Key words: Austromenidia, silverside fishes.

Resumen - Austromenidia fue creada por Hubbs para agrupar a especies que se distinguen de Odontesthes por tener escamas pequeñas y la primera aleta dorsal muy adelantada de la cola, y de Atherinopsis en tener prominencia del maxilar superior. Austromenidia fue puesto en la sinonima de Odontesthes por de Buen y luego por White en el contexto filogenético de la familia Atherinidae. Dyer realizó un estudio filogenético de las pejerreyes sudamericanas, combiniendo al género Odontesthes con un grupo monofilético reconocido como el subgénero Caupo y Austromenidia. El subgénero Austromenidia es diagnosticado por cinco caracteres que son únicos dentro de los pejerreyes sudamericanos: una musculatura lateral ampliada y redondeada, y expansiones alares laterales de la aleta del pez con proyecciones ante-mortem. Aunque O. plana es del mismo tamaño que el subgénero, otras especies como O. regia y O. australis son alternativas como indicado en la clasificación resultante. El subgénero Austromenidia está compuesto de las especies marinas O. regia (Bolivian), O. armata (Somali), y O. plana (Perú, Chile), y se distribuye a lo largo de las costas sureñas de la Argentina desde el Cabo de Pata (km 38.3) hasta el sur de Tierra del Fuego, Patagonia, y Islas Malvinas, e intrusión hacia el océano Pacífico al sur de la línea de demarcación del extremo norte de Punta Norte (33°S), Chile. Odontesthes regia se diagnostica por la extensión posterior de la aleta alar hasta el final de la aleta dorsal, y se distribuye a lo largo de las costas sureñas del océano Pacífico en Perú y Chile, desde Pata (km 36.1) hasta el Archipiélago de Las Canarias, Aysén (km 48.4). Odontesthes armata se diagnostica por dientes relativamente pequeños, tres filas de escamas subadultas, sin dientes de comisura, y un tamaño máximo registrado de 120 mm LSL. Es una especie endémica del Archipiélago de Las Canarias, Aysén (km 48.4). Dyer realizó un estudio de variación merística de Odontesthes regia y O. australis. Debido a la gran variación intraspecífica de distribución de O. regia y O. australis, se presentó un estudio de variación merística. Debido a la amplia superposición de rango de variación de estas características son inapropiadas como claves diagnósticas, pero ciertamente útiles como características descriptivas. Mientras que los escamas del costado aumentan con latitud, siguiendo, sin embargo, el regla de las escamas, todos los escamas del ramo inferior aumentan rápidamente en número con la edad. Mientras que los aletas pueden aumentar sólo ligeramente con latitud, los dientes de la aleta dorsal pueden aumentar en número en número.
diagnosticada por una reducida placa ventral del urobel. Se encuentra distribuida por la costa argentina del Atlántico suroccidental, desde Mar del Plata (aprox. 39ºS) hasta el canal de Beagle en Tierra del Fuego, en las islas Malvinas, y adentrándose al Pacífico noreste por el estrecho de Magallanes hasta el Seno de Última Esperanza, Puerto Natales (21ºS), Chile. Odontesthes regina está diagnosticada por la extensión posterior del embudo balenal que se extiende hasta el extremo posterior de la aleta anal. Se encuentra distribuida por la costa del Pacifico suroriental de Perú y Chile, desde Pisco (3ºS) hasta el archipiélago de Los Chonos, Aysén (46ºS). Odontesthes gracilis está diagnosticada por dientes relativamente pequeños, tres corrientes de escamas suborbitales, ausencia de dientes vómeros, y un tamaño máximo de 130 mm de longitud estándar. Es una especie endémica del archipiélago de Juan Fernández (aprox. 35ºS, 79ºW), Chile. Debido al gran espectro latitudinal de distribución de las especies O. regina y O. smithi, se presenta un estudio de la variabilidad morfométrica registrada. Debido a la amplia subspeccion 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 branquias de la nariz 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 Bassischichys 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), Matsu (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 monotypic group, including Austromenidia as a junior synonym. In his hypothesis, Odontesthes is the sister group of Bassischichys (White 1985) and both constitute the tribe Sargentiniini (White 1989). Odontesthes is the most diverse atherinopsine genus, composed of between 17 and 22 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 Cuvace Eirignanae and Austromenidia were recognized as subgenera, and the latter composed of three species: O. regina Humboldt, O. gracilis Steinacher, and O. smithi Lahille.

In a revision of the marine pejerreyes of Argentina, García (1987) discussed the striking similarity between the Pacific species O. regina and the Atlantic species O. smithi 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 “Urania” at the Falkland or Malvinas Islands. Whitley (1943-137) argued convincingly that this species is a South American atherinopsine, possibly close to O. latilitoria (=O. regina) according to C.L. Hubbs, rather than an Old World atherine. Schulte (1948) also discussed the issue of Atherina 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 nomenclatural problem because it predates all atherinopsine names, but it has never been used to describe a sargentine.

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, Harlow 1961, Fowler 1970, Chernoff 1982, Lindsey 1988, Blaxter 1992). The number of species described from different latitudes along the coasts of Chile and Peru (O. affinis, O. latilitoria, and O. regina), and Argentina (O. smithi, O. smithi var. australis, and O. madranyensis) 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
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 *Bastichthys* by various authors (Fowler 1945, 1951, Mann 1954, de Buen 1955, Seqvalveda & Pequeño 1985), and properly placed by Campos (1984) in *Astromenidia* 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 (Ringuetti & Azambuja 1960, López 1964, Menini *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* Quay & Gaimard, 1822, 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 (1944) 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 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 preaxial vertebrae (PCV) as having a neural 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 (Backups 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.

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 supraorbital 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 Schultze (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 05), 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 tentatively supported and could change with only an additional character or two. This is indicated in the classification (Table 1) by sects mutabilis. An alternative hypothesis of relationships within Node 05 of Figure 5 that is one step longer, places O. inscula 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 paraphroenoid ventral ridge (Fig. 6; Ch. 27).

Systematics
Subfamily Atherinopsinae Fowler, 1903
Tribe Serrugentini Piasta de Risso & Risso, 1953
Genus Odontesthes Evermann & Kendall, 1906
Subgenus Austromenidia Hubbs, 1918
Type Species= Basilichthys regilus Abbott, 1899
Table 1
Sequenced classification of Sargentinini, Atherinopsinae. Order of genera or species is chronological unless noted by an asterisk
(∗= included taxa are phylogenetically sequenced)

<table>
<thead>
<tr>
<th>Genus</th>
<th>Species group</th>
<th>Description</th>
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<td>Order Atheriniformes Raney, 1964</td>
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<td>Sargentinini</td>
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<td>Subfamily Atherinopsinae Fowler, 1903</td>
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<td></td>
<td>Subfamily Atherinopsinae Fowler, 1903</td>
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<td>Tribe Sargentini</td>
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<td></td>
<td>Genus Basilichthys Girard, 1854</td>
<td>micropliodae species group</td>
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<td></td>
<td></td>
<td>†B. micropigidio (Jenys, 1842)</td>
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<td></td>
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<td>†B. australis Eigenmann, 1927</td>
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<td></td>
<td></td>
<td>xenotilus species group</td>
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<td></td>
<td></td>
<td>†B. xenotilus (Cope, 1876)</td>
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<td></td>
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<td>perigaeae-retroplontis species group</td>
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<td>†O. perigaeae Evermann &amp; Kendall, 1906</td>
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<td></td>
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<td>†O. orientalis de Bon, 1950</td>
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<td></td>
<td></td>
<td>†O. micrantha Benavides, 1995</td>
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<td>†O. bonanaeorum (Valenciennes, 1835)</td>
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<td>Subgenus Caeruleus Eigenmann, 1927 seda mutabilis</td>
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<td></td>
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<td>†O. brasiensis (Gardner, 1886)</td>
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<td></td>
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<td>†O. maculatum (Steindachner, 1890)</td>
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<td>†O. pictus (St Nehoff, 1859) seda mutabilis</td>
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<td></td>
<td>Subgenus Austromenidia Hubbs, 1938 seda mutabilis</td>
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<tr>
<td></td>
<td></td>
<td>†O. smithi (Lahille, 1929)</td>
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<td></td>
<td></td>
<td>†O. regina (Randall, 1921)</td>
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<td></td>
<td></td>
<td>†O. gracilis (Steindachner, 1896)</td>
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<td>Superorder Cypriodontomorpha Dyer &amp; Chenoff</td>
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Diagnosis: Species of Odontesthes with an enlarged lacrimal endolyte of the lateral ethmoid (Fig. 3; Ch. 14), postocular shelf along entire length of dermopalatine (Fig. 7; Ch. 23), two rows of teeth on jaws (Ch. 50), ophthalmic 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 diagnostic features: Species of Odontesthes with an endopterygoid tooth patch (Ch. 59), hyomandibular nerve divided inside of hyomandibula (Dyer 1997: Ch. 60), opercular posterooral border straight (Fig. 8; Ch. 68) and posteroventral border concave (Fig. 8; Ch. 69), ventral postcleithrum between pleural rib 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. 83), first pleural rib long (Ch. 87), posterior pleural rib anterior to first anal-fin pterypyalophore (Fig. 4; Ch. 88), haemal-funnel floor bulged dorsally (Fig. 4; Ch. 93), anterior haemal spine 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 - 32; pectoral-fin tip anterior of pelvic-fin origin, and lateral band wide.

Distribution: Marine, with juveniles sometimes found in estuaries; from the Tijuca del Fuego to Piura, Peru - 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).

Odonotesthes smithi (Lahille 1929a)
Basilichthys smithi Lahille, 1929a: 84 (types missing).
Type locality: "Fin de Barrantes", Golfo San Matías, SE Atlantic, Argentina.
†Atherina jacksoniana Quoy & Gaimard, 1825: 333 (Syntypes MNHN-P A.2895, MNHN-P 3060). Type locality: unknown (original label, Port Jackson, NSW, Australia).
†Menidia patagoniensis Eigenmann, 1909: 280 (types missing). Type locality: Straits of Magellan (Tres de Añuas), Chile.
Basilichthys madreymensis Lahille, 1929b: 326 (types missing). Type locality: Puerto Madryn, Golfo Nuevo, Chubut, Argentina.
Basilichthys smithi var. australis Lahille, 1929a: 84 (types missing). Type locality: Rio Gallegos, Argentina, and Puerto Natales, Chile.

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

Additional diagnostic features: Species of subgenus Austromenidia with three vomerine tooth patches (Dyer 1997: fig. 7; Ch. 8), paraphenodal ventral ridge tapered anteriorly (Fig. 6b; Ch. 27), opercular fenestration covering an enlarged surface area of the opercle (Fig. 4; 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 regis (UMMZ 215521).
Vista lateral de las aletas impares y esqueleto axial de Odontesthes regis (UMMZ 215521).
Alternative hypotheses of relationships among taxa of Node OS; A, Subgenus Caque is sister to the other members of Node OS (L=403); B, Odontesthes incisa is sister to the other members of Node OS (L=404). O. platensis is sister to subgenus Astromenida, to the Cauque clade, or sister to Cauque, O. nigricans, and Astromenidae.

Hypótesis alternativas de relaciones entre taxa del Node OS; A, el subgénero Cauque es hermana de los otros miembros del Node OS (L=403); B, la especie Odontesthes incisa es hermana de los otros miembros del Node OS (L=404). La especie O. platensis es hermana del subgénero Astromenidae, del clado Cauque - O. nigricans, o hermana de Cauque, O. nigricans, y Astromenidae.

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.

Distribución: Inshore marine of southwestern Atlantic along the coast of Argentina from Mar del Plata (38°S, 57°23’W) to the Beagle Channel in southern Tierra del 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).

Comentarios: Lack of collections between Puerto Natales (ab. 53°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. smithi in the Pacific, or both. Odontesthes regia and O. smithi could either allopatric or sympatric in this region. Verbal accounts on the presence of unidentified "pajicurrés" in Puerto Eden (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 Elias et al. (1984) and Gostonyi 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 (Elias 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).
Additional descriptive features: Species of *Austromenidia* with three vomerine tooth patches (Dyer 1997: fig 7; Ch. 8), parapophyseal ventral ridge rounded anteriorly (Fig. 6A; Ch. 27), endopodites with enlarged tooth patch (Ch. 29), 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, 30-56; 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 Peru, to the Archipelago of Los Chinos or Guatapacays, Aysén (ab. 48°S), XI Region, southern Chile (Fig. 9). Juveniles are sometimes found in estuaries.


*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 parapophyseal 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, 14-12; anal-fin rays, 17-18; total number of vertebrae, 56-52; precaudal vertebrae, 24-28; caudal vertebrae, 26-27; total number of gill rakers, 32-46; gill rakers of upper branch, 7-8; gill rakers of lower branch, 24-28.

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 labrace (UMMZ 193463); B, Odontesthes regia (UMMZ 215521); C, O. smithi (UMMZ 218448).

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

Vistas lateral y ventral del urohial; A, Odontesthes regia (UMMZ 215521); B, O. smithi (UMMZ 218448).
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 2: 23-27). *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. 12). 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: 15-16), 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
Phylogenetic systematics of *Austrorhadinus*.

locally, 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, Sikes 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.

**Figure 12**
Variation in the number of precaudal vertebrae (PCV) with latitude South. Each circle represents at least one individual.

**Figure 13**
Variation in the number of caudal vertebrae (CV) with latitude South. Each circle represents at least one individual.
Table 2

<table>
<thead>
<tr>
<th>Locality</th>
<th>TV</th>
<th>PCV</th>
<th>CV</th>
<th>Anal</th>
<th>D1</th>
<th>D2</th>
<th>GRU</th>
<th>GRT</th>
<th>SL (mm)</th>
<th>N</th>
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</thead>
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**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 basiarcus funnel. The subgenus *Austromenidia* is composed of three marine species: *Odontesthes smittii*, *O. regia*, and *O. gracilis*. *Odontesthes smittii* 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 the southwestern reaches of the Strait of Magellan. *Odontesthes regia* is the sister species to the eastern Pacific *O. regia* - *O. gracilis* clade. *Odontesthes regia* is diagnosed by the basal funnel extended posteriorly to the middle of the anal fin, and distributed along the Pacific coast from northern Peru (ab. 5°S) to southern Chile (ab. 48°S). *Odontesthes gracilis* is diagnosed by the lack of vomerine teeth and relatively small jaw teeth, and is endemic to the Juan Fernandez 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 smittii* 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. smittii*. The range of variation of vertebral and Gill raker means in *O. smittii* 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 meristic in this study.
## Table 3

Meristics of *Odontesthes rega* by locality. Meristics (min-max-xavg/SD): TV, total vertebrae; PCV, precaudal vertebrae; CV, caudal vertebrae; Anal, anal-fin rays; DI, 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 1–7, from Chile 8–18. 1, Lobos Alca Island, Lima; 2, Chacabuco, Aysén; 18, Quirschlo, Aysén.

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<th>Locality</th>
<th>TV (mm)</th>
<th>PCV</th>
<th>CV (mm)</th>
<th>Anal</th>
<th>D1</th>
<th>D2</th>
<th>GRU</th>
<th>GRL</th>
<th>GRT</th>
<th>SL (mm)</th>
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<td>51-51</td>
<td>25-25-25</td>
<td>26-26-26</td>
<td>18-18-17</td>
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<td>6-6</td>
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<td>9 (1%)</td>
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<td>11 (1%)</td>
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<td>12 (1%)</td>
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Average (avg) = 50.95, standard deviation (sd) = 1.65.
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.

<table>
<thead>
<tr>
<th>Locality</th>
<th>TV</th>
<th>PCV</th>
<th>CV</th>
<th>Anal</th>
<th>D1</th>
<th>D2</th>
<th>GRU</th>
<th>GRL</th>
<th>GRT</th>
<th>SL(mm)</th>
<th>N</th>
</tr>
</thead>
</table>

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.

Variable 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 anal en 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 brânquias 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 brânquias 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 brânquias (GRT), brânquias de la rama inferior (GRL) y brânquias 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.
Acknowledgements

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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 (Skejbyhaven Institute of Oceanographic Sorting Center). In parenthesis, cleared and stained, or dried and dissected. Uncataloged material is abbreviated as 'unca'. 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. Overgroup taxa examined are listed in Dyer (1997).

O. (Austrometridia) simi

BMNH 1936.5.18.15[1], Stanley Harbour, Falkland; CENPAT 23[64], Po. Madryn, Chubut, Argentina; CENPAT 28 [116], Po. Destado, Santa Cruz, Argentina, LACM unc[2], Tierra del Fuego, MNHN A.2895[4], MNHN 306[1], Po. 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 11124[2], Po. Galileu, Santa Cruz, Argentina; NRM 11131[2], Seno Última Esperanza, Magallanes, Chile; NRM 11135[1], Po. Madryn, Chubut, Argentina; UMZM 7549[1], Neochen, Buinot Asis, Argentina; UMMZ 218448[10], Punta Arenas, Chile; UMMZ 218990[9], UMMZ 218998[21], UMMZ 219094[6], Camilla Creek, Estancia Falkland or Malvinas; UMMZ 218439[4], Po. Madryn, Chubut, Argentina; UMMZ 218707[1], Straits of Magellan, Tierra del Fuego, Chile; USNM 83716[2], USNM 83719[1], Po. Stanley, Falkland or Malvinas; USNM 250719[5], Punta Arenas, Chile; USNM 305073[0], Dawson Island, Straits of Magellan, Chile; ZMH 75921[1], ZMH 7593, ZMH 7594[3], Punta Arenas, Chile.

O. (Austrometridia) gracilis

MCZ 50000[20], Juan Fernández Islands, Chile; NRM 10970[120], Robinson Crusoe Island, Juan Fernández Islands, Chile; LACM 215529[6], Cumberland Bay, Robinson Crusoe Island, Juan Fernández Islands, Chile; USNM 28024[43], Cumberland and Padres Bay, Robinson Crusoe Island, Juan Fernández Islands, Chile.

O. (Austrometridia) regia

BMNH 1900.9.29.185[1], Perú; CAS 45176[3], Antofagasta, Chile; CAS 45980[8], mixed Valparaiso and Valdivia, Chile; CAS-SL 6006[1], Callao Bay, Lima, Perú; CAS-SU 6070[1], CAS-SU 6072[3], CAS-SU 6073[1], Callao Bay, Lima, Perú; CAS-SU 37431[11], Chorrillos Islands, Pisco, Perú; LACM unc[20], LACM unc[41], LACM 44143[1], Valparaiso Harbor, Valparaiso, Chile; MCZ 18126[9], Paracas Bay, Pisco, Perú; MCZ 18142[2], Perú; MCZ 18187[4], Perú; SOSC LWK66-723[1], Navidad, Chilen; SOSC LWK66-733[1], Iquique, Chile; SOSC LWK66-764[1], Punta Lastras, Arequipa, Perú; SOSC LWK66-82[12], opp. mouth of Baja, Ica, Perú; SOSC LWK66-1[1], Colonia, Chilen; SOSC LWK66-98[11], Lobos Island, Malevique, Perú; SOSC 308[1], Montevideo, Valparaiso, Chile; UMMZ 215522[5], Quinto Bay, Valparaiso, Chile; UMMZ 215523[13], Valdivia monte, Valdivia, Chile; UMMZ 215523[10], Limari River mouth, Limari, Chile; UMMZ 215524[4], Male River, Talca, Chile; UMMZ 215525[5], Arica, Chile; UMMZ 215526[1], Iquique, Chile; UMMZ 215527[12], Quillota, Camarín, Perú; UMMZ 215528[1], Callao, Lima, Perú; UMMZ 215529[1], Iquique, Chile; UMMZ 218453[11], Quimo, Aysén, Chile; UMMZ 218454[2], Coquimbo, Chilen; UMMZ 218456[14], Puerto Chacabuco, Aysén, Chile; UMMZ 220600, Mejillones, Antofagasta, Chile; UMMZ 756001, Temucuipilla Antofagasta, Chile; USNM 776314[1], Paracas Bay, Pisco, Perú; USNM 77564[1], Callao Bay, Lima, Perú; USNM 12853[2], off Piata, Piata, Perú; USNM 17653[13], Quito, Chilen, Perú; ZMH 7595[1], Pisco, Punta, Chilen, Perú; ZMH 7599[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 polarizations see Dyer (1997). Character states 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 coded in the data matrix, as well as the consistivity 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. Multivariate 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 eutherian and metridae are in a single U or V-shaped band along the anterioventral border of the bone. A derived condition is found in sargodontinae 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 conacle, are found in Oedenthes peregrina (Dyer 1959: fig. 7), O. anguernoni, O. platymeri, O. smithi, and O. regia. (Vomeronine teeth in a band: 1 median vomeronine tooth patch; 3 three vomeronine tooth patches;
14. Lacrimal conchyle shape. The pleomorphic condition of the lateral ethmoid is to be articulated with the lacrimal along the lateral ridge and cartilagenous conchyle of the preorbital wing. The ventral half of the lateral ridge is formed by a roughly oval cartilagenous conchyle (Dyer 1993). A derived condition found in *O. smitti*, *O. regia*, and *O. gracilis* is for the lacrimal conchyle to be distinctly enlarged and rounded (Fig. 1). *(=lacrimal conchyle of lateral ethmoid oval in shape; 1= lacrimal conchyle 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 pleomorphic 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. 1A) 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. 1B). *(=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. Parapharynoid ventral ridge. The parapharynoid 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 parapharynoid, 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 shorted, 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). *(= anterior end of parapharynoid ventral ridge, smoothly tapered; 1= anterior end of parapharynoid ventral ridge, rounded; 0.50)*

Jaws, suspensorium and associated ligaments.

50. Tooth rows on oral jaws. Pleomorphic for atheriniforms is presence of more than three rows of teeth on oral jaws as seen in *magilida*, cyprinodontiforms, beloniforms, and atherinids except for netrostahirs which have two rows only. Adult argentissines have three rows of teeth except for the *Basilichthys semiotus* species group and *Odontesthes hitcheri* 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. *(=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; 3= polymorphic: 0.29, 0.58; n= add)*

59. Endopterygoid tooth patch. The presence of teeth on the ventrolateral surface of the endopterygoid is considered pleomorphic in atheriniforms, though absent in *Cyprinodontidae*. 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. hitcheri*, and *O. humensis*. Large tooth patches are present in *O. regia*. *(Endopterygoid teeth present: 1= endopterygoid teeth absent: 0.30, 0.48)*

60. Hyomandibular nerve. *(Only hyomandibular nerve divided external to hyomandibular; 1= hyomandibular nerve divided inside of hyomandibula; 2= dorsal foramen of hyomandibular nerve perforates hyomandibula [see Dyer 1997]: 0.40, 0.67; 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 pleomorphic feature of atheriniforms (Fig. 8A). The dilator opercularis muscle is attached to the medial face of this laminar flange which is extended posteroventrally to the lateral face of the opercle. A derived condition found in *Atheringopis*, *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). *(= opercular dorsal process blade-like; 1= opercular dorsal process not blade-like: 0.25, 0.27)*

65. Opercular fenestration (White, 1985). A smooth surface at the base of the opercular process is a pleomorphic 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. argentissima*, *O. platensis*, *O. nigricans*, *O. smitti*, *O. gracilis*, and *O. regia* (Fig. 8 B, C). *(= 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, Garcia 1987), more so than *O. nigricans*.

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

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

Branchial basket

74. Urohyal ventral plate. *(= urohyal ventral plate present; 1= urohyal ventral plate absent [see Dyer 1997]: 0.36, 0.00)
The pleiomorphic condition of the ventral border of the urohyal is it is widened in an oval-shaped plate (Fig. 10A). A derived condition found only in Odonesthes smithi is the ventral plate reduced, folded medially, and more elongate (Fig. 10B).

Pectoral girdle

77. Ventral postcleithrum position. (0=ventral postcleithrum posterior to pleural rib one; see Dyer & Cherwowitz 1995); 1=ventral postcleithrum between pleural ribs one and two (see Dyer 1997); 2=ventral postcleithrum between pleural ribs one and three; 3=polymorphic; 0.67, 0.91; add). The position of the ventral postcleithrum in O. brevianalis and O. graciosus is variable in that it is placed between pleural ribs one and two or one 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 ever or posterior to anus; 0.36).

85. Number of interdorsal pterygophores. (0=six or fewer interdorsals; 1=more than six interdorsals; 2=polymorphic; 0.35, 0.65 / 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 pleiomorphic condition of artheriniforms is for the posterior ribs to be anterior to the dorsal tip of the first anal-fin pterygophore (Dyer 1997). Presence of two or more pleural ribs posterior to the dorsal tip of the first anal-fin pterygophore is a derived feature of melanochromids (Dyer & Cherwowitz 1995) and artherinoids apart from for Membris, Melanochromis, Odonesthes platypterus, O. nigricans, O. inca, O. smithi, O. regia, and O. graciosus (Fig. 4). (0=pleural ribs anterior to dorsal tip of first anal-fin pterygophore; 1=presence of two or more pleural ribs posterior to dorsal tip of first anal-fin pterygophore; 0.50, 0.80).

91. Haemal-arch funnel and expansions (White 1982). The haemal arches as artheriniforms and outgroups have no expansions or modifications, except in Atherinae and Atherinases (Schultz 1948). A derived feature of sargontines except for Odonesthes inca 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 sargontines is present in four conditions, each state inclusive of the previous: 1=hatcheri and O. rostrimimus have a haemal funnel but lack any form of flaring or projections; sargontines except for the four species mentioned above, have flaring expansions of the haemal arches; Odonesthes 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. smithi, O. regia, O. graciosus 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=anterior and posterior 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 sargontines, the haemal-arch funnel is extended posteriorly to the vertebrae 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 vertebrae above mid-anal fin. This derived condition is found only in Odonesthes platypterus, O. smithi, O. graciosus, 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 pleiomorphic 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 pterygophores one to three, forming a dorsal bulge of the funnel floor (Fig. 4). This derived condition is found in Odonesthes argentinensis, O. platypterus, O. brevianalis, O. smithi, O. regia, and O. graciosus. (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=caudal vertebrae over posterior half of anal fin; 2=first caudal vertebrae over anterior half of anal fin; 3=polymorphic; 0.50, 0.80; add)

Scales

97. Number of subbital scale rows. Three rows of scales below the middle of the orbit in adult specimens is considered the pleiomorphic condition in artheriniforms. In sargontines, this condition is found in Atherinopsini except Atherina, in Odonesthes hatcheri, O. humensis, O. bernardensis, O. inca, and O. graciosus. Four subbital scale rows are found in Basileichthys, Odonesthes argentinensis, O. platypterus, O. nigricans, O. regia, O. smithi and O. brevianalis (Dyer 1997: fig. 2). BC1 (3=three subbital scale rows; 4=four subbital scale rows; 5=two subbital scale rows; 0.25, 0.58; add)

98. Cleithrum scales. No scales on the lateral shaft of the cleithrum is a pleiomorphic feature of artheriniforms. 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 atherinopterines except
for Atherinops, and in Odontesthes species except O.
bennesis, O. benneensis, O. nattereri, and O.
perugiae. A derived condition is present in Odontesthes
nigricans, O. brevimanus, O. smittii, 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; 0.20, 0.47, 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 silver scales, 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 pleiomorphic condition of atheriniformes. Small
scales are the derived condition and in some species they
are found in Basilichthys, Odontesthes hatcheri, O.
nigricans, O. planus, O. brevimanus, O. smittii, O. regia
and O. gracilis. (0=large scales [111 dorsal scales];
1=small scales [112 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)