The South American and Australian percichthyids and perciliids. What is new about them?

Gloria Arratia¹ and Claudio Quezada-Romegialli²,³

A study including morphological characters and mitogenomics of South American and Australian fishes previously assigned to Percichthyidae was conducted. Results generated from these different data sets reveal major disagreements concerning the content and interpretation of the so-called percichthyids. A phylogenetic analysis based on 54 morphological characters suggests the existence of two major clades: (1) Percichthyidae, including the South American *Percichthys* and the Australian taxa *Macquaria australasica*, *Macquaria* (= *Plectroplites*), and *Maccullochella*; (2) Perciliidae with the South American genus *Percilia* at the base plus more advanced Australian genera *Nannoperca*, *Nannatherina*, *Bostockia*, and *Gadopsis*. In contrast, molecular and mitogenomic evidence suggests only one clade (Percichthyidae), with the exclusion of species of *Macquaria* (= *Percalates*). Additionally, the results reveal the existence of various taxonomic problems, such as the current interpretation of only one species of *Percichthys* in Argentina, an interpretation that is not supported by the present study; the existence of cryptic species of *Percilia* as well as of *Gadopsis*, *Nannoperca*, and *Macquaria* that will increase the diversity of the genera; and the need for an extensive revision of species previously assigned to *Percalates versus Macquaria*. Disagreements point to the need to develop further research on the so-called percichthyids and perciliids.

**Keywords:** Biogeography, Endemism, Morphology, Phylogeny, Taxonomy.

Se realizó un estudio de peces sudamericanos y australianos incluyendo caracteres morfológicos y mitogenómicos, para taxa previamente asignados a la familia Percichthyidae. Los resultados generados de estos conjuntos de datos diferentes revelaron desacuerdos importantes entre el contenido y la interpretación de los así llamados percicthyidos. Un análisis filogenético basado en 54 caracteres morfológicos sugiere la existencia de dos clados importantes: (1) La familia Percichthyidae, incluyendo el género sudamericano *Percichthys* y los taxa australianos *Macquaria australasica*, *Macquaria* (= *Plectroplites*) y *Maccullochella*. (2) Perciliidae con el género sudamericano *Percilia* en la base, y géneros australianos más avanzados como *Nannoperca*, *Nannatherina*, *Bostockia* y *Gadopsis*. En contraste, la evidencia molecular y mitogenómica incluye la mayor parte de los géneros dentro de la familia Percichthyidae, excluyendo a las especies de *Macquaria* (= *Percalates*). Adicionalmente, los resultados revelan la existencia de variados problemas taxonómicos, tales como la existencia de una sola especie de *Percichthys* en Argentina, cuya interpretación no es soportada por este estudio; la existencia de especies crípticas de *Percilia*, *Gadopsis*, *Nannoperca* y *Macquaria* que aumentarán la diversidad específica del género; y la necesidad de una revisión extensiva de especies previamente asignadas a *Percalates versus Macquaria*. Los desacuerdos encontrados apuntan a la necesidad de investigar más profundamente sobre los así llamados percicthyidos y perciliids.

**Palabras claves:** Biogeografía, Endemismo, Filogenia, Morfología, Taxonomía.

**Introduction**

Gondwanan continents are characterized, in general, by a notable endemism due to their isolation, exemplified by there being only a few fish taxa that are common to two or more continents. For example, dipnoans have representati- ves in Africa, Australia, and South America, with each continent having its distinct family, and osteoglossomorphs are broadly diversified in Africa, but have one monotypic family inhabiting South America. The so-called temperate perch belonging to the family Percichthyidae are currently interpreted as inhabitants of southern South America and Austra- lia, including Tasmania, while Perciliidae are only in South America (Arratia, 2003a, 2003b; Fricke et al., 2018).

---

¹Department of Ecology and Evolutionary Biology and Biodiversity Institute, University of Kansas, USA. garratia@ku.edu, https://orcid.org/0000-0002-7363-1319 (corresponding author)
²Departamento de Biología, Facultad de Ciencias Naturales y Exactas, Universidad de Playa Ancha, Valparaíso, Chile. claudio.quezada@upla.cl, https://orcid.org/0000-0003-3380-389X
³Núcleo Milenio INVASAL, Concepción, Chile.
Among neoteleosts, the family Percichthyidae is one with a most confusing history that began when Jordan (1923) created the family—without a diagnosis—for the austral South American freshwater species of *Percichthys* Girard, 1855. At the same time, the family Perciliidae was created by Jordan (1923) for the Chilean genus *Percilia* Girard, 1854, an approach followed later by Arratia (1982, 2003a, 2003b), Nelson (2006), Nelson et al. (2016), and Fricke et al. (2018). Initially, the South American genera *Percichthys* and *Percilia* were included in the Serranidae by Girard (1854, 1855) and in the subfamily Percichthyinae by Jordan, Eigenmann (1890). Based on morphological evidence, Percichthyidae, as well as Serranidae, were considered to be in the order Perciformes (Tabs. 1, 2) until recently, when molecular studies gave a new interpretation, with the family Percichthyidae as part of the order Centrarchiformes (Chen et al., 2014; Lavoué et al., 2014; Betancur-R et al., 2017) within the Subdivision Percor- 
omorphacea. Additionally, the genus *Percalates* was removed from Percichthyidae *sensu* Johnson (1984)—now considered as a junior synonym of *Macquaria* and making *Macquaria* par- phylectic—and included in its own suborder Percalatoidei within Centrarchiformes (e.g., Betancur-R et al., 2017).

Gosline (1966; Tab. 1), based on a few characters that prove to be not unique for Percichthyidae, removed numerous genera from the Serranidae that he considered to be percichthyids. Although Gosline (1966) acknowledged that his understanding of Percichthyidae did not represent a natural assemblage, his Percichthyidae was followed for more than 20 years by most ichthyologists. Johnson (1984:p. 469) restricted the family Percichthyidae to the freshwater (and one brackish: *Percalates*) genera living in southern South America and Australia, a view supported recently by molecular studies (Nar et al., 2012; Chen et al., 2014; Lavoué et al., 2014; Betancur-R et al., 2017; see Tab. 2). Johnson’s study is the only one that until now has provided morphological sym- 
apomorphies for the South American plus Australian percichthyids, as well as for other percoid families (e.g., Coraci- 
didae and Moronidae). In Johnson’s (1984) study, the South American genera *Percichthys* and *Percilia* were classified as Percichthyidae, contrary to Arratia (1982) that placed them in separate families. Micklich’s (1987) study of the middle Eocene fossil *Amphiperca* is the only one that up to now has provided alternative phylogenetic hypotheses, including fos- sil and extant percoids, where South American and Australian temperate perches were included (see Fig. 1), but contrary to Johnson (1984), Perciliidae and Percichthyidae *sensu stricto* were interpreted as separate families. *Amphiperca*, previously included within Serranidae, was interpreted by Micklich (1987) as part of Percichthyidae *sensu* Gosline (1966). Des- 
pite this progress, Gosline’s (1966) apparent influence, and the incomplete knowledge of Serranidae and Percichthyi- dae, many studies of the next 50 years still included a mix of genera. For instance, “*Fishes of the World*” kept *Howella* within Percichthyidae up to 2006 (see Tab. 1), whereas *Percil- lia* was included in Perciliidae (Nelson, 2006). Additionally, Nelson (1994:p. 334) stated that “there is no firm evidence” that Johnson’s (1984) percichthyids “forms a monophyletic group”. Later, it was suggested that *Percilia* and the Austral- ian genera *Edelia, Nannoperca*, and *Nannatherina* are more closely related to each other than with *Percichthys* and other Australian forms (Arratia, 2013b). Nelson et al. (2016) rec- 
ognized the family Percichthyidae, while the genus *Percilia* was excluded and kept in Perciliidae.

Starting in 2001, molecular studies (see Tab. 2, Figs. 2 and supplementary S1), including mitochondrial, nuclear and genomic markers, gave different interpretations of the content of Percichthyidae *sensu* Johnson (1984). The first molecular study (Jerry et al., 2001) included 20 Australian temperate perches, but not *Percichthys* and *Percilia* (Fig. sup- 
plementary S1a), so the monophyly of Percichthyidae was not evaluated. An important finding was that *Macquaria (= 
Percalates)* and *Macquaria sensu stricto* were found to be par- phylectic. Smith, Craig (2007) addressed the limits and relationships of Serranidae and Percidae families, consid- 
ering *Bostockia, Gadopsis, Howella, Macquaria (= Percala- 
etes)* and *Nannoperca* as representatives of Percichthyidae. In their results, Smith, Craig (2007) found a polyphyletic Percichthyidae with three distinct lineages (Fig. supple- 
mental S1b). Near et al. (2012) investigated the phylogenetic relationships of *Elassoma* using nuclear markers and in- cluded 68 species across a diversity of percomorph fishes. They found a par- phylectic Percichthyidae, where the catadromous *Percalates colonorum* and *Percalates novemaculeata* were distantly related to the other freshwater percichthyids (Fig. supplementary S1c), and given that *Percilia irwini* was nests- ed within this group, they suggested that Perciliidae should be synonymized with Percichthyidae (Near et al., 2012). Later, both Betancur-R et al. (2013) and Near et al. (2013) found again a par- phylectic Percichthyidae because of *Percalates*, whereas the phylogenetic placement for Percichthyidae *sensu stricto* was incertae sedis for the former and within Centrarchiformes for the latter (Fig. supplementary S1d-e). Similar results regarding the par- phylectic condition of Percichthyidae and the phylogenetic position within Cen- 
trarchiformes was found by Chen et al. (2014; Fig. supple- 
mementary S1f) and Lavoué et al. (2014) using nuclear and mitogenomic markers, and *Percichthys trucha* and *Percilia irwini* were resolved as allied taxa (Figs. 2a, b). Finally, Sanciangco et al. (2016; Fig. 2c) and Betancur-R et al. (2017; Fig. 2d) using a combined supermatrix of mitochondrial and nuclear genes largely confirmed the par- phylectic condition of Percichthyidae *sensu* Johnson (1984).

One of the problems that ichthyologists studying ser- ranids, percichthyids, and other euteleosts face is the high morphological variability of many structures. Such variabili- 
ity involving meristic and morphometric features, as well as osteological features, was reported for the South American genera *Percilia and Percichthys* by Arratia (1982) and López- 
-Arbarello (1999, 2004), and for the Australian percichthyids, by MacDonald (1978). Ontogenetic variability also affects cephalic sensory canal configuration (compare Arratia, 1982; López-Arbarello, 2004; and especially Vega, Viozzi, 2016).
Tab.1. Genera of Percichthyidae according to various authors starting 1923.

|                      | Jordan, 1923 | Gosline, 1966 | MacDonald, 1978 | Arratia, 1982 | Johnson, 1984 | Paxton *et al.*, 1989 | Eschmeyer, 1990 | Nelson, 2006 | Nelson *et al.*, 2016 | Fricke *et al.*, 2018 | This study |
|----------------------|-------------|---------------|-----------------|---------------|---------------|----------------------|----------------|--------------|----------------------|-----------------------|-----------|
| **Perciformes**      |             |               |                 |               |               |                      |                |              |                      |                       |           |
| Acropomidae          |             |               |                 |               |               |                      |                |              |                      |                       |           |
| Acropoma             |             |               |                 |               |               |                      |                |              |                      |                       |           |
| Apogonops            |             |               |                 |               |               |                      |                |              |                      |                       |           |
| Bostockia            |             |               |                 |               |               |                      |                |              |                      |                       |           |
| Coreoperca           |             |               |                 |               |               |                      |                |              |                      |                       |           |
| Ctenolates           |             |               |                 |               |               |                      |                |              |                      |                       |           |
| Doderleinia          |             |               |                 |               |               |                      |                |              |                      |                       |           |
| Edelia               |             |               |                 |               |               |                      |                |              |                      |                       |           |
| Gadopsis             |             |               |                 |               |               |                      |                |              |                      |                       |           |
| Guyu                 |             |               |                 |               |               |                      |                |              |                      |                       |           |
| Howella              |             |               |                 |               |               |                      |                |              |                      |                       |           |
| Lateolabrax          |             |               |                 |               |               |                      |                |              |                      |                       |           |
| Macullocichthydia    |             |               |                 |               |               |                      |                |              |                      |                       |           |
| Macquaria            |             |               |                 |               |               |                      |                |              |                      |                       |           |
| Malakichthys         |             |               |                 |               |               |                      |                |              |                      |                       |           |
| Macullocichthys      |             |               |                 |               |               |                      |                |              |                      |                       |           |
| Neoscombrops         |             |               |                 |               |               |                      |                |              |                      |                       |           |
| Niphon               |             |               |                 |               |               |                      |                |              |                      |                       |           |
| Percalates           |             |               |                 |               |               |                      |                |              |                      |                       |           |
| Percilia             |             |               |                 |               |               |                      |                |              |                      |                       |           |
| Plectroplites        |             |               |                 |               |               |                      |                |              |                      |                       |           |
| Synagrops            |             |               |                 |               |               |                      |                |              |                      |                       |           |

Note: *=Macquaria (Perc.)*
### Tab. 2. Genera of Percichthyidae according to various authors (molecular and mitogenomic publications) starting 2001.

| Year | Author(s)                          | Genera                                      |
|------|------------------------------------|---------------------------------------------|
| 2001 | Hughes et al.                      | *Siniperca*, *Macquaria*                   |
| 2012 | Møbjerg et al.                     | *Plectroplites*                             |
| 2013 | Betancur-R et al.                  | *Percalates*                                |
| 2014 | Chen et al.                        | *Percilia*, *Percichthys*                   |
| 2014 | Van der Laan et al.                | *Oligorus*, *Siniperca*                     |
| 2014 | Lavocat et al.                     | *Howella*, *Gadopsis*                       |
| 2014 | Bacigalupo et al.                  | *Maccullochella*, *Nannoperca*              |
| 2013 | Neave et al.                       | *Bostockia*, *Burtonichthys*                |
| 2013 | Brouat et al.                      | *Nannatherina*, *Coreoperca*                |
| 2012 | Smith, Craig                       | *Coreoperca*                                |
| 2011 | Near et al.                        | *Nannatherina*, *Coreoperca*                |
| 2007 | Lavocat et al.                     | *Percichthys*, *Percilia*                   |
| 2001 | Jerry et al.                       | *Percichthys*, *Percilia*                   |
|      | Betancur-R et al.                  | *Nannotherina*, *Coreoperca*                |
|      | Near et al.                        | *Nannotherina*, *Coreoperca*                |
|      | Smith, Craig                       | *Coreoperca*                                |
|      | Hughes et al.                      | *Siniperca*, *Macquaria*                   |
Fig. 1. Speculative phylogenetic hypotheses (a, b) concerning the relationships of the Eocene genus *Amphiperca* and certain percoids within serranids and percichthyids based mainly on an unpublished hypothesis by GD Johnson. Slightly modified from Micklich (1987:fig. 16).

Fig. 2. Phylogenetic hypotheses based on mitochondrial, nuclear and genomics markers concerning the content of Percichthyidae *sensu* Johnson (1984). a, Mitogenomic maximum likelihood [ML] tree of Lavoué *et al.* (2014), b, total evidence ML of Lavoué *et al.* (2014), c, Sanciangco *et al.* (2016), and d, Betancur-R *et al.* (2017). Representatives of Percichthyidae are shown in pink, *Percilia irwini* (Perciliidae) is shown in light blue and *Macquaria* (= *Percalates*) is shown in green.
South American and Australian percichthyids and perciliids

The purposes of this contribution are: 1) to study and interpret certain morphological characters of the South American genera *Percichthys* and *Perca*; 2) to understand South American percichthyids in their historical and biogeographic scenarios; 3) to investigate their phylogenetic relationships; and 4) to analyze and discuss current interpretations of percichthyids and perciliids. A brief presentation of the South American and Australian temperate perches follows.

**Percichthys.** The content of the genus *Percichthys* is very different depending on taxonomic or molecular approaches. *Percichthys*—the type-genus of Percichthyidae—is currently known by five morphologically distinct species living in the Andean Region of Austral South America (Figs. 3, 4; Fricke *et al.*, 2018). The species are: (1) *Percichthys chilensis* Girard, 1854 (commonly identified as *P. trucha* in Chile; Eigenmann, 1927; Arratia, 1982; Campos, Gavilán, 1996; Arratia, 2003a; López-Arbarello, 2004); (2) *Percichthys colhuapiensis* MacDonagh, 1955 (Argentina; Ringuelet *et al.*, 1967; López-Arbarello, 2004); (3) *Percichthys laevis* Jenyns, 1840 (Argentina; Ringuelet *et al.*, 1967; López-Arbarello, 2004); (4) *Percichthys melanops* Girard, 1855 (Eigenmann, 1927; Arratia *et al.*, 1981; Arratia, 1982; Campos, Gavilán, 1996); and (5) *Percichthys trucha* Valenciennes, 1833 (Argentina; Ringuelet *et al.*, 1967; López-Arbarello, 2004).

The first mention of percichthyids or “Chilean trout” is from Molina (1782) in his description of the natural history of Chile. About 50 years later, *Perca* (= *Percichthys trucha*), was formally described from freshwaters of southern Argentina. Such taxonomic assignment was accepted also for the Chilean percichthyids (Guichenot in Gay, 1848; Jordan, Eigenmann, 1890; Duarte *et al.*, 1971; Arratia *et al.*, 1981; Arratia, 1982; Dyer, 2000). In contrast, López-Z-Arbarello (2004) restricted *P. trucha* to Argentina and recognized *Percichthys chilensis* Girard, 1854 (commonly accepted as a synonym of *P. trucha*, but see Fricke *et al.*, 2018), which was described, however, based on specimens from the Maipo Basin, Chile. For the purpose of this contribution, we consider *P. trucha* as an inhabitant of Argentina and *P. chilensis* of Chile (Fig. 3).

*Percichthys chilensis* (Figs. 3a, 4a-b), *P. melanops* (Fig. 4c), and *P. laevis* are characterized as having a small mouth, with the articulation between lower jaw and quadrate positioned below the mid-region of the orbit (Figs. 5a-c), whereas the mouth is large in *P. colhuapiensis*, with the articulation of the lower jaw-quadrate positioned behind the posterior margin of the orbit (Fig. 5d) so that the fish is identified with the common name “perca bocona” (= “large-mouth perch”). In addition, there are differences in the musculature associated with feeding mechanism among these species (see Results below). However, differences in the upper jaw length from larval through juvenile to adult stages and the causal relationship between diet and shape of the head of the Argentinian species were interpreted as the result of high morphological plasticity of *P. trucha* by Crichigno *et al.* (2014). Those authors follow Ruzzante *et al.* (2006) whose results based on molecular evidence suggested that only one species, *Percichthys trucha*, inhabits both sides of the Andean Range, whereas *P. melanops* (Fig. 4c) lives on its west side.

In general, comparisons through the years show that in the past *Percichthys* was abundant, forming large schools in the main rivers of central-south Chile. Because of its fine taste, the fishes were used as food, and they were caught by artisanal fishermen using dynamite (a common practice at the beginning of the last century). This kind of fishing produced a big fish mortality until the use of explosives was prohibited in the last century. Thus, *Percichthys* had a broader distribution in Chile in the past, from Aconcagua Basin (ca. 33º S) in the north reaching up to Punta Arenas in the south (ca. 54º S, where it is now locally extinct) as demonstrated by specimens collected by J. B. Hatcher during his expedition to Patagonia at the end of the 19th century (Haller, 2004; Fig. 4a herein). The records cited in Eigenmann (1927; collected by the Irwin expedition during 1918-1919) are deposited in the California Academy of Sciences (Figs. 4b-c). Currently, species of *Percichthys* live in southern Argentina and central-southern Chile (Fig. 3b).

The fossil record of South American percichthyids is known from three genera—†*Santosius* Arratia, 1982, *Percichthys* (Fig. 6b), and †*Plesiopercichthys* Agnolin *et al.*, 2014; one of them (†*Santosius*) was living in the Neotropical Region and the other two in the Austral region of South America. The oldest known percichthyid is †*Santosius anti-quis* (Woodward, 1898) from the Tremembé Formation (in the lacustrine unit of the Taubaté Basin) in the eastern part of São Paulo (Oligocene to early Miocene, ca. 30-25 Ma; Malabarba, 1988). Later, an incomplete specimen assigned to †*Santosius*? sp. was described and illustrated from the Miocene of the Cura-Mallín Formation, Lonquimay, Bio-Bio Region (Rubilar, 1994); however, this assignment needs revision. Fossil *Percichthys* are known from four species: †*P. hondoensis* Schaeffer, 1947 from the lower Eocene of Cañadón Hondo, Chubut Province, Argentina, †*Percichthys lonquimayensis* Chang *et al.*, 1978 (Fig. 6a), †*Percichthys sandovalli* Arratia, 1982, and †*Percichthys sylviae* Rubilar, Abad, 1990 from the middle Miocene of Cura-Mallín (Río Pedregoso) Formation (ca. 12.6 Ma), Lonquimay, Bio-Bio region, Chile (Pedroza *et al.*, 2017). In addition, *Percichthys* sp. specimens from the same locality and formation were described and illustrated by Rubilar (1994:pl. 2, figs. 7-10). All these fossils are known from almost complete specimens, whereas †*Plesiopercichthys dimartinoi* is known from disarticulated bones that were recovered in the Pliocene of Farola Monte Hermoso, southern region of Buenos Aires Province, Argentina. Additionally, fragmentary bones (e.g., spines and preopercles) assigned to *Percichthys* sp. and undetermined percichthyids from the Upper Cretaceous of Bolivia were cited by Gayet in de Muizon *et al.* (1983), in Marshall *et al.* (1985), and in the Maastrichtian-Paleocene of Santa Lucia Formation, Bolivia, by Gayet *et al.* (1991).
Poorly preserved specimens from La Palca, lower Paleocene (Danian) of Bolivia were interpreted as *Percichthys hondoensis* Schaeffer, 1947, an assignment that is not supported by the preservation of the Bolivian material (Gayet, Meunier, 1998:fig. 25). An indeterminate percichthyid from the Upper Cretaceous of Brazil was mentioned by Gayet, Brito (1989). To the best of our best knowledge, the South American percichthyid spines and preopercles are not diagnostic to the familial or generic levels. Therefore, there is not well-supported evidence for the presence of percichthyids in the Upper Cretaceous of South America—their fossils are only confidently known from the Cenozoic.

**Fig. 3.** *Percichthys trucha* (CAS 79013), type species of the genus in lateral view (a) and current distribution of South American percichthyids (b). Occurrence records downloaded from GBIF.org (https://doi.org/10.15468/dl.ivxhrw) and courtesy of Jorge Liotta (Museo de Ciencias Naturales “P. Antonio Scasso”, Argentina).
Fig. 4. Lateral view of specimens of *Percichthys*. **a**, Photograph of historical specimen (CAS 70005) collected in southern Chile (Punta Arenas), where the species is currently extinct. **b**, *Percichthys chilensis* (CAS 79019) from Maule River, central Chile; **c**, *Percichthys melanops* (CAS 70183) from Todos Los Santos Lake, Chile.

Fig. 5. Head of percichthyids in lateral view illustrating the position of the quadrate-mandibular articulation (small arrows) and the extension of the maxillary blade in comparison to the orbit. **a**, *Percichthys trucha* from southern Chile, Punta Arenas (CAS 70005); **b**, *Percichthys chilensis* from Maule River (CAS 79019); **c**, *Percichthys trucha* from Limai River (Argentina; CAS 79015); **d**, *Percichthys colhuapiensis* (CAS[SU] 31714) from Buenos Aires Market (Argentina).
Fig. 6. South American fossil percichthyids. 

a, *Percichthys lonquimayensis* (SNGM 7656 [old catalogue number IIG MA-21]) under ultraviolet light; 
b, distribution of fossil percichthyids during the Oligocene-Miocene; fragments preliminarily assigned to percichthyids are from the Upper Cretaceous-Paleocene of Bolivia; Cura-Mallín (= Rio Pedregoso) Formation after Pedroza et al., 2017.
Percilia. The genus *Percilia* was created for one species—*Percilia gilissi* Girard, 1855—living in freshwaters of central-south Chile, from ca. 33° S to ca. 41° S (Fig. 7). A second species, *Percilia irwini* Eigenmann, 1927 is restricted to some tributaries of Bio-Bio river, Bio-Bio Region, at about 39° S. In other words, both species are endemic to the western side of the Andean Region of South America. The most recent taxonomic revision includes these *Percilia* species within the family Perciliidae (Fricke *et al*., 2018), following Jordan (1923) and Arratia (1982, 2003b).

Fig. 7. *Percilia gilissi*, type species of the genus in lateral view (a) and current distribution of South American perciliids (b). Occurrence records downloaded from GBIF.org (https://doi.org/10.15468/dl.cyqxvf).
The two species are represented by small fishes reaching a maximum length of 80 mm, *Percilia irwini* being a little smaller. They have an oblong or slightly elongate body covered with large ctenoid scales, relatively larger than those present in *Percichthys*, and with differences in scale characters, e.g., the position of the focus of the scales and length of ctenii. *Percilia* species lack scales on the frontal cranial region, infraorbital 1 and upper jaw; however, cycloid scales cover the opercular and cheek regions. The head profile is smoothly rounded with the snout region projecting slightly anteriorly to the lower jaw (compare figs. 95 and 108 in Arratia, 1982; see below). Their infraorbital bones, opercle, subopercle, interopercle, and posttemporal have smooth margins, whereas the preopercle is poorly serrated. These features make their identification easy when comparing with species of *Percichthys*. For a description of morphological features of *Percilia gillisi* and *P. irwini* see Arratia (1982).

Information concerning the biology and behavior of both species is incompletely known. There are a few reports about the reproduction and behavior of *Percilia gillisi* (Kilian, Campos, 1969; Chiang et al., 2011; Chiang et al., 2012) and ontogenetic changes of *P. irwini* (Aedo, Habit, 2009). There is concern about the present situation of the two species, which are currently catalogued as threatened in Chile.

A few fragments assigned preliminarily to *Percilia* sp. were described by Rubilar (1994) from the Miocene of Curamilla, Campos, 1969; Chiang et al., 2011; Chiang et al., 2012) and ontogenetic changes of *P. irwini* (Aedo, Habit, 2009). There is concern about the present situation of the two species, which are currently catalogued as threatened in Chile.

So-called Australian percichthyids. Under this subheading, we include all Australian genera that were interpreted as members of the family Percichthyidae by Johnson (1984; Tab. 1). However, new interpretations about them are addressed below and also in the sections Results and Discussion (see below).

According to Fricke et al. (2018; Tab. 1), Australian percichthyids currently comprise the following genera (and species): 1) *Macquaria* Cuvier, 1830 with three species [*M. australasica* Cuvier, 1830, *M. (= Plectroplites) ambigua* Richardson, 1845, and *M. (= Guyu) wualwjaalensis* Pusey, Kennard, 2001]; 2) *Percalates* Ramsay, Ogilby, 1887 with two species [*P. colornorum* (Günther, 1863) and *P. noveamaculeata* (Steindachner, 1866)]; 3) *Maccullochella* Whitley, 1929 with four species [*M. macquariensis* (Cuvier, 1829); *M. ikei* Rowland, 1986; *M. mariensis* Rowland, 1993; and *M. peelli* (Mitchell, 1838)]; 4) *Gadopsis* Richardson, 1848 with two species (G. bispinosus Sanger, 1984 and G. marmoratus Richardson, 1848); 5) *Bostockia* Castelnau, 1873 with one species (*B. porosa* Castelnau, 1873); 6) *Namnatherina* Regan, 1906 with one species (*Namnatherina balstoni* Regan, 1906); and 7) *Nannoperca* Günther, 1861 with six species [*N. australis* Günther, 1861; *N. obscura* (Klunzinger, 1872); *N. oxleyana* Whitley, 1940; *N. pygmaea* Morgan, Beatty, Adams, 2013; *N. variegata* Kuitter, Allen, 1986, and *N. vittata* (Castelnau, 1873)].

The genus *Macquaria* currently includes *Plectroplites (=Ctenolates)*, which was synonymized by MacDonald (1978) after examining morphological and electrophoretic characters, and *Guyu* Pusey, Kennard, 2001, which was informally synonymized based on the personal communication of Peter Unmack to Frickie et al. (2018). MacDonald (1978) found that the Australian percichthyid species *sensa* Gosline (1966) fall into two subgroups, the genus *Maccullochella* (see below) and the *Macquaria* group, the latter including *Plectroplites*.

Cuvier (1830) described *Macquaria australasica*, the type species of the genus, based on specimens collected in the Macquarie River, although the species was historically distributed across both sides of the Great Dividing Range (GDR), Australia’s most significant mountain range (about 3,500 km in length, up to ca. 300 km in width and 2,228 m in height) in South East Australia (Faulks, Gilligan, Beheregaray, 2010; Fig. 8). *Macquaria australasica* typically inhabits the cooler upper reaches of the Murray-Darling river system (MacDonald, 1978), is still present in the headwaters of this river system (Faulks, Gilligan, Beheregaray, 2010) and appears to have adapted to the environment of manmade lakes, thus is also found in some coastal streams of New South Wales and Victoria (MacDonald, 1978). Although the GDR, the most prominent geographical barrier within the distribution of *M. australasica*, is likely the major factor in shaping freshwater fish lineages for the last 90 million years, more recent and geographically small-scale processes must have been responsible for shaping the evolutionary history of freshwater taxa on either side of the GDR (Faulks, Gilligan, Beheregaray, 2010).

*Macquaria (= Plectroplites) ambigua* is a moderate to large fish known to reach 760 mm and 23 kg (Pusey, Keenan, Artington, 2004) that is commonly found in warm, turbid, slow-moving waters. It is restricted to the lower reaches of the Murray-Darling river system (Hammer et al., 2012) and inhabits some river systems of coastal south-eastern Queensland (MacDonald, 1978). In addition, it is reported to occur in coastal streams of northern New South Wales and to have been introduced into Western Australia and into streams and dams of northern coastal Australia (MacDonald, 1978; Fig. 8). Based on electrophoretic genetic differentiation, Musyl, Keenan (1992) recognized two distinct subspecies: *M. ambiguorum* (subsp.) *Macquaria* sp. B (subsp.). *Macquaria* sp. B also occurs in the Bulloo River and was suggested as a distinct subspecies based on the presence of a unique array of alleles (Pusey, Keenan, Artington, 2004 and citations therein). *Macquaria (= Guyu) wualwjaalensis* is a small fish [maximum length of the type series being 101 mm SL (Pusey, Kennard, 2001)], limited to the Bloomfield River of north-eastern Queensland (145°20’E 15°55’S). It appears to be confined to the main channel between the Bloomfield River Falls and Roaring Meg Falls, being undetectable by snorkeling or electrofishing in other tributaries of the Bloomfield River either upstream or downstream (Pusey, Kennard, 2001). As recent phylogenetic molecular analysis placed *M.
Macquaria (= Percalates) novemaculeata was originally described as *Dules novemaculeatus* by Steindachner (1866), and there has been considerable uncertainty about the taxonomy and systematics of the Australian bass *P. novemaculeata* and the morphologically similar estuary perch *M. colonorum* (Pusey, Keenan, Artington, 2004). Historically, these forms have been considered to represent a single species (often designated *colonorum*), two subspecies within a single species, or two distinct species (Pusey, Keenan, Artington, 2004 and references therein). According to Nelson et al. (2016) and Frickle et al. (2018), *Percalates* is considered a valid taxon, but MacDonald (1978), based on morphological and electrophoretic evidence, synonymized *Percalates* with *Macquaria*. Thus, some authors considered *Percalates* as a junior synonym of *Macquaria* (see Tabs. 1-2 and Figs. 1-2). Recently, Betancur-R et al. (2017) removed the genus *Percalates* from Percichthyidae (*sensu* Johnson, 1984) and included it in the suborder Percalatoidei within Centrarchiformes; however, both the Family and Suborder are awaiting a formal nomenclatural description in compliance with the International Code of Zoological Nomenclature (ICZN; Betancur-R et al., 2017).

*Percalates colonorum* is essentially estuarine, rarely being found above tidal influence, whilst *Percalates novemaculeata* spends a large part of its life cycle in fresh water, periodically descending to waters under tidal influence to breed (MacDonald, 1978). These species occur in coastal southeastern Australian drainages between southern Queensland and eastern South Australia, commonly co-occurring from northern New South Wales to eastern Victoria (Trenski, Hay, Fielder, 2005; Fig. 8).

**Fig. 8.** Distribution of Australian percichthyids. (a) *Macquaria (= Plectroplites) ambigua* (blue circles) and *Macquaria australasica* (green squares); the Great Divide Range is shown with the black line. (b) *Maccullochella* species (red hexagons. (c) *Macquaria (= Percalates) colonorum* (yellow pentagon) and *Macquaria (= Percalates) novemaculeata* (orange triangle). The illustrated specimens are represented by *Macquaria (= Plectroplites) ambigua* (CAS-ICN 23516, reversed); *Macquaria (= Percalates) colonorum* (CAS-ICN 20765); and *Maccullochella peelii* (CAS-ICN 24432). Occurrence records downloaded from GBIF.org (*Macquaria*, https://doi.org/10.15468/dl.54hpar; *Guyu*, https://doi.org/10.15468/dl.zwq5wo; *Maccullochella*, https://doi.org/10.15468/dl.nbei5c).
Australia’s cod were described as *Gr克斯 macquariensis* by Cuvier (1829), while other generic names were made available prior to 1929 (e.g., *Grytes, Grystes* and *Oligorus*), when Whitley erected the genus *Maccullochella* (Berra, Weatherley, 1972). Using morphological and electrophoretic characters, Berra, Weatherley (1972) concluded that only two species (*Ma. peeli* and *Ma. macquariensis*) were found in southeastern Australia. Later, Jerry et al. (2001) suggested and Nock et al. (2010) confirmed that four extant taxa should be recognized within the genus: *Ma. macquariensis*, *Ma. peeli*, *Ma. mariensis*, and *Ma. ikei*.

*Maccullochella* spp. occur on both sides of the GDR, which has had a key role in the freshwater fish speciation in eastern Australia (Fig. 8). The Murray River cod (*Maccullochella peeli*) and trout cod (*Ma. mariensis*) are endemic to the Murray-Darling Basin on the inland side of the GDR and the eastern freshwater cod (*Ma. ikei*), whereas the Mary River cod (*Ma. mariensis*) persists in isolated coastal catchments to the east of the GDR (Harrisson et al., 2016 and references therein). Species of *Maccullochella* are highly regarded for their cultural, historical, angling and edible characteristics, and there have been significant declines in the distribution and/or abundance of each species, which are classified as vulnerable (*Ma. peeli*) or endangered (the other species; Nock et al., 2010).

The taxonomic placement of *Gadopsis* had proven problematic until Johnson (1984) placed it within Percichthyidae and interpreted it as more closely related to the Australian genera *Bostockia, Nannatherina*, and *Nannoperca*, than to other percichthyids. In the past, *Gadopsis* was first included within the Blenniidae by Richardson (1848), an assignment that was followed by Steindachner (1866) and Goodrich (1909). Regan (1913) established a division within the Percoidae to contain *Gadopsis* based mainly on the absence of the entopterygoid, the jugular position of the pelvic fins (each reduced to a pelvic spine and a bifid soft ray), and 48 vertebrae, an assignment that was later followed by Jordan (1923). Berg (1947) placed *Gadopsis* in its own superfamily, the Gadopsoidae, whereas Scott (1962) placed it in its own order, the Gadopsiformes or it was included in its own family, Gadopsidae, within the Percoidae (Greenwood et al., 1966) or Ophioidei (Gosline, 1968).

Although *Gadopsis* is known by two species, new molecular evidence has suggested that *Gadopsis marmoratus* represents a complex of several cryptic species (Unmack et al., 2017). This is one of the largest temperate perch that may reach 60 cm in length (Bray, 2011). Species of *Gadopsis* are restricted to rivers and streams of southeastern Australia, including Tasmania (Hammer et al., 2014; Unmack et al., 2017; Fig. 9).

*Bostockia porosa* is a moderately small fish (16 cm maximum length, commonly reaching 9 cm SL) with nocturnal habits (hence the common name of “nightfish”), endemic to the streams of the southwestern drainage area in Western Australia (MacDonald, 1978; Fig. 9). Little is known regarding *B. porosa*, although its biology has been described based on monthly data obtained over three years during the 1980’s by Pen, Potter (1990). *Bostockia porosa* sampled had most age classes belonging to 0+ and 1+ (81.8 and 12.5% of the 2,463 fish caught), and hardly reaches 6+ years old (only one individual of this age was found). Sexual maturity is attained commonly at the end of the first year for males and at the end of the second year for females. This species is carnivorous, feeding on a wide range of benthic organisms (Pen, Potter, 1990).

Originally *Nannatherina balstoni* was placed in the Atherinidae, but later was positioned in the Kuhlidae (Regan, 1940), until Johnson (1984) placed it in the Percichthyidae. *Nannatherina balstoni* is the rarest of all the endemic freshwater fishes of southwestern Australia (Morgan, Hill, Potter, 1998; Fig. 9). It is moderately abundant in a few shallow pools and creeks that dry up in summer, and in winter and spring this species typically is found amongst inundated riparian vegetation, where it presumably feeds and spawns. It is generally restricted to the small area of coastal peat flats in the southwestern corner of Australia and to two populations that have recently been found well to the north of this area (Morgan, Hill, Potter, 1998); however, the contemporary area of occurrence is now ca. 69% of its historical distribution (Morgan et al., 2014).

*Edelia* Castelnau, 1873—a synonym of *Nannoperca* according to Jerry et al. (2001)—was described with *E. obscura* and *E. vittata*, which are currently assigned to the genus *Nannoperca*. All these species are considered “pygmy perch” due to their small size that may reach a maximum length of 7 or 8 cm. Among these, *Nannoperca pygmaea* reaches a maximum length of 4 cm. Classification of pygmy perches has long posed problems for taxonomists. Over the years these species have been placed in Nannopercidae, the Kuhlidae, within the kuhlid subfamily Nannopercinae (see Jerry et al., 2001 and Hoese et al., 2006). Johnson (1984) interpreted the genera *Nannatherina, Nannoperca* and *Edelia* as part of the Percichthyidae.

Recent molecular studies suggested that there are cryptic species within *Nannoperca* (Unmack et al., 2011; 2013). A phylogenomic study published recently confirmed the paraphyletic nature of *N. vittata*, revealing two new cryptic lineages within the species and recognizing informally the existence of *N. ‘flindersi’* (Buckley et al., 2018). However, Buckley et al. (2018) emphasized that a more comprehensive sampling may reveal the full geographic range of the delimited species, including morphological and ecological characters for establishing species boundaries.

These species are endemic to the southeast (e.g., Murray–Darling Basin and coastal drainages) and the southwest of Australia and have a puzzling biogeographic disjunction across southern Australia (Buckley et al., 2018; Fig. 9). Pygmy perches prefer lowland habitats, including low gradient rivers and creeks, as well as floodplain habitats with aquatic macrophyte cover in general, and occur in virtually all drainages inhabited by fishes across southern Australia (Unmack et al., 2011).
Material

For institutional acronyms see Sabaj (2016). The material of South American and Australian temperate basses examined is listed below in alphabetic order. sp = specimen; cl&st = cleared and stained specimen. Considering the taxonomic discrepancies concerning certain species, the possible synonyms are identified below. High-level classification follows Betancur-R et al. (2017).

Order Centrarchiformes. Suborder Percichthyoidei. Bostockia diagramma: MCZ:Ich: 33108, 2 sp., 34.1 and 34.6 mm SL. Bostockia porosa: USNM 218841, 1 cl&st, ca. 34 mm SL. USNM 272935, 1 cl&st, ca. 34 mm SL.

Gadopsis marmoratus: CAS-ICH 024428, 18 sp., 48 mm to 92.3 mm SL and 1 cl&st, dissected. MCZ:Ich: 27554, 1 sp., 177 mm SL. USNM 308109, 2 cl&st partially dissected; 31.8 mm and 62.7 mm SL. USNM 344900, 1 cl&st, 130.7 mm SL.

Maccullochella macquarensis: CAS-ICH 20790, 1 sp., 212 mm SL. Maccullochella peeli: CAS-ICH 24432, 1 sp., ca. 200 mm SL. USNM 287440, 1 cl&st partially dissected; 67.6 mm SL.

Macquaria ambigua (= Plectroplites ambiguus): CAS-ICHSU 20971, 1 sp., 156 mm SL. USNM 287446, 1 cl&st, 101.5 mm SL.

Nannatherina balstoni: USNM 289205, 1 cl&st, 52.06 mm SL. USNM 315892, 2 cl&st partially dissected; 41 mm and 49.1 mm SL. Nannoperca australis: UMMZ 187418, 10 sp., 28.7 mm to 49.6 mm SL and 3 cl&st, 17.5 mm, 36.93 mm, and 42.5 mm SL. USNM 218843, 2 cl&st, 39.7 mm and 41.5 mm SL. USNM 399435, 2 sp., 38.34 mm and 43.4 mm SL. Nannoperca (= Edelia) vittata: MCZ:Ich: 33109, 2 sp., 33.2 mm and 36.4 mm SL. USNM 315895, 2 cl&st partially dissected; 36.3 mm and 39.9 mm SL. USNM 33109, 2 sp., 34.7 mm and 39.9 mm SL.

Percichthys colhuapiensis: CAS(SU)-ICH 31614, 2 sp., 224 and 231 mm SL. KU:KUI uncat: 2 cl&st dissected. *Percichthys longimayensis*: I.I.G. MA 21; I.I.G. 2990.
Percichthys melanops: CAS-ICH 70006, 18 sp., 48 to 150 mm SL; CAS-ICH 70183, 5 sp. LBUC, 1 cl&st, 156 mm SL. KU:KUI 19283, 1 cl&st, ca. 150 mm SL; KU:KUI 19326, 3 cl&st.; KU:KUI 19376, 1 cl&st, 110 mm SL. USNM 290487, 3 cl&st. Percichthys chilensis: CAS:I(UUM) 15559, 2 sp.; CAS 70005, 3 sp., ca. 135 to 185 mm SL; CAS 79013, 3 sp., 61.2 mm, 103.7 mm and 172 mm SL. CAS-ICH 79015, 1 sp.; CAS-ICH 79019, 2 sp. KU:KUI 19283, 1 cl&st, 157 mm SL; KU:KUI 19326, 3 cl&st.; KU:KUI 19376, 1 cl&st., LBUC 10101982, 4 sp., 120 to 250 mm SL; 1 cl&st, 120 mm SL. MHNV3258, 6 cl&st; 52.6 mm, 55.2 mm, 56.04 mm, 60.6 mm, 63.0 mm, and 63.2 mm SL. Only specimens collected in Chilean freshwaters, except CAS-ICH 79015 (IU 15552), 1 sp. *Percichthys trispinosis*: CAS-ICH 70189, 13 sp., 23.7 mm to 62.6 mm SL; CAS-ICH 70190, 10 sp. KU:KUI 21924, 47 sp., 2 cl&st.; KU:KUI 19303, 5 cl&st.; KU:KUI 19314, 1 cl&st.; KU:KUI 19334, 2 cl&st. MVNV 3252, 6 cl&st, 55.9 mm and 62 mm SL. USNM 290487, 4 sp. 51.5 mm, 54.3 mm, 63 mm, and 65.9 mm SL. *Percilia irwinii*: KU:KUI 19246, 30 sp., 23 mm SL to 60 mm SL. *Percilia* sp.: MHNV 3257, 5 cl&st, 49.0, mm, 49.1 mm, 49.7 mm, 54.1 mm, and 56.8 mm SL.

The material listed below was used for comparisons and is ordered alphabetically.

**Centrarchiformes. Centrarchidae.** *Lepomis gibbosus*: KU:KUI 13983, 4 cl&st. *Lepomis megalotis*: KU:KUI 21928, 21 sp. *Pomoxis annularis*: KU:KUI 21463, 8 cl&st.

**Pampheroformes. Acropomatidae.** *Acropoma japonicus*: CAS-ICH 6733, 3 sp., 1 cl&st; CAS-ICH 20776, 2 sp. *Doederleinia berycoides*: CAS-ICH 17563, 21 sp., 2 cl&st.; CAS-ICH 22631, 2 sp. 210 mm SL; CAS(SU) 23488, 2 sp. *Malakichthys griseus*: CAS(SU) 17756, 4 sp, 140 mm SL. *Synagrops trispinosis*: CAS-ICH 70185, 10 sp., 1 cl&st.

**Hollowellidae.** *Howella broidei*: CAS 52432, 1 sp.

**Lateolabridae.** *Lateolabrax japonicus*: CAS(SU) 7298, 1 sp; CAS 9999, 10 sp.; CAS 28746, 1 sp.

**Percalatoidei.** *Percalates colonorum* (= *Macquaria colonorum* in Betancur-R *et al., 2017*): CAS 2913, 2 sp.; CAS 20786, 3 sp, 1 cl&st, 114.8 mm SL, 163 mm CAS 20787, 4 sp.; CAS 24427, 145 mm SL. *Percalates novemaculeatus* (= *Macquaria novaemaculatus* in Betancur-R *et al., 2017*): CAS(SU) 20765, 3 sp., 148 mm SL; CAS(SU) 20786, 1 sp., 114.8 mm SL. USNM 312977, 1 cl&st, ca. 115 mm SL.

**Perciformes. Percidae.** *Perca flavescens*: KU:KUI 3741, 10 sp. *Stizostedion vitreum*: KU:KUI 4955, 2 sp.; KU:KUI uncat., 40 cl&st larvae.

**Eupercaria, order incertae sedis.** *Moronidae. Morone chrysops*: KU:KUI 13147, 3 cl&st, dissected; KU:KUI 9881, 4 sp., 210 mm SL; KU:KUI 22669, 10 sp., ca. 114 to 200 mm SL; KU:KUI 16011, 1 cl&st; KU:KUI 16799, 10 cl&st; KU:KUI 18024, 5 cl&st. *Morone saxatilis*: KU:KUI 18212, 2 sp., 1 cl&st, 71 mm SL.

**Methods.** Ethanol specimens were included for studies on the external morphology of fishes and its squamation. Muscles were studied in dissected specimens; dissections were done by GA on the left side of specimens. Ligaments and tendons were observed with stereomicroscopes equipped with polarized light and phase contrast. Osteological structures were studied in cleared and double stained specimens for cartilage and bone following the techniques of Dingerkus, Uhler (1977) and Arratia, Schultze (1992). Scales from comparable body regions were studied on ethanol specimens; some scales were stained with a weak solution of alizarin to observe details under an Olympus compound microscope equipped with polarized light and phase contrast.

**Phylogenetic methodology for morphological characters.** Our major difficulty for this analysis is the controversy between the composition and taxonomic placement of percichthyids, perciliids and other percomorphacean taxa (see Tabs. 1, 2). For instance, between percichthyids *sensu* Johnson (1984) and other percomorphacean families and genera *incertae sedis*, the only morphological phylogeny published on the subject is that of Micklich (1987: fig. 16; see Fig. 1 herein), and percichthyids and perciliids were considered within the order Perciformes, as in Arratia (1982) and Johnson (1984). The most recent molecular hypotheses interpreted percichthyids as part of the Centrarchiformes (Betancur-R *et al., 2017*; Arcila *et al., 2017; Hughes et al., 2018). Considering the current information concerning the placement of percichthyids, we use in morphological comparisons different percomorphaceans belonging to a variety of families including other centrarchiforms, such as species from Acropomatidae, Centrarchidae, and Percalatoidei and further representatives, for instance Moronidae (see list of comparative material). Species of *Morone* and *Macquaria (= Percalates)* were used as the outgroup (see Material studied).

The phylogenetic analysis was conducted using TNT version 1.5 (Goloboff, Catalano, 2016) and tested with PAUP (Phylogenetic Analysis Using Parsimony) software (version 4.0b10) for 32-bit Microsoft (Swofford, 2000). In TNT, the optimal score was hit 20 times independently, using xmult plus 10 cycles of tree-drifting, while a heuristic search using a random addition sequence with 1000 replicates, and the three bisection and reconnection (TBR) branch-swapping algorithm was performed in PAUP. The character matrix was constructed using MacClade for the analysis to run in PAUP. All characters are unweighted, unordered, and considered to be independent of one another. The phylogenetic analysis used a list of 54 characters for 12 taxa. The data were analyzed in PAUP, including both ACCTRAN and DELTRAN optimization. Bootstrap support was done with 1000 replicates by TBR-swapping the trees found in TNT.
Mitogenomic analyses. We compiled published mitogenomes considered as part of Percichthyidae according to current molecular hypotheses (Lavoué et al., 2014; Betancur-R et al., 2017) from Prosdocimi et al. (2012; Nannoperca australis, Genbank accession no. JF519732; Nannoperca obscura, Genbank accession no. JF519733), Lavoué et al. (2014; Bostockia porosa, Genbank accession no. AP014529; Gadopsis bispinosus, Genbank accession no. AP014530; Nannoperca variegata, Genbank accession no. AP014535; Macquaria ambiguа, Genbank accession no. AP014533; Percichthys trucha, Genbank accession no. AP006791; and Percilia irwini, Genbank accession no. AP014528), Harrisson et al. (2016; Maccullochella macquaricensis, Genbank accession no. KT337329; Maccullochella peelli, Genbank accession no. KT337334; Maccullochella mariaensis, Genbank accession no. KT337327 and Maccullochella ikei, Genbank accession no. KT337324), Gan et al. (2016; Gadopsis marmoratus, Genbank accession no. KJ539519) and Pavlova et al. (2017; Macquaria australasica, Genbank accession no. KT152235).

Additionally, we sequenced the whole mitogenome of Percilia gillissi from the Maipo River (type locality), a second sample from south of Chile, and Percilia irwini from the Bureo River, Bio-Bío Basin, following Quezada-Romegialli et al. (2016a, 2016b). Briefly, total genomic DNA was extracted from dorsal muscle (Aljanabi, Martínez, 1997) and purified with the DNA Clean and Concentrator Kit (ZymoResearch, Irvine, CA, USA). Total DNA was sent to a next-generation sequencing facility (OMICS-Solutions, Santiago, Chile) and subjected to a shared run on an Ion Torrent PGM Sequencer (chip 318). Total reads per each sample were trimmed (at 5’ and 3’ low quality ends), filtered by quality (Q15/90% with FASTX-toolkit: http://hannonlab.cshl.edu/fastx_toolkit) and mapped to the closely related species Percilia irwini (Genbank accession no. AP014528; Lavoué et al., 2014) in GenoBios v8.0.5 (Biomatters Ltd., Auckland, New Zealand). Annotations of 13 protein-coding genes, ribosomal units and tRNA genes were confirmed in DOGMA (Wyman et al., 2004) and MitoFish (Iwasaki et al., 2013).

Considering the molecular hypotheses regarding the content and sister groups of Percichthyidae sensu stricto (Lavoué et al., 2014; Betancur-R et al., 2017), we explicitly excluded Macquaria (= Percalates) novemaculeata from the phylogenetic analysis (see Fig. 2), and used as outgroups the siniperbrids Coreoperca herzi (Park et al., 2015; Genbank accession no. KR075132), C. whiteheadi (Lv et al., 2016; Genbank accession no. KJ498111), Siniperca obscura (Chen et al., 2014; Genbank accession no. KC567664), S. roulei (Chen et al., 2014; Genbank accession no. KJ644782) and S. scherzeri (Chen et al., 2012; Genbank accession no. JN084101) and the cirrhitids Cirrhichthys aprinus (Yagishita et al., 2009; Genbank accession no. AP006011) and Paracirrhites arca~tus (Miyaj et al., 2013; Genbank accession no. AP006012); the ellosomatids Elassoma evergladei (Miyaj et al., 2001; Genbank accession no. AP002950) and E. zonatum (Setiamarga et al., 2008; Genbank accession no. AP006813); the centrarchids Micropterus dolomieu (Mukai, Sato, 2008; Genbank accession no. NC011361), M. salmoides (Brough-ton, Reneau, 2006; Genbank accession no. NC008106), Lepomis macrochirus (Li, Bai, 2001; Genbank accession no. JN389795) and L. gibbosus (Unpublished, Genbank accession no. KP013097); the enoplosid Enoplosus armatus (Yagishita et al., 2009; Genbank accession no. AP006008) and the cheilodactylids Cheilodactylus variegatus (Quezada-Romegialli et al., 2016c; Genbank accession no. KP704218), Ch. zonatus (Lavoué et al., 2014; Genbank accession no. AP006013) and Ch. quadricornis (Wang, Sun, Wu, 2016; Genbank accession no. KT357695).

Considering the 34 taxa, separate alignments were done with MAFFT (Katoh et al., 2002; algorithm FFT-NS-i × 1000, scoring matrix 1PAM / k = 2; excluding the control region) for (i) the 12S and 16S rRNA sequences, (ii) all the concatenated 22 tRNA genes, and (iii) the protein-coding genes. The protein-coding genes alignment was checked by eye with respect to the translated amino acid sequences. We inferred phylogenetic trees for three different character matrices: first, a partitioned data matrix concatenating the 13 protein-coding genes except third codon positions (7712 positions), 22 rRNA genes (1545 positions) and the two ribosomal RNA genes (2921) as an initial matrix (Mt1, three partitions). Second, a partitioned data matrix with the first (3856 positions) and the second codon positions (3856 positions) of 12 protein-coding genes concatenated, 22 tRNA genes (1545 positions) and the two rRNA genes (2921 positions; following Lavoué et al., 2014) as Mt2 (four partitions). Finally, a third data matrix (Mt3) was partitioned according to the best fit partitioning scheme calculated with PartitionFinder2 (Lanfear et al., 2016), considering as input the three codon positions of the protein-coding genes per separate (29 data blocks), plus the 22 tRNA genes (1 data block) and the two rRNA genes (1 data block). We searched for maximum likelihood (ML) phylogenetic trees using RAxML (Stamatakis, 2014) at the CIPRES Science Gateway (Miller, Pfieffer, Schwartz, 2010) under a GTR + Γ model (general time reversible model, following a discrete gamma distribution) and the rapid bootstrapping and search for best-scoring ML tree as search algorithm, with 1000 bootstrap replicates for assessing robustness of the internal branches.

Anatomical Terminology. The terminology of the skull roof bones follows the traditional terminology that differs from that based on homologization (e.g., Schultze, 2008). The skull roof traditional terminology is fundamentally based on human anatomy. For instance, the bone called “frontal” in traditional terminology actually corresponds to the parietal bone in actinopterygians. Identification and nomenclature of cephalic sensory canals follows Northcutt (1989). Identification and terminology of muscles follow Datovo, Vare (2013, 2014), with comparisons of previous terminologies used by Winterbottom (1974), Stiassny (1981), and Johnson (1984). We indicate some of the differences below. Scale types follow Schultze (1966) and Roberts (1993), even though we are not dealing specifically with different types of ctenoid scales, but those of percichthyids (McCully, 1970).
Results

Morphological characters and analysis. For explanation of characters see text below and for their coding see Tab. 3. [0] represents the plesiomorphic state; [1] and [2] the apomorphic states of a character. Non-applicable condition is represented with [-]. Presentation of characters follows body regions, except for a few miscellaneous ones presented at the end of this section. Most characters from Johnson (1984) are considered below; however, the construction of each character, including its character states, is based on our polarization depending on our outgroup (see Material and Methods).

Scales. Ch. 1. Ctenoid scales bearing simple, slightly amputated needle-like ctenii (during most of the life of the individual or late in ontogeny): absent [0]; present [1]; see Fig. 10. Character modified from Johnson, 1984.

Ch. 2. Whole posterior field of ctenoid scales filled with slightly amputated needle-like ctenii: absent [0]; present [1]; non-applicable because of other condition, e.g., cycloid scales [-]. See Fig. 10.

Ch. 3. Only cycloid scales present on cheek region: absent [0]; present [1].

Ch. 4. Skin of maxilla covered with scales: present [0]; absent [1].

Comments. Fossil stem teleosts may have ganoid scales of lepisosteid-type and amnoid-type (Schultze, 1966), whereas the presence of cycloid scales is a synapomorphy at the level of Leptolepis coryphaenoides plus more advanced teleosts or “true” teleosts (Arratia, 1997, 2015, 2017). The crown teleosts share the presence of cycloid scales and its further transformations (e.g., ctenoid and serrated scales) in some euteleost groups. The posterior exposed field of a scale may be smooth or with a serrated or pectinated posterior border or bear small ctenii (Schultze, 1966; Roberts, 1993; Fig. 10). In strict terms, scales bearing ctenii are ctenoid scales; however, pectinated and serrated scales have also been named ctenoid.

Both ctenoid and serrated scales develop from cycloid scales, and they represent evolutionary transformation of the cycloid pattern (Schultze, 1966). This is also supported by ontogenetic changes, as shown by small specimens bearing cycloid scales that develop ctenii in their posterior field. Ctenoid scales (Fig. 10) may lose their ctenii in the oldest individuals—as shown in large Percichthys chilensis and P. melanops—but always keep remnants of the ctenoid condition. Radial furrows or radii may develop in the anterior field of cycloid scales and are consistently present in percichthyids bearing ctenoid scales (Fig. 10). Ctenoid scales may adopt a variety of shapes and modifications of the ctenii within percomorphaceans (Robert, 1993), which are features in need of further investigation.

The presence of scales with simple, only slightly amputated needle-like ctenii (Fig. 10) was noticed first by McCully (1970) and later was proposed as a synapomorphy of percichthyids by Johnson (1984:p. 469). It is interesting to clarify that this feature is absent in some of the Australian temperate basses or perciliids with only cycloid scales (e.g., Bostockia, Gadopsis and Nannatherina; see Tab. 3), and their scales were interpreted as secondarily cycloid by Johnson (1984), but see section of Results. The ctenii develop as needle-like with sharp tips, and they lose their tips during growth. Thus, needle-like ctenii are observed at the posterior margin of the scale, whereas oldest rows near the focus of the scale present truncated ctenii.

Lateral line canal. Ch. 5. Series of scales carrying the lateral line sensory canal: complete [0]; interrupted or reduced [1].

Comments. The lateral line may be continuous and positioned through a complete series of scales along the body (the common condition observed in percichthyids), or it may be interrupted or continuous, but runs throughout an interrupted series of scales (e.g., Percilia; Arratia, 1982). Ramifications of the lateral line at the level of its maximum curvature have been observed in some individuals of Percichthys colhuapiensis. A reduced, interrupted or absent lateral line canal is present in the Australian genera Nannoperca, Nannatherina, and Bostockia among the studied fishes (see also Johnson, 1984). In contrast, Gadopsis has a continuous lateral line (see Tab. 3).

Position of lower jaw versus anterior margin of snout. Ch. 6. Anterior tip of the lower jaw: projecting in front of premaxilla/upper jaw [0]; premaxilla placed at the same level [1]; slightly posterior to premaxilla [2]. See Figs. 11 and 12.

Comments. A lower jaw (Fig. 11) that projects anterior to the anterior margin of the snout is the generalized condition among the studied percomorphaceans. Among the studied specimens, three conditions are present:

1) The lower jaw extends anterior to the premaxilla (e.g., Bostockia diagramma, Macquaria (= Percalates) colonomum, Percichthys colhuapiensis, and Macquaria (= Plectrotipes) ambigua; Figs. 11b-d). This pattern represents the primitive character state by comparison to the outgroup (Fig. 11a).

2) The anterior tip of the lower jaw and premaxilla are at the same level (e.g., Nannoperca australis, Nannatherina balstoni, and Percichthys melanops; Figs. 12b, c).

3) The premaxilla projects anterior to the lower jaw (e.g., Gadopsis marmoratus, Macrochelota macquarensis and Percilia gillissi; Figs. 12a, d); however, in certain individuals of Percilia the lower and upper jaws are at the same level.

Given the differences on the position of the premaxilla relative to the lower jaw, the osteology and ligaments of the anterior part of the head of all mentioned fishes were investigated without finding synapomorphies that could characterize the percichthyids; though variation among the fishes was used for comparisons.
Fig. 10. Scale structure. a, ctenoid scale of *Percichthys chilensis* from the dorsal region of the trunk, posterior to the pectoral girdle; b, detail of the posterior region of the scale showing needle-like ctenii and amputated ctenii (some are indicated by arrows); c, detail of a ctenoid scale of *Percilia gillisi* from the dorsal region of the trunk, posterior to the pectoral girdle; d, cycloid scale on the head and/or body of some percichthyids. af = anterior field; ct = ctenii; fc = focus; pf = posterior field; rd = radii.

Tab. 3. Character-taxon data matrix for 54 characters used in the phylogenetic analysis. State [N] represents the character is not applicable. State P represents a polymorphic character coded as 0/1 in the matrix.
Position of the quadrate-mandibular articulation. Ch. 7. Quadrate-mandibular articulation placed: below the middle of the orbit [0]; below the anterior half of the orbit or anterior to it [1]; below the posterior half of the orbit or posterior to it [2]. See Fig. 13.

Comments. In most examined taxa, the quadrate-mandibular articulation (Fig. 13b) is placed below the posterior half of the orbit or posterior to it (e.g., Gadopsis, Maccullochella, Nannatherina, and Percichthys colhuapiensis). In Percilia, the quadrate-mandibular articulation is placed below the anterior margin of the orbit (Fig. 13d), a condition also observed in Bostockia. In Percichthys chilensis and P. melanops, the articulation is placed at the mid-region of the orbit or posterior to it (Fig. 13c) so that the lower jaw is short. Among Percichthys, the quadrate-mandibular articulation is placed below the middle region of the orbit or posterior to it. Consequently, the longest lower jaw, is present in P. colhuapiensis (Fig. 13b) with the quadrate-mandibular articulation posterior to the orbit. The length of the lower jaw justifies its common name “perca bocona” (= perch with a big mouth), a feature used to characterize this percichthyid (MacDonagh, 1955; Ringuette et al., 1967).

Fig. 11. Anterior section of the head of certain percomorphaceans in lateral view; arrow points to the position of the anterior margin of the lower jaw. a, Morone chrysops (KU:KUI 22669); b, Macquaria (= Percalates) colonorum (CAS 24427); c, Percichthys colhuapiensis (CAS 31614); d, Macquaria (= Plectroplites) ambigua (CAS 24429).
Position of posterior margin of maxilla. Ch. 8. Posterior end of maxilla positioned: below the anterior half of the orbit or anterior to the orbit [0]; below the posterior half of the orbit [1]. See Figs. 4, 11–13.

Comments. Although the maxilla presents differences in the shape of the articular process for the palatine, or in the curvature between the articular anterior processes and the body of the palatine, we could detect no significant character that could be unique to percichthyids. However, the length of the maxilla may be of some value. A maxilla whose posterior end lies below the anterior half of the orbit or in front of the orbit is interpreted here to represent the plesiomorphic condition (e.g., in Bostockia, Gadopsis, Macquaria australasica, and Percichthys melanops; Figs. 11, 13c) by comparison with the outgroup (Fig. 11a). In contrast, a maxilla that extends below the middle or posterior half of the orbit is interpreted here as an advanced feature (e.g., Nannatherina, Percichthus colhuapiensis, Maccullochella macquarensis, and Macquaria (= Plectroplites) ambigua; Figs. 11, 12).

Fig. 12. More anterior sections of percomorphacean heads in lateral view; arrow points to the position of the anterior margin of the lower jaw. a, Maccullochella macquarensis (CAS 20790); b, Macquaria australasica (CAS[SU]) 20971; c, Percichthys melanops (CAS 1555); d, Percilia gillissi (KU:KUI 19243).
The length of the maxilla varies in *Percichthys colhuapiensis*; it ranges from the posterior half of the orbit to posterior to it (Figs. 4d, 11c, 13b). The position of the posterior end of the maxilla, and therefore the maxillary length, may be of taxonomic value; for instance, in *Percichthys melanops* the maxilla is short, usually reaching the anterior rim of the orbit (Fig. 12); in contrast, the maxilla is longer, reaching the anterior half of the orbit in *Percichthys chilensis* (Figs. 4a-c).

**Skin and mandibular sensory canal.** *Ch. 9. Large depressions on the skin that cover the dentary (the last one lies between dentary and anguloarticular):* Less than 3 [0]; three [1]; four [2]; without depressions [3]. See Figs. 14 and 15.

*Ch. 10. Only slit-like pores opening in the skin that cover the dentary: absent [0]; present [1]. See Figs. 14, 15.*

*Ch. 11. Slit-like pores and numerous small round pores present together in the skin that cover the dentary in large individuals: absent [0]; present [1]. See Figs. 14, 15.*

*Ch. 12. Only a few, independent round pores on the skin of the dentary: absent [0]; present [1]. See Figs. 14, 15.*

**Comments.** The mandibular canal extending from the posterolateral side of the anguloarticular to the anterior part of the dentary exits to the skin through a series of pores (most examined species). The external exits of the mandibular canal perforate the skin in young specimens (e.g., *Macquaria (= Plectroplites) ambigu*a, *Percichthys colhuapiensis, P. chilensis, and P. melanops*). However, in large specimens the count of pores and their size may be difficult, because the fish may still have all pores opened or a few of them closed (e.g., individual of 345 mm standard length of *Percichthys colhuapiensis*). Therefore, the study of the pores of the mandibular canal opening on the skin may be misleading if someone does not consider their ontogenetic variation.

Those regions of the skin of the lower jaw where pore(s) will open during ontogeny are associated with oval or round depressions (Figs. 14, 15) that are easy to observe in an external examination of the skin. Three or four depressions are commonly present in percichthyids. *Percilia* (Fig. 14d), as well as *Nannatherina* and *Nannoperca*, does not have depressions. Less than three depressions are found in *Morone* (Fig. 14a; see Tab. 3).

As above stated, pores begin to perforate the skin of the depressions of the lower jaw during growth. The common condition found in the taxa used for comparisons is the presence of numerous small pores irregularly placed in such depressions (e.g., *Acropoma, Synagrops*, and *Lateolabrax*); this condition is also present in *Macquaria (= Percalates) colonorum* (Fig. 14b). The pores may be slit-like or oval-shaped and placed at the posterior corner of a depression (e.g., *Macullochella, Macquaria australasica, Macquaria (= Percalates) ambigu*a and *Percichthys*; Figs. 14, 15), or round (*Percilia; Fig. 14d), or there may be a combination of slit-like pores and small numerous pores (e.g., *Macquaria (= Percalates) colonorum*; Fig. 14b).

The presence of “enlarged sensory pores of the dentary” is a character mentioned by Johnson (1984:p. 469) for *Plectroplites, Macquaria, Macullochella, Percichthys,* and *Percilia*. However, this statement is not supported by the specimens studied and illustrated in Figs. 14-16 herein.

*Ch. 13. Pore 1 or the most anterior of the mandibular sensory canal placed on the skin: at the most anterior portion of the dentary [0]; absent [1].

**Comments.** The first pore of the mandibular canal usually is round or oval, and it may open late in ontogeny (e.g., *Percichthys chilensis, P. melanops, and P. colhuapiensis*). The first pore is on the skin that covers the anterior part of the dentary. The first pore location varies. It may be positioned anteriorly or ventrally in the jaw (Figs. 14-16). When the first pore has an anterior placement, it is not observed in a ventral view of the head, with the exception of *Macullochella* (Fig. 14c). The anterior position of the pore represents the generalized condition among the studied fishes. The first pore is absent in *Percilia, Bostockia, Nannatherina, and Nannoperca* (e.g., Figs. 16a, b).

*Ch. 14. Mandibular canal is: enclosed in a bony tube in the dentary [0]; on a groove along most of the dentary [1]. See Figs. 12, 16 and 17.*

**Comments.** The mandibular canal (Figs. 12a, d, 16a) is placed in the dentary and the angular portion of the anguloarticular, enclosed in a bony tube that has openings to the skin (most common condition). The mandibular canal (Figs. 12b, c, 16b, c) is placed in a groove on the lateral aspect of the dentary and anguloarticular in *Bostockia, Macquaria australasica, Percichthys chilensis* and *P. melanops* (see Tab. 3).

There are some differences in the size of the openings in the dentary that may be of taxonomic value. For instance, *Percilia irwini* has the most enclosed canal among all examined taxa, and in *Percilia gillissi*, the pores are comparatively larger.

**Skin, infraorbital canal and infraorbital bones.** *Ch. 15. Slit-like or oval pores on the skin covering infraorbital 1: absent [0]; present [1]. See Figs. 11 and 12.*

*Ch. 16. Infraorbital sensory canal on infraorbital 1: is enclosed by bone, in a tube with small or large openings [0]; is in a groove, without forming openings in the bone [1]. Figs. 11-13, 17.*

*Ch. 17. Infraorbital canal emerges from infraorbitals 3 to 5 throughout (or posterodorsal infraorbitals): short, simple tubules [0]; ramified tubules [1]; no tubules [2].
Fig. 13. Position of the quadrate-mandibular articulation—indicated by arrows—in certain percomorphaceans with the mouth open. **a**, Morone saxatilis (KU:KUI 18212); **b**, Percichthys colhuapiensis (KU:KUI uncat.); **c**, Percichthys melanops (USNM 312977); **d**, Percilia gillissi (KU:KUI 19241). ang-ar = anguloarticular; de = dentary; fr = frontal bone of traditional terminology; io1 = infraorbital 1; max = maxilla; na = nasal bone; pmx = premaxilla; rar = retroarticular; smax = supramaxilla.
Fig. 14. Anterior part of the head in ventral view illustrating the position of depressions (darker oval or round regions) and slit-like pores of the mandibular canal in certain percomorphaceans. Small, round pores are indicated by arrows. a, *Morone chryssops* (KU:KUI 22699); b, *Macquaria (= Percalates) colonorum* (CAS 24427); c, *Percichthys colhuapiensis* (KU:KUI uncat.).
Fig. 15. More anterior parts of the head in ventral view illustrating the position of depressions (darker oval or round regions) and slit-like pores of the mandibular canal in certain percomorphaceans. Small, round pores are indicated by arrows. a, *Maccullochella macquariensis* (CAS 20790); b, *Percichthys melanops* (CAS 15555); c, *Percilia gillissi* (KU:KUI 19423).
Fig. 16. Lower jaws in lateral view illustrating the trajectory of the mandibular sensory canal (oblique lines) and its pores and their sizes (in black). a, Percilia gillissi; b, Bostockia porosa (USNM 218841); c, Percichthys chilensis; a and c modified from Arratia (1982). ang-ar = anguloarticular; de = dentary; p1–6 = pores 1–6; rar = retroarticular.

Comments. The pores of the infraorbital canal that open through the skin of infraorbital bones 1 and 2 have different shapes within the studied fishes. Usually they are round (the generalized condition), however, slit-like or oval pores are characteristic of percichthyids.

The infraorbital sensory canal is partially or totally enclosed by bone in infraorbital 1 in most examined taxa (Figs. 13a, b, 17); however, it is in a groove, only partially protected by a small ossification at its anterior portion in fossil and extant species of Percichthys chilensis, P. melanops and P. colhuapiensis (Figs. 13b, c). A similar condition is observed in †Santosius antiquus from the Tertiary of Brazil (Arratia, 1982:text-fig. 91).

The infraorbital canal associated with infraorbital bones 3 to 5 may exit to the skin by short, simple and few (two or three, usually) tubules, each opening to the skin through a round pore (e.g., Percilia gillissi and P. irwini), or ramified tubules (Figs. 11d, 12b) exit through many pores (e.g., Macquaria australasica, Macquaria [= Plectroplites] ambiguа) and specimens used in comparisons.

Ch. 18. Additional bones between infraorbitals 1 and 5: absent [0]; present [1]. See Fig. 17 and Arratia (1982).

Comments. Six infraorbitals (including the most dorsal bone that may correspond to the dermosphenotic at the junction of the supraorbital, infraorbital, and otic canals; otic and postotic canals were named temporal canals by Vega, Viozzi, 2016) represent the common condition found in most fishes examined herein (Figs. 13b, c). In contrast, Percilia commonly presents more infraorbitals (7 or 8), because of the presence of an additional bone-bearing canal between infraorbitals 1 and 2. Arratia (1982:p. 34) interpreted the presence of a high number of infraorbitals in Percilia as the primitive condition from which would be a reduction of elements due to fusion. Additional infraorbitals are also observed in Nannotherina and Nannoperca (Fig. 17). The high number of infraorbitals is re-interpreted herein as an apomorphic condition by comparison with the outgroup and other fishes examined (see Material studied). A reduction of infraorbitals is found in some individuals of Percichthys trucha and P. melanops (Arratia, 1982) that is due to fusion of infraorbitals 3 and 4 or 4 and 5, as illustrated by the size of the bones and the presence of fusion lines.

Ch. 19. Ventral margin of infraorbital 1: smooth [0]; serrated [1]. See Figs. 13 and 17 and Arratia (1982).

Ch. 20. Ventral margin of infraorbital 2: smooth [0]; serrated [1]. See Figs. 13 and 17 and Arratia (1982).

Comments. The presence of a serrated ventral margin of infraorbital 1 (Figs. 13b, c) is the common condition found in most perichthyids. An infraorbital 1 bearing a smooth ventral margin (Figs. 13d, 17) is present in Bostockia, Gadopsis, Nannotherina, Nannoperca, and Percilia, among fishes studied here. The degree of serrations on infraorbitals 1 and 2 may be diagnostic at the species level. For instance, infraorbital 1 and 2 are highly serrated from early ontogeny in Percichthys melanops. In contrast, P. chilensis develops fewer serrae during growth in comparison to P. melanops (Arratia, 1982). Among fossil percichthyids, infraorbital 3 bears serrae in both fossil species, †Percichthys lonquimayensis (Arratia, 1982:text-figs. 88, 89) and †Santosius antiquus (Arratia, 1982:text-figs. 85, 91).

Ch. 21. Subocular shelf: present in infraorbital bone 3 [0]; in infraorbital 2 [1]; absent [2].
The absence of a subocular shelf was mentioned first by Johnson (1984) for *Bostockia*, *Gadopsis*, *Nannatherina*, and *Nannoperca*. The study of this structure has shown that when the subocular shelf is present, it may be associated with infraorbital 2 or 3 in different species, indicating that the bone bearing the shelf should be identified to make comparisons possible, and consequently, homology statements.

**Supraorbital canal and epiphyseal pore. Ch. 22.** One epiphyseal pore opens in the skin that covers the frontal bone just at the postorbital region: absent [0]; present [1].

**Comments.** One medial pore associated with both epiphyseal tubules (named “supraorbital commissure” by Vega, Viozzi, 2016) of the supraorbital canal is present in most examined taxa. The median epiphyseal pore is placed between both orbital margins of the frontal bones, at the mid-region of the preorbital region in *Percilia*. It lies at the level of the autosphenotic or posterior to the preorbital region of the frontal bones in most examined taxa. In some of the species used for comparisons, the pore is confused among the ramifications and pores of the supratemporal canal (*e.g.*, *Morone* and *Percalates* [= *Macquaria* colonorum]).

**Ch. 23. Basisphenoid: present [0]; absent [1]. Character from Johnson (1984).**

**Comments.** Among the studied taxa, *Bostockia* and *Gadopsis* share the absence of the basisphenoid.

**Ch. 24. Palatine (auto + dermopalatine) extending posterior to the orbital process of the lateral ethmoid by: a short posterior process or no process [0]; a long posterior process [1]. See Fig. 18.**

**Comments.** The auto plus dermopalatine (the so-called palatine) is a compound bone that results from the early ontogenetic fusion of the chondral autopalatine that originates at the anterior corner of the palatoquadrate, the *pars autopalatina* (Arratia, Schultze, 1991), and a dermal component bearing teeth, which is named dermopalatine.
An elongate auto + dermopalatine or palatine (Fig. 18a) that extends posterior to the lateral ethmoid is present in all examined taxa, except Nannoperca and Percilia (Fig. 18b). In Percilia and Nannoperca (as well as in the outgroup), the palatine is only represented by its anterior section that articulates anteriorly with the maxilla and posteriorly with the lateral ethmoid. The articulation between palatine and lateral ethmoid is a hinge joint in all studied percomorphaceans.

Ch. 25. Palatine (auto + dermopalatine) bearing: few or no teeth [0]; numerous teeth [1]. See Fig. 18.

Comments. All taxa examined herein—with the exception of Nannoperca, Percilia, and the outgroup, Morone—have numerous teeth along the complete or almost complete length of the palatine (Fig. 18a). In Percilia, a few (1 to 5, commonly 2) are present on the ventrolateral margin of the palatine (Arratia, 1982:text-figs. 23, 24); the teeth are so small and scarce in number that former authors described Percilia as lacking teeth on the palatine and vomer (Eigenmann, 1927; Fowler, 1951).

Ch. 26. Toothed ectopterygoid: absent [0]; present [1].

Comments. Among the studied taxa, Nannatherina and the outgroup Macquaria (= Percalates) colonorum have ectopterygoid dentition.

Ch. 27. Supramaxilla: absent or atrophic [0]; present [1].

Comments. The presence of a supramaxilla represents the generalized condition in percomorphaceans; however, the bone is absent in the outgroup (Morone). Most percichthyids have a small, elongate, well-ossified supramaxilla abutting on the postero-dorsal margin of the maxilla, a condition that is absent in Percilia. An atrophic supramaxilla is present in Percilia (Fig. 18a; Arratia, 1982:text-figs. 13, 14), whereas the bone is absent in the Australian genera Gadopsis, Nannatherina, and Nannoperca (Fig. 17).

Ch. 28. Dorsoposterior region of dentary (part of coronoid process): broad, and slightly rounded [0]; elongate and narrow [1]. See Figs. 16 and 17.

Ch. 29. Preopercle with numerous strong serrae in lower arm [0]; with few or no serrae [1].

Ch. 30. Opercle with a well-defined main spine and a smaller dorsal one: present [0]; absent [1].

Ch. 31. Anterior ceratohyal with: a “beryciform-like” foramen opening dorsally [0]; with its dorsal margin slightly concave [1]; a round or oval foramen (= beryciform foramen) that is bony enclosed [2].

Comments. Among the studied species, a beryciform foramen is present in Percilia (Arratia, 1982:text. figs. 26-29); see Tab. 3 for distribution of character states.

Ch. 32. Number of branchiostegal rays: seven or more [0]; six or fewer [1].

Comments. This character was mentioned first (= “reduced number of branchiostegals”) by Johnson (1984:p. 369) for Nannatherina, Nannoperca, and Bostockia, but a number was not given. This feature is problematic due to its variability; for instance, Percichthys chilensis, P. colhuapiensis, and Percilia may have seven or six branchiostegals (see Tab. 3 and Arratia, 1982:tab. 1).

Fig. 18. Palatine or auto + dermopalatine and associated bones in (a) Percichthys melanops (USNM 312977) and (b) Percilia gillissi (KUI:KU 19241). apa+dpa = auto plus dermopalatine or palatine; fr = frontal bone of traditional terminology; lat.et = lateral ethmoid; l.na-max = ligament extending between nasal and maxilla; max = maxilla; met = mesethmoid; na = nasal bone; pmx = premaxilla; ro.c = rostral cartilage; smax = supramaxilla; vo = vomer.
South American and Australian percichthyids and perciliids

Vertebral column and fins. Ch. 33. Number of vertebrae: less than 55 [0]; 25 to 30 [1]; 30 to 40 [2].

Comments. A similar vertebral number (29-33) was interpreted as a synapomorphy of *Bostockia*, *Nannatherina*, and *Nannoperca* by Johnson (1984). However, and based on the variation present in the studied taxa, the character is re-interpreted here with three states. Among the Australian taxa, *Gadopsis* has 48 or 49 vertebrae. The number of vertebrae of the Chilean species of *Percichthys* and *Percilia* varies between 30 and 36 (Arratia, 1982:tab. 1).

Ch. 34. Supraneural (= predorsal) bones: three to five [0]; two or one [1]; none [2].

Comments. The number of predorsal bones (= supraneurals of Mabee, 1988) is considered an important taxonomic feature in the identification of percomorphaceans (e.g., Johnson, 1984:tab. 120; Arratia et al., 2004), including the so-called percichthyids (e.g., Arratia, 1982; Micklich, 1987). However, as shown by Arratia (1982), the number can vary from 2 to 5 in *Percilia* and is less variable in *Percichthys chilensis* and *P. melanops* with 3 or 4 bones. The Australian *Gadopsis* and *Bostockia* are characterized by one supraneural or its absence. Additionally, when this element is present, it does not resemble a pterygiophore-like supraneural, but the thin, elongate supraneural of teleosts outside percomorphaceans.

Ch. 35. Lateral line or postotic canal enclosed by a tube-like canal on the upper third of the supracleithrum: present [0]; absent [1]. Modified from Johnson (1984).

Comments. The absence of the supracleithral sensory canal or lateral line was proposed as a synapomorphy of the Australian genera *Bostockia*, *Nannoperca*, and *Nannatherina* (Johnson, 1984) and also *Gadopsis* (see Tab. 3 for distribution of this character).

Ch. 36. Postpelvic process in basipterygium: well-defined and elongate [0]; short or rudimentary [1].

Comments. Gosline (1966) considered a relatively long postpelvic process a diagnostic feature of his Percichthyidae. A well-defined elongate process (ca. 5 to 10 times in the basipterygium length) is common to the outgroup and most of the studied taxa, with the exception of the Australian *Bostockia*, *Gadopsis*, and *Maccullochella*, which have a short or rudimentary process. See Arratia (1982:tb. 5) for variation concerning the elongate postpelvic process.

Ch. 37. Pectoral fin with a long filament: absent [0]; present [1].

Comments. A pectoral ray projected in a long filament is present in *Percichthys chilensis* and *Maccullochella* (see Tab. 3).

Ch. 38. Long dorsal fin, reaching or almost reaching the origin of caudal fin: absent [0]; present [1].

Ch. 39. Number of rays in the dorsal fin: 10-15 [0]; over 16 rays [1].

Comments. Among the studied taxa, the greatest numbers of dorsal fin rays are found in *Bostockia* (with more than 16 rays) and *Gadopsis* (with about 30). A reduced number of dorsal spines was suggested as a synapomorphy of *Bostockia*, *Nannatherina*, and *Nannoperca* by Johnson (1984). Two or three dorsal spines are present in *Gadopsis* (among the studied taxa), a feature that has been used to distinguish *G. marmoratus* (commonly 3) and *G. bispinosus* (commonly 2).

Ch. 40. Number of uroneurals in the caudal endoskeleton: two or more [0]; one [1]. Arratia (1982) and Johnson (1984). See Fig. 19.

Fig. 19. Caudal skeleton in lateral view. a, *Percichthys chilensis* (slightly modified from Arratia, 1982). b, *Nannatherina balstoni* (USNM 289205). CC = compound terminal centrum; E1-3 = epurals 1-3; H1, H5 = hypural 1, 5; PH, parhypural; ST = modified uroneural or stegural; UN2 = second uroneural (numeration of uroneural does not imply homology).

e180102[28]
Comments. Part of the taxa studied here (including the out-group) present two uroneurals; however, only one uroneural (= stegural) is present in Percilia (Arratia, 1982:text-figs. 79-81) and the Australian Bostockia, Gadopsis, Nannatherina, and Nannoperca; the second, splint-like uroneural presents in percichthyids, is absent.

Ch. 41. Number of epurals: three [0]; two [1]. See Fig 19.

Comments. The “absence of a third epural” was proposed as a synapomorphy of Bostockia and Gadopsis by Johnson (1984:p. 469). In contrast, all other taxa studied here have three epurals.

Ch. 42. Procurrent spur: present [0]; absent [1].

Comments. A procurrent spur at the ventral margin of the base of the posteriormost ventral procurrent ray is a character present in most perciforms (Johnson, 1975). However, a spur is missing in several taxa studied here, e.g., Bostockia, Nannatherina, and Nannoperca (see also Johnson, 1984). In others, its presence may be intraspecifically variable, as for instance in Percichthys chilensis and P. melanops, with a very small spur when it is present. A spur is absent in most specimens of Percilia, and when it is present, is rudimentary.

Ch. 43. Number of dorsal procurrent: 10 or more rays [0]; less than 10 rays [1].

Comments. Reduced numbers of procurrent rays was mentioned as a synapomorphy shared by Bostockia, Nannatherina, and Nannoperca by Johnson (1984:p. 469), without establishing differences between the dorsal and ventral series of procurrent rays. Thus, the character has been changed, and both series are treated as separated for comparative and homology purposes.

Ch. 44. Number of ventral procurrent: 8 or more rays [0]; 7 or less [1].

Comments. See character 43.

Adductor mandibulae muscle. Ch. 45. Adductor mandibulae muscle includes: a large mass formed by pars malaris plus pars rictalis (= ricto-retromalaris) [0]; distinct pars malaris and pars rictalis [1]. See Fig. 20.

Comments. The generalized condition among perciformaceans, particularly among lower forms, is a single muscle mass (Fig. 20a) present on the lateral aspect of the supensorium (e.g., Winterbottom, 1974; Stiassny, 1981; A. Datovo, pers. communication; November, 2018). The presence of a single mass (pars malaris plus pars rictalis) is the condition found in the outgroup Morone (Fig. 20a), as well as in Maccullochella and Percichthys colhuapiensis (Fig. 20c). (However, two separate masses were observed in Morone mississippiensis by Datovo, pers. communication). Two separate muscle masses (pars malaris and pars rictalis) are found in various fishes here studied, e.g., Macquaria (= Plectroplites) ambiguus, Macquaria australasica (Fig. 20f, g), Gadopsis, and Nannoperca (see Tab. 3 for distribution of the character). However, both conditions may be found in some individuals of Percichthys chilensis. In Macquaria (= Percalates) novemaculata and Macquaria (= Percalates) colonorum, there are two muscle masses (Fig. 20b).

Ch. 46. Promalaris: absent [0]; present [1]. See Fig. 20.

Comments. A separated inner division of adductor mandibular section A1 (= promalaris sensu Datovo, Vari, 2013) is a synapomorphy of the family Percichthyidae sensu Johnson (1984). However, a promalaris is not found in all the so-called percichthyids sensu Johnson, 1984 (see Fig. 20 and Tab. 3). The promalaris is not present in Percilia, Nannatherina, and Nannoperca (Fig. 20d; Tab. 3).

Ch. 47. Promalaris: absent [0]; a fleshy connection unites it the main muscle mass of pars malaris [1]; separated from pars malaris and has a tendinous connection to hyomandibula and maxilla [2]. See Fig. 20.

Comments. In Percichthys trucha and P. melanops the promalaris may be separated from pars malaris (Fig. 20e) and connects by independent tendons to the hyomandibula and maxilla. Promalaris may have a fleshy attachment to the main section of pars malaris (e.g., Maccullochella macquarenensis and Percichthys colhuapiensis; Fig. 20c) and to the buccopalatal membrane plus imbedded ligaments (e.g., Macquaria australasica; Fig. 20g).

Levator arcus palatini muscle. Ch. 48. Large subdivision of the levator arcus palatine muscle with fibers almost 90 degrees to the cranial roof bones: absent [0]; present [1]. See Fig. 20.

Ch. 49. Dilatator operculi placed almost horizontal to the main section of the muscle: absent [0]; present [1]. See Fig. 20.

Comments. Commonly, the levator arcus palatine (Fig. 20) is a small muscle in all taxa examined, except in Maccullochela macquarenensis and Percichthys colhuapiensis (Fig. 20c). In these fishes, the muscle is particularly large, with most fibers lying almost 90 degrees to the cranial roof bones. The enlargement of the muscle seems to be correlated with the enlargement of the autosphenetic. In addition, the position of a separate section of the dilatator operculi (Fig. 20c) dorsal to the lateral surface of the autosphenetic and pterotic is unique to Percichthys colhuapiensis and Maccullochela macquarenensis among the examined percichthyids.

Miscellaneous characters. Ch. 50. Distinctive (asymmetric) nasal rosette: absent [0]; present [1]. Character from Johnson (1984).
Fig. 20. Semi-diagrammatic illustrations of the *adductor mandibulae* and *dilatator opercula* muscles in certain percomorphaceans. **a**, *Morone chrysops* (KU:KUI 22669); **b**, *Macquaria (= Percalates) colonorum* (CAS 20786); **c**, *Maccullochella macquarensis* (CAS 20790) and *Percichthys colhuapiensis*; **d**, *Percilia gillissi* (KU:KUI 19243); **e**, *Percichthys melanops* (CAS 70006); **f**, *Macquaria (= Plectroplites) ambiguа* (CAS 24429); **g**, *Macquaria australasica* (CAS 20971). bp.m = bucco-palatal membranes with embedded ligaments; d.lap = division of *levator arcus palatini* that covers laterally the *dilatator operculi* muscle; d.op = *dorsalis opercularis* muscle; l.ap = *levator opercularis* muscle; rmal = *ricto-retromalaris* muscle; pmal = *promalaris* or inner section of adductor mandibulae; pop = preopercle; ri = *rictalis* muscle; sl.ap = subdivision of *levator arcus palatini* muscle; t = tendon.
Ch. 51. Tubular anterior nostril placed near the margin of the lip: absent [0]; present [1]. Character from Johnson (1984).

Comments. A distinctive nasal rosette and a tubular anterior nostril placed near the margin of the upper lip are morphological features shared by Bostockia and Gadopsis and were first mentioned by Johnson (1984). A similar anterior nostril is also present in Maccullochella peeli (Fig. 12a) among the studied fishes.

Ch. 52. Premaxillary frenum: absent [0]; present [1]. Character from Johnson (1984).

Comments. A premaxillary frenum has been observed in Gadopsis and Maccullochella among the studied fishes.

Ch. 53. Trigeminal pterygiophores: absent [0]; present [1]. Character from Johnson (1984).

Comments. Trigeminal pterygiophores have been observed in Bostockia, Nannatherina, and Nannoperca.

Ch. 54. Semidemersal, non-adhesive eggs: absent [0]; present [1].

Comments. The reproductive mechanism is unknown in most percichthyids; however, MacDonagh (1955) suggested that Percichthys trucha (from Argentina) and Percichthys colhuapiensis are protandrous hermaphrodites. Percilia gillissi is a protandrous hermaphroditic (GA pers. observation). Hermaphroditism is known in other percoids, such as Centropistes (Lavenda, 1949), Diplectrum and Prionodes (Longley, Hildebrand, 1941), Alphestes, Cephalopholis, Epinephelus, Myctoperca, and Petrometodon (Smith, 1959).

The eggs of the studied specimens may be:
1) Pelagic (Percalates, probably; Breder, Rosen, 1966).
2) Demersal and adhesive (e.g., Percichthys colhuapiensis [Fuster de Plaza, Plaza, 1955]; Nannoperca oxleyana [Knight, Trnski, 2011]; and probably Maccullochella [Lake, 1959]).
3) Slightly demersal and non-adhesive (e.g., Macquaria [= Plectroplites] ambigua and probably other species of Macquaria [Lake, 1959]).
4) Eggs of Percilia gillissi are deposited in the gastric cavity of the freshwater sponge Spongilla ilgiformis wherever they develop (Kilian, Campos, 1969). To the best of our knowledge no percichthyid or centrarchiform is known for this behavior.

Phylogenetic analysis and results: morphological characters. Phylogenetic Analysis. To assess the phylogenetic relationships of Percilia and percichthyids, we have performed a cladistic analysis including 12 taxa and 54 morphological characters. The coding of 54 characters is presented in Tab. 3. Two parsimony analyses were performed using Morone as the outgroup. The parsimony analysis recovered one tree of 116 steps (retention index = 0.647; consistency index = 0.566).

Figure 21 represents the topology of the tree found, which suggests two well-supported clades identified here, in a preliminary way, as Perciliidae (Node B) and Percichthyidae (Node C).

Node B. Perciliidae. The monophyly of the family Perciliidae is supported by eight synapomorphies: Absence of scales on the skin of maxilla (Ch. 4[1]); series of scales carrying the lateral line canal interrupted or reduced (Ch. 5[1]); without large depressions on the skin that covers the dentary (Ch. 9[1]); with a few independent round pores on the skin of the dentary (Ch. 12[1]); pore 1 or the most anterior of the mandibular sensory canal placed at the most anterior portion of the dentary absent (Ch. 13[1]); with more than five infraorbital bones (Ch. 18[1]); preopercle with few or no serrae in lower arm (Ch. 29[1]); and one uroneural (= stegalural) present (Ch. 40[1]). The family Perciliidiae comprises the South American genus Percilia and the Australian genera Bostockia, Gadopsis, Nannatherina, and Nannoperca.

Node B1. The branching of all other Australian perciliids [Nannoperca + [Nannatherina + [Gadopsis + Bostockia]]] is supported by eight synapomorphies: Infraorbital canal without sensory tubules (or occasionally a few may be present) at the posterodorsal infraorbital bones (Ch. 17[2]); subocular shelf absent (Ch. 21[2]); with 30 to 40 vertebrae (Ch. 33[2]); lateral line or postotic sensory canal not enclosed by the upper third of the supracleithrum (Ch. 35[1]); less than 10 dorsal procurent rays [1] (Ch. 43[1]); with 7 or less ventral procurent rays (Ch. 44[1]); adductor mandibulae muscle with distinct pars malaris and pars rictalis (Ch. 45[1]); and trigeminal pterygiophores present (Ch. 53[1]).

Node B2. Five synapomorphies support the branching of Nannatherina + [Bostockia + Gadopsis]: Cycloid scales present (Ch. 1[0]); palatine (auto + dermopalatine) extending posterior to the orbital process of the lateral ethmoid by a long posterior process [1] (Ch. 24[1]); and palatine (auto + dermopalatine) bearing numerous teeth (Ch. 25[1]).

Node B3. The clade comprising Bostockia plus Gadopsis is supported by the following synapomorphies: Absence of additional bones between infraorbitals 1 and 5 (Ch. 18[0]); basisphenoid absent (Ch. 23[1]); dorso posterior region of dentary (part of coronoid process) elongate and narrow (Ch. 28[1]); long dorsal fin, reaching or almost reaching the origin of caudal fin (Ch. 38[1]); number of rays in the dorsal fin over 16 (Ch. 39[1]); two epurals present (Ch. 41[1]); tubular anterior nostril placed near the margin of the lip (Ch. 51[1]); and with a distinctive (asymmetric) nasal rosette (Ch. 50[1]).

Node C. Percichthyidae. The monophyly of the family Percichthyidae is supported by nine synapomorphies: Slit-like or oval pores on the skin covering infraorbital 1 present (Ch. 15[1]); infraorbital sensory canal on infraorbital 1 tube-like and enclosed by bone (Ch. 16[0]); smooth ventral margin of
infraorbital 1 (Ch. 19[0]); palatine (auto + dermalpalatine) extending posterior to the orbital process of the lateral ethmoid by a short posterior process or the process is absent (Ch. 24[0]); palatine (auto + dermalpalatine) bearing few or no teeth (Ch. 25[0]); supramaxilla present (Ch. 27[1]); dorso-posterior region of dentary (part of coronoid process) elongated and narrow (Ch. 28[1]); promalaris present (Ch. 46[1]); and promalaris separated from pars malaris with a tendinous connection to hyomandibula and maxilla (Ch. 47[2]).

Node C1. The clade comprising *Macquaria australasica* + *Macquaria (= Plectroplites) + (Percichthys colhuapiensis + P. trucha)* is supported by two synapomorphies: Only slit-like pores opening in the skin that covers the dentary (Ch. 10[1]) and mandibular canal placed on a groove along most of the dentary (Ch. 14[1]).

Node C2. The sister relationship formed by *Macquaria australasica* and *Macquaria (= Plectroplites)* is supported by two synapomorphies: *Adductor mandibulae* with distinct *pars malaris* and *pars rictalis* (Ch. 45[1]) and semidemersal, non-adhesive eggs present (Ch. 54[1]).

Node C3. The sister relationship formed by *Percichthys colhuapiensis* and *P. chilensis* is supported by three synapomorphies: Cycloid scales present on check region (Ch. 3[1]); ventral margin of infraorbital 2 serrated (Ch. 20[1]); and one epiphyseal pore opening in the skin that covers the frontal bone just at the postorbital region (Ch. 22[1]).

When the phylogenetic analysis included *Macquaria (= Percalates)* as the outgroup, there was no change in the topology of the tree (Fig. 21), with the exception that *Percalates* was included in a polytomy at node A.

Phylogenetic analysis and results: Mitogenomics. A total of 303,853 (mean 240 bp, sd 88 bp), 324,606 (mean 243 bp, sd 100 bp) and 308,889 (mean 228 bp, sd 97 bp) reads were sequenced for the samples of *Percilia gillissi* from the Maipo River and southern Chile, and *Percilia irwini* from the Bureo River, respectively. The complete mitochondrial genomes of *Percilia gillissi* were assembled with 372 (mean coverage 5x) and 292 (mean coverage 4x) reads, whereas the mitogenome of *Percilia irwini* had 717 (mean coverage 10x) reads mapped. Gene composition and structure of the newly assembled mitogenomes were similar to *Percilia irwini* (Genbank accession no. AP014528; Lavoué et al., 2014), and comprised of 13 protein-coding genes, 2 ribosomal RNA units, 22 tRNA genes and a control region, the latter being excluded for further analyses. The length of these mitogenomes were 16,622 bp (Maipo River sample), 16,624 bp (southern Chile sample) and 16,624 bp (*P. irwini* from Bureo River). Genbank accession numbers are MK239311, MK239310 and MK239312, respectively.

Phylogenetic analyses considering mitogenomic characters recovered different topologies of percichthyids and perciliids, depending on the partition scheme used. For example, when considering the first matrix (M1) there were two groups: *Gadopsis* spp. + *Maccullochella* species (BSs = 66 %) nested along *Bostockia porosa* (BSs = 70 %) in a clade with *Nannoperca* species (BSs = 68 %); and *Macquaria + Macquaria (=Plectroplites)* sister group of *Percichthys trucha + Percilia* species (BSs = 100 %; Fig. supplementary S2a). When analyzing the second matrix (M2) *Gadopsis* spp. remain as sister group of *Maccullochella* species (BSs = 62 %) in one clade, whereas a second clade comprises *Bostockia porosa* and *Nannoperca* species (BSs = 35 %) as sister group (BSs = 18 %) of *Macquaria + Macquaria (= Plectroplites) (BSs = 100 %) along with *Percichthys trucha + Percilia* species (BSs = 100 %; Fig. supplementary S2b). The third matrix (M3; Fig. 22) recovered the same topology as the second analysis, in all cases with low BS support for the intergeneric relationships, except when considering *Percichthys trucha* as sister group of *Percilia* species (BSs = 100 %), *Macquaria + Macquaria (= Plectroplites) (BSs = 100 %) and the clade formed by these two groups (BSs = 100%). An interesting finding is that, instead of recovering a sister group relationship between *Percilia gillissi* and *Percilia irwini*, *Percilia gillissi* appeared as polyphyletic in our mitogenomic reconstruction. In terms of its genetic distance, both mitogenomes of *P. irwini* have 99.04 % similarity (110 SNPs [single nucleotide polymorphisms]), whereas mitogenomes of *P. gillissi* have 95.46 % similarity (519 SNPs). *Percilia gillissi* from the Maipo River (type locality) has 95.71 and 95.78 % similarity with both published and new mitogenome of *Percilia irwini* (490 and 483 SNPs, respectively), whereas *Percilia gillissi* from southern Chile has 97.56 and 97.61 % similarity with the published and the new mitogenome of *P. irwini* (275 and 274 SNPs, respectively).

Discussion

Percichthyid and perciliid relationships. The results presented herein are the first published effort to analyze the possible phylogenetic relationships among fishes currently interpreted as percichthyids *sensu* Johnson (1984) that includes South American and Australian taxa. Prior research established the possible content of the families Percichthyidae and Perciliidae (Arratia, 1982; Micklich, 1987) or only Percichthyidae (Johnson, 1984) without a formal phylogenetic analysis and hypothesis of possible relationships. According to Johnson (1984:p. 469), “The monophyly of Percichthyidae is supported by a series of nested synapomorphies only a few of which are mentioned here. The scales of most of those genera are similar and unlike those of the excluded genera in having the posterior field filled with simple only slightly amputated (see McCully, 1970) needle-like ctenii (those of *Bostockia, Gadopsis* and *Nannatherina* are secondarily cycloid).” The parsimony analysis (TNT) does not interpret this feature as a synapomorphy of Perciliidae and/or Percichthyidae, an interpretation also supported by PAUP analysis. *Nannoperca* has ctenoid scales as in *Percilia* and percichthyids; thus, the absence of ctenoid scales is interpreted as a synapo-
morphy of the clade [Nannatherina + [Bostockia + Gadopsis]] = Node B2 in Fig. 21 (see Tab. 3 for distribution of characters). Johnson (1984:p. 469) provided 13 morphological characters supporting the taxa that he assigned to the family, and added five more specific characters (p. 470) supporting a probable relationship between the Australian Bostockia and Gadopsis and one shared by Bostockia and Maccullochella. From those, only two characters were not considered in the present study: (1) a reduced number of branchiostegal rays, because there is not much variation among the studied taxa, just one ray that can be variable (see Arratia, 1982:tb. 1); and (2) absence of a medial tabular (= medial extrascapula; only in Gadopsis and Bostockia).

The phylogenetic analyses performed herein differs from Johnson’s (1984) hypothesis in recognizing two clades that we identify preliminarily as Perciliidae and Percichthyidae (Fig. 21: nodes B, C). The two families are supported by numerous morphological characters. In addition, each branch has bootstrap support over 90 % (see Fig. 21).

According to this new hypothesis, the family Perciliidae includes the Australian genera Nannoperca, Nannatherina, Bostockia and Gadopsis with the South American genus Percilia at its most basal node (Fig. 21: node B). The enigmatic genera Bostockia and Gadopsis are interpreted as perciliids; they are sister to each other, as already suggested by Johnson (1984), and the most advanced taxa within the family. On the other hand, the family Percichthyidae has a new understanding, including the South American genus Percichthys and the Australian Macquaria australasica, Macquaria (= Plectroplites) ambiguа, and Maccullochella.

The new phylogenetic hypothesis (Fig. 21) based on morphological characters is not congruent with previous molecular studies (e.g., Near et al., 2012, 2013; Chen et al., 2014; Lavoué et al., 2014; Betancur R et al., 2017)—where Percilia and Percichthys are part of the same clade, the family Percichthyidae sensu Johnson (1984). Those results are not confirmed either by the mitogenomic analysis performed herein (Figs. 22 and S2a-b). For example, Bostockia and Gadopsis (Fig. 21: node B3) are not recovered as sister taxa in any molecular study (i.e., Figs. 2, 22, and supplementary S2a-b). According to molecular hypotheses, percichthyids such as Maccullochella spp. are commonly found as sister taxa with perciliids (i.e., Gadopsis spp.; Near et al., 2013; Lavoué et al., 2014; Betancur-R et al., 2017; Figs. 2d, g, i-j). Nevertheless, it is important to note that a major problem is the differences in the taxonomic sampling used in the various studies. The morphological analysis performed here is the only one that includes representatives of all genera suggested as percichthyids by Johnson (1984). Consequently, the results between morphological and molecular analyses are not comparable, and even the results among the differently sampled molecular studies are not comparable.  

**Taxonomy of percichthyids and perciliids.** The content and understanding of the so-called family Percichthyidae have been controversial from its beginning when Jordan (1923) created the family (see Tabs. 1 and 2). Over the decades, only a few papers revised the taxonomy and/or morphology of the South American percichthyids (e.g., Ringuet et al., 1967; Arratia, 1982; López-Arbarello, 1999, 2004) and Australian ones (e.g., Berra, Weatherley, 1972; MacDonald, 1978; Johnson, 1984; Nock et al., 2010). In the most recent morphological and taxonomic reviews of the Argentinian species of Percichthys, only three species were recognized: Percichthys trucha, P. colhuapiensis and P. laevis (López-Arbarello, 1999, 2004), whereas only one species of Percichthys was recognized by the phylogeographic study of Ruzzante et al. (2006), an approach followed later by other researchers. Thus, under this paradigm, the genus Percichthys would be represented by two species in South America, P. trucha inhabiting both Andean slopes and P. melanops restricted to central-southern Chile (Fig. 3b). However, the results of this study—based on morphological characters—suggests that Percichthys colhuapiensis, as well as Percichthys chilensis, are valid species and should be re-investigated. Percichthys colhuapiensis is characterized by two autapomorphies: dilatator operculi placed almost horizontal to the main section of the muscle and a large subdivision of the levator arcus palatine muscle with fibers almost 90 degrees to the cranial roof bones (Fig. 20c). In addition, the position of a separate section of the dilatator operculi dorsal to the lateral surface of the autosphenotic and pterotic is a character shared by Percichthys colhuapiensis and Maccullochella macquariensis among the examined percichthyids. The presence of a large muscle mass formed by the ricto-retromalaris (rectalis + malaris) is another character shared by P. colhuapiensis and Maccullochella.

Currently, the taxonomy of the Australian percichthyids needs revision. MacDonald (1978), based on an electrophoretic analysis of protein variation at 19 genetic loci, proposed Percalates and Plectroplites as a synonym of Macquaria and recognized Maccullochella as a valid genus that differs extensively from Macquaria. However, as discussed in the previous sections, Macquaria and Percalates should be revised, because they have different positions and relationships in previous molecular studies (see for instance Lavoué et al., 2014 or Betancur R et al., 2017) and herein (Fig. 2), as well as the morphological phylogenetic analysis performed herein. The family Perciliidae was created by Jordan (1923) for the Chilean genus Percilia, an approach followed later by a few others. The results of the morphological phylogenetic analysis (Fig. 21) suggest that representatives of the genera Nannatherina and Nannoperca and the enigmatic Bostockia and Gadopsis are also members of Perciliidae.

Thus, under the new interpretation presented here, the family Perciliidae includes three genera (Percichthys, Macquaria, and Maccullochella) and 12 species; five species are restricted to southern South America and seven to Australia. The family Perciliidae contains five genera (Percilia, Bostockia, Gadopsis, Nannatherina, and Nannoperca) and 12 species; two are restricted to central-southern Chile and 10 to Australia.
The results of the mitogenomic analysis (Fig. 22) reveal that under the names *Percilia gillissi* and *P. irwini* are other cryptic species. Similar results have been published concerning *Macquaria* (Musyl, Keenan, 1992; Beheregaray et al., 2017), *Gadopsis* (Hammer et al., 2014; Unmack et al., 2017), and *Nannoperca* (Unmack et al., 2011; Buckley et al., 2018). Consequently, there is much more work needed to clarify the taxonomy of the South American and Australian percichthyids and perciliids.

**Geographical distribution and endemism.** Percichthyids and perciliids are distributed in freshwaters of southern South America and Australia (Figs. 3-5, 7-9). Three freshwater fish families (Aplochitonidae, Percichthyidae, and Perciliidae), the diadromus fish family Galaxiidae, and the cyclostomata *Geotria* inhabit these two regions. Despite the fact that percichthyids and perciliids are distributed in freshwaters of the two continents, we are unable to establish sister group regions between South America and Australia with the available information.

**Fig. 21.** Hypothesis of phylogenetic relationships of South American and Australian percichthyids and perciliids based on 54 morphological characters.

**Fig. 22.** Mitogenomic maximum likelihood tree of Percichthyidae *sensu* Lavoué et al. (2014) and Betancur-R et al. (2017) considering newly assembled and available mitogenomic sequences. Numbers at nodes are bootstrap support [bs], black circles represent bs = 100 %.
Percichthysids and perciliids present a high endemism. For instance, *Percichthys colhuapiensis* is restricted to southern Argentinian Patagonia (Fig. 3b) and *Percichthys melanops* to central-southern Chile (Fig. 3b). Conversely, *Macquaria, Macquaria (= Plectroplites)* and *Maccullochella* are endemic to southern Australia, whereas *Macquaria (= Wuyu)* is the only percichthyid distributed as north as 15º S (Fig. 8; Pusey, Kennard, 2001). According to the evidence presented above, perciliids appear to be endemic to both continents, with *Percilia* restricted to central-southern Chile (Fig. 7b) and all Australian perciliids (*e.g.*, *Bostockia, Gadopsis, Nanotherina* and *Nannoperca [= Edelia]*) have restricted areas of distribution. Freshwater percichthysids and perciliids are unknown from Africa, New Zealand, or New Caledonia.

The current distribution of percichthysids and perciliids is interesting, because it suggests an Antarctic connection to explain it. However, fossil and extant percichthysids and perciliids have not been reported from the Antarctica yet. The extant South American and Australian percichthysids and perciliids are not diadromous, and it is difficult to explain their present distribution as result of transoceanic dispersion as has been proposed for galaxioids (McDowall, 1970). In contrast, Campos (1984) suggested that the present distribution of galaxioids is merely the result of the disruption of the supercontinent Gondwana. The same suggestion is put forward here to explain the actual distribution of percichthysids and perciliids. We can hypothesize that the ancestral stock of percichthysids and perciliids inhabited southern South America, Antarctica, and Australia before the break-up of Gondwana. During the Late Cretaceous the three continents were continuous, although there were breaks between all crustal blocks; final separation took place in the Eocene-Oligocene (*e.g.*, Craddock, 1982; Woodburne, Zinsmeister, 1984). According to the morphological analysis, the phylogenetic positions of the South American genus *Percichthys* as the sister group of *Macquaria australasica* and *Macquaria (= Plectroplites)* and of the South American genus *Percilia* as the sister group of all Australian perciliids (Fig. 21) suggest that the separation between the South American and Australian stocks occurred not so long ago, because of the few divergent morphological changes. However, the group seems to have a longer evolutionary history in Australia than in South America as shown by a major generic differentiation, a condition also observed in other fish families—Aplodinotidae and Galaxiidae—that occur in both continents. Regarding the molecular and mitogenomic hypotheses, *Macquaria* (including *M. ambiguia* and *M. australasica*) were recovered as the sister group of *Percichthys* and *Percilia* (Chen et al., 2014; Betancur-R et al., 2017; mitogenomic analysis herein; Fig. 22 and supplementary S1a-b). Thus, considering the time-calibrated phylogeny of Betancur-R et al. (2017), the split between *Percichthys chilensis* and *Percilia* occurred about 20 Ma, whereas the split of these genera and *Macquaria (= Plectroplites) ambiguia + Nannoperca australis* occurred ca. 45 Ma. In this view, *Percilia* would have appeared within the South American continent during the Cenozoic. A Paleocene-Oligocene origin for crown Percichthysidae sensu Johnson (1984) was suggested previously by Near et al. (2013) and Chen et al. (2014), which agrees with the age of the fossil percichthysids recovered in Chile (further research on this subject is in progress by the authors).

**Acknowledgments**

Our sincerest thanks to José Birindelli and the Organizing Committee of the II Symposium of Phylogeny and Classification of Neotropical Fishes (October-2017, Londrina, Brazil) for the invitation to participate in the meeting and to Luiz Malabarba and Carla Pavanelli for their invitations to submit a manuscript for the special symposium volume. Special thanks to William Eschmeyer and David Catania (CAS), Andrew Williston (MCZ), Hernán López-Fernández and Douglas Nelson (UMMZ), G. David Johnson, Jeff Williams and technical staff (USNM) for loans of specimens; Sergio Quiroz (MHNV) for cataloguing specimens; and Andrew Bentley (KU:KUI) for managing the loans. To Sebastien Lavoué for sharing his data matrix from Lavoué et al. (2014). To Jorge Liotta for sharing distribution of *Percichthys* spp. from Argentina. To Luis A. Cione for information on fossil percichthysids from Argentina. To Alessio Datovo for assistance with his new muscle terminology. To Alfonso Rubilar for facilities to check and photograph fossil percichthysids from Cura-Mallín (= Río Pedregoso) Formation, Lonquimay, Chile. To TJ Meehan for checking the English style of the manuscript. Our special thanks to the editor H. López-Fernández and to G. D. Johnson and an anonymous reviewer for comments on the manuscript. CQR was supported by CONICYT Fondecyt 3160659, 11181259 and by Nucleo Milenio INVASAL funded by Chile’s government program, Iniciativa Científica Milenio from Ministerio de Economía, Fomento y Turismo.

**References**

Aedo JR, Belk MC, Habit EM. Geographic variation in age, growth and size structure of *Percilia irwini* from south-central Chile. J Fish Biol. 2009; 74:278-84. DOI: 10.1111/j.1095-8649.2008.02113.x
Agnolin FL, Bogan S, Tomassini SL, Manera T. Nuevo Percichthyidae (Teleostei, Perciformes) del Plioceno temprano de la Provincia de Buenos Aires (Argentina) y sus implicancias biogeográficas. Rev Mus Argentino Cien Nat n.s. 2014; 16:19-31.
Aljanabi SM, Martinez I. Universal and rapid salt-extraction of high quality genomic DNA for PCR-based techniques. Nucleic Acids Res. 1997; 25(22):4692-93.
Arcila D, Ortí G, Vari RP, Armbruster JW, Staissny MLJ, Ko K, Sabaj MH et al. Genome wide interrogation advances resolution of recalcitrant groups in the Tree of Life. Nature Eco Evo. 2017; 17:162. DOI: 10.1186/s12862-017-0958-3
Arratia G. A review of freshwater percoids from South America (Pisces, Ostechthyes, Perciformes, Percichthyidae, and Perciliidae). Abh Senckenb Naturforsch Ges 1982; 540:1-52.
South American and Australian percichthyids and perciliids

Arratia G. Family Percichthyidae. In: Reis R, Ferraris C, Kullander S, editors. Check list of the Freshwater Fishes of South and Central America. CLOFFSA. Fish Base Data of Neotropical Fishes. Porto Alegre: Edipucrs; 2003a: p.596-597.

Arratia G. Family Perciliidae. In: Reis R, Ferraris C, Kullander S, editors. Check list of the Freshwater Fishes of South and Central America. CLOFFSA. Fish Base Data of Neotropical Fishes. Porto Alegre: Edipucrs; 2003b: p.598.

Arratia G, Cione LA. The fossil record of fossil fishes of Southern South America. In: Arratia G, editor. Contributions of Southern South America to Vertebrate Paleontology, Münchner Geowiss Abh. (special volume). München: Verlag Dr. F. Pfeil; 1996: p.9-72.

Arratia G, López-Arbarello A, Prasad GVR, Parmar V, Kriwet J. Late Cretaceous-Paleocene percomorphs (Teleostei) from India - Early radiation of Perciformes. In: Arratia G, Wilson MVH, Cloutier R, editors. Recent advances in the origin and early radiation of vertebrates. München: Verlag Dr. F. Pfeil; 2004: p.635-663.

Arratia G, Rojas G, Chang A. Géneros de peces de aguas continentales de Chile. Publicación Ocasional 34, Museo Nacional de Historia Natural (Chile). 1981:3-108.

Arratia G, Schultz H-P. The palatoquadrate and its ossifications: Development and homology within osteichthians. J Morphol. 1991; 208:1-81.

Arratia G, Schultz H-P. Rerevaluation of the caudal skeleton of certain actinopterygian fishes. III. Salmonidae. Homologization of caudal skeletal structures. J Morphol. 1992; 2:1-63.

Beheregaray LB, Pfeiffer LV, Attard CRM, Sandoval-Castillo J, Domingos FMCB, Faulks LK et al. Genome-wide data delimits multiple climate-determined species ranges in a widespread Australian fish, the golden perch (Macquaria ambigua). Mol Phylogenet Evol. 2017; 111:65-75.

Berra TM, Weatherley AH. A systematic study of the Australian freshwater Serranid fish genus Maccullochella. Copeia. 1972; 1972(1):53-64.

Betancur-R R, Broughton RE, Wiley EO, Carpenter K, López JA, Li C et al. The tree of life and a new classification of bony fishes. PLoS Currents Tree of Life. 2013. DOI: 10.1371/currents.tol.53ba26640fd0cacee75bb165ec826288)

Betancur-R R, Wiley EO, Arratia G, Acero A, Bailly N, Miya M et al. Phylogenetic classification of bony fishes. BMC Evol Biol. 2017. DOI: 10.1186/s12862-017-0958-3

Bray DJ. Gadopsis marmoratus in Fishes of Australia. Cited 25 July 2018. Available from http://fishesofaustralia.net.au/home/species/3877

Breder CM, Rosen DE. Modes of reproduction in fishes. Garden City, New York: Natural History Press. 1966.

Broughton RE, Reneuc PC. Spatial covariation of mutation and nonsynonymous substitution rates in Vertebratemitochondrial genomes. Mol Biol Evol. 2006; 23(8):1516-24.

Buckley SJ, Domingos FMCB, Attard CRM, Brauer CJ, Sandoval-Castillo J, Lodge R et al. Phylogenetic history of enigmatic pygmy perches: Implications for biogeography, taxonomy and conservation. R Soc Open Sci. 2018; 5(6).

Campos H. Gondwanaland and neotropical galaxiid fish biogeography. In Taret T, editor. Evolutionary ecology of neotropical freshwater fishes. The Hague: Dr. W. Junk Publishers. 1984: p. 113-25.

Campos H, Gavilán JF. Diferenciación morfológica entre Percichthys trucha y Percichthys melanops (Perciformes; Percichthyidae) entre 36° y 41° L.S. (Chile y Argentina), através de análise multivariados. Gayana Zool. 1996; 60(2):99-120.

Chang A, Arratia G, Alfar G. Percichthys longimayiensis n. sp. from the Upper Paleocene of Chile (Pisces, Perciformes, Serranidae). J Paleont. 1978; 32(3):727-36.

Chen DX, Chu WY, Liu XL, Nong XX. Phylogenetic studies of three sinipercid fishes (Perciformes: Siniperidae) based on complete mitochondrial DNA sequences. Mitochondr DNA. 2012; 23(2):70-76.

Chen WJ, Lavoué S, Beheregaray LB, Mayden RL. Historical biogeography of a new antitropical clade of temperate freshwater fishes. J Biogeogr. 2014; 41(9):1806-18.

Chiang G, Munkttrick KR, McMester ME, Tucca F, Saavedra MF et al. Seasonal changes in oocyte development, growth and population size distribution of Percilia gillissi and Trichomycterus areolatus in the Itata basin, Chile. Gayana (Concepción). 2012; 76:131-141. DOI:10.4067/S0717-65382012000300006

Chiang G, Munkttrick KR, Saavedra MF, Tucca F, McMester ME et al. Seasonal changes in reproductive endpoints in Trichomycterus areolatus (Siluriformes: Trichomycteriidae) and Percilia gillissi (Perciformes, Perciliidae), and the consequenc es for environmental monitoring. Stud Neotrop Fauna Environ. 2011; 46:185-196. DOI: 10.1080/01650521.2011.598296

Crichigno SA, Battini MA, Cussac VE. Diet induces phenotypic plasticity of Percichthys trucha (Valenciennes, 1833) (Perciformes, Percichthyidae) in Patagonia. Zool Anz. 2014; 253:192-202.

Croadcock C. Antarctic and Gondwanaland. In: Craddock C, editor. Antarctic Geosciences (Internt. Union Geol. Sci), ser. B(4). München: Verlag Dr. F. Pfeil; 1996: p.9-72.

Cruces H, Gavilán JF. Diferenciación morfológica entre 36° y 41° L.S. (Chile y Argentina), através de análise multivariados. Gayana Zool. 1996; 60(2):99-120.

Cuvier G, Valenciennes A. Histoire naturelle des poissons. Tome troisième. Suite du Livre troisième. Des percoides à dorsale unique à sept rayons branchiaux et à dents en velours ou en cardes. 1829; 3: i-xxvii + 2 p. + 1-500.

Cuvier G, Valenciennes A. Histoire naturelle des poissons. Tome cinquième. Livre cinquième. Des Sciénoïdes. 1830; 5: i-xxviii + 1-499 + 4 p.

Cuvier G, Valenciennes A. Histoire naturelle des poissons. Tome neuvième. Suite du livre neuvième. Des Scombéroïdes. 1833: v. 9: i-xxix + 3 pp. + 1-512, Pls. 246-279.

Datovo A, Hari PR. The jaw adductor muscle complex in teleostean fishes: Evolution, homologies and revised nomenclature (Osteichthyes, Actinopterygii). PLoS One. 2013; 8(4):e60846. DOI: 10.1371/journal.pone.0060846

Datovo A, Hari RP. The adductor mandibulae muscle complex in lower teleostean fishes (Osteichthyes, Actinopterygii): comparative anatomy, synonyms, and phylogenetic implications. Zool J Linn Soc. 2014; 171:554-622. DOI: 10.1111/zpl.12142
Dingerkus G, Uhler LD. Enzyme clearing of alcian blue stained whole small vertebrates for demonstration of cartilage. Stain Technology. 1977; 52:229-32.

Duarte W, Feito R, Jara C, Moreno C, Orellana AE. Ictiofauna del sistema hidrográfico del río Maipo. Bol Mus Nac Hist Nat (Chile). 1971; 32:227-68.

Dyer B. Systematic review and biogeography of the freshwater fishes of Chile. Estudios Oceanol. 2000; 19:77-98.

Eigemann K. The fresh water fishes of Chile. Mem Nat Acad Sci. 1927; 22:1-63

Eschmeyer WN. Catalog of the genera of recent fishes. California Acad Sci San Francisco, CA. 1990.

Faulks LK, Gilligan DM, Beheregaray LB. Evolution and maintenance of divergent lineages in an endangered freshwater fish, Macquaria australasica. Conserv Genet. 2010; 11(3):921-34.

Fowler H. Analysis of the fishes of Chile. Revista Chilena Hist Natur. 1951; 51:263-326.

Fricke FR, Eschmeyer WN, van der Laan R (eds). 2018. Catalog of the families of fish: Genera, species, references. (http://researcharchive.calacademy.org/research/ichthyology/catalog/fishcatmain.asp). Electronic version accessed 2018.

Fuster de Plaza ML, Plaza J. Nuevos ensayos para obtener la reproducción artificial de las percas o truchas criollas (Percichthys spp.). Publ Misc Ministerio Agric Ganad. 1955:1-48.

Gan HM, Tan MH, Lee YP, Austin CM. The complete mitogenome of the river blackfish, Gadopsis marmoratus (Richardson, 1848) (Teleostei: Percichthyidae). Mitochondrial DNA. 2014; 1736:1-2.

Gay C. Historia física y política de Chile. Museo Nacional de Historia Natural, Santiago. 1848.

Gayet M, Brito PM. 1989. Ichthyofauna nueva del crétacé supérieur du groupe Bauru (États de Sao Paulo et Minas Gerais, Brésil). Geobios. 1989; 22, fasc. 6:641-47.

Gayet M, Marshall L, Sempere T. The Mesozoic and Paleocene vertebrates of Bolivia and their stratigraphic context: a review. Revista Técnica de YPFB. 1991; 12:393-433.

Gayet M, Meunier F. Maastrichtian to Early Late Paleocene freshwater Osteichthyes of Bolivia: Additions and Comments. In: Phylogeny and classification of Neotropical fishes. Part 1 - Fossils and geological evidence. Malabarba LR, Reis RE, Vari RP et al., editors. Porto Alegre: EDIPUCRS. 1988; p. 85-110.

Girard C. Abstract of a report to Lieut. Ja. M. Gilliss, U.S.N., upon the fishes collected during the U.S.N. astronomical expedition to Chili. Proc Acad Nat Sci Phila. 1854; VII:197-99.

Girard C. Appendix F. Fishes. In: Gilliss JM, editor. The United States naval astronomical expedition to the Southern hemisphere, during the years 1849-'50-'51-'52. Vol. II. A. O. P. Washington: Nicholson Printer. 1855. p.230-253.

Goloboff PA, Catalano SA. TNT version 1.5, including a full implementation of phylogenetic morphometrics. Cladistics. 2016; 32(3):221-38.

Goodrich ES. Vertebra trunks of the sardine and other tunas. Fish. 1909; 9. i-xvii + 1-518.

Gosline W. The limits of the fish family Serranidae, with notes on other lower percoids. Proc Calif Acad Sci. 1966; 33(6):91-112.

Gosline W. The suborders of perciform fishes. Proc United States Nat Mus. 1968; 124(3647): 1-78.

Greenwood PH, Rosen DE, Weitzman SH, Myers GS. Phylogenetic studies of teleostean fishes, with a provisional classification of living forms. Bull Amer Mus Nat Hist. 1966; 131(4):341-455.

Haller MJ. En memoria de John Bell Hatcher (1861-1904) y las expediciones de la Universidad de Princeton a la Patagonia de 1896 a 1899. Rev Asoc Geol Argentina. 2004; 59(4):523-24.

Hammer MP, Adams M, Foster R. Update to the catalogue of South Australian freshwater fishes (Petromyzontida & Actinopterygii). Zootaxa. 2012; 3593:59-74.

Hammer MP, Unmack PJ, Adams M, Raadik TA, Johnson JB. A multigene molecular assessment of cryptic biodiversity in the iconic freshwater blackfishes (Teleostei: Percichthyidae: Gadopsis) of south-eastern Australia. Biol J Linn Soc. 2014; 111(3):521-40. https://doi.org/10.1111/bij.12222

Harrison K, Pavlova A, Gan HM, Lee YP, Austin CM, Sunnucks P. Pleistocene divergence across a mountain range and the influence of selection on mitogenome evolution in threatened Australian freshwater cod species. Heredity. 2016; 116(6):506-15.

Hill ES. Fossil Murray cod (Maccullochella macquariensis) from the diatomaceous earths in New South Wales. Rec Australian Mus. 1946: 21:380-82.

Hoese DE, Bray DJ, Paxton JR, Allen GR. Fishes. Australia Part 2. In: Zoological Catalogue of Australia, vol 35. ABRS and CSIRO Publishing, Australia; 2006.

Hughes LC, Ortì G, Huang Y, Sun Y, Baldwin CC, Thompson AW et al. Comprehensive phylogeny of ray-finned fishes (Actinopterygii) based on transcriptomic and genomic data. PNAS. 2018; www.pnas.org/cgi/doi/10.1073/pnas.1717358115

Iwasaki W, Fukunaga T, Isagozawa R, Yamada K, Maeda Y, Satoh TP et al. Mitofish and mitoannotator: A mitochondrial genome database of fish with an accurate and automatic annotation pipeline. Mol Biol Evol. 2013; 30(11):2531-40.

Jenyns L. Fish. In: The zoology of the voyage of H. M. S. Beagle, under the command of Captain Fitzroy, R. N., during the years 1832 to 1836. London: Smith, Elder, and Co. 1840. Issued in 4 parts. i-xvi + 1-172.

Jerry DR, Elphinstone MS, Baverstock PR. Phylogenetic relationships of Australian members of the family percichthyidae inferred from mitochondrial 12S rRNA sequence data. Mol Phylogenet Evol. 2001; 18(3):335-47.

Johnson GD. The recurrent spur: an undescribed perciform caudal character and its phylogenetic implications. Occas Pap Calif Acad Sci. 1975:1-23.

Johnson GD. Percoidei: Development and relationships. In: Moser HG, Richards WJ, Cohen DM et al., editors. Ontogeny and systematics of fishes. Amer Soc Ichthyol Herp. Spec. Public. 1. 1984; p.464-498.

Jordan D. A classification of fishes including families and genera as far as known. Stanford Univ, Pub Univ Ser Biol. 1923; 3:79-243.
South American and Australian percichthyids and perciliids

Jordan DS, Eigenmann CH. A review of the genera and species of Serranidae found in the waters of America and Europe. Bull United States Fish Comm. 1888. 1890; 8:329-441.

Kilian EF, Campos H. Süßwasserschwämme als Ort der Brutpflege eines Fisches. Naturwissenschaften. 1969; 56:333. DOI: 10.1007/BF00602187

Knight JT, Trnski T. Early development of the endangered Oxleyan pygmy perch Nanoperca oxleyana Whitley (Percichthyidae). Australian Zoologist. 2011; 35:895-909.

Lake JS. The freshwater fishes of New South Wales. Res Bull State Fish, New South Wales, Sydney. 1959; 5:1-19.

Lanfear R, Calcott B, Ho SYW, Guindon S. PartitionFinder: Combined selection of partitioning schemes and substitution models for phylogenetic analyses. Mol Biol Evol. 2012; 29(6):1695-701.

Lavenda N. Sexual differences and normal protogynous hermaphroditism in the Atlantic sea bass, Centropristis striatus. Copaea. 1949; 3:185-94.

Lavoüé S, Nakayama K, Jerry DR, Yamanoue Y, Yagishita N, Suzuki N et al. Mitogenomic phylogeny of the Percichthyidae and Centrarchiiformes (Percomorphaceae): Comparison with recent nuclear gene-based studies and simultaneous analysis. Gene. 2014; 549(1):46-57.

Li SJ, Cai L, Bai JJ. Mitochondrial genome sequence of the bluegill sunfish (Lepomis macrochirus). Mitochondrial DNA. 2011; 22(5-6):194-96.

López-Arbarello A. Estudio taxonómico de los percíctidos (Osteichthyes: Perciformes) actuales de Argentina. Dr. Thesis, Universidad de Buenos Aires, Facultad de Ciencias Exactas y Naturales. 1999.

López-Arbarello A. Taxonomy of the genus Percichthys (Perciformes, Percichthyidae). Ichthyol Expl Freshwaters. 2004; 15(4):331-50.

Lv L, Tian C, Liang X, Yuan Y, Zhao C, Song Y. The complete mitochondrial genome sequence of Coreoperca whiteheadi (Perciformes: Serranidae). Mitochondrial DNA. 2016; 27(1):301-03.

Mabee P. Supraneural and predorsal bones in fishes: development and homologies. Copaea. 1988; 4: 827-38.

MacDonald CM. Morphological and biochemical systematics of Australian freshwater and estuarine percichthyid fishes. Austr J Mar Freshwater Res. 1978; 29:667-98.

Malabarba MC. Phylogeny of fossil Characiformes and palaeobiogeography of the Tremembé Formation, São Paulo, Brazil. In: Malabarba LR, Reis RE, Vari RP et al., editors. Phylogeny and Classification of Neotropical Fishes. Part 1 - Fossils and Geological Evidence. Porto Alegre: EDIPUCRS. 1988: p. 69-85.

Marshall LG, De Muizon C, Gayet M, Lavenu A, Sigé B. The “Rossetta Stone” for mammalian evolution in South America. National Geogr Res. 1985; 1:274-88.

McCully H. Amputation and replacement of marginal spines in ctenoid percoid scales. California Acad. Sci. 1970.

McDowall RM. The galaxiid fishes of New Zealand. Bull Mus Comp Zool. 1970; 139:341-431.

Micklich N. Neue Beiträge zur morphologie, ukologie und systematik messeler knochenfische. I. Die Gattung Amphiherca Weitzel 1933 (Perciformes, Percioidei). Cour Forsh-Inst Senckenberg. 1987; 91:36-96.

Miya M, Kawaguchi A, Nishida M. Mitogenomic exploration of higher teleostean phylogenies: a case study for Moderate-scale evolutionary genomics with 38 newly determined complete mitochondrial DNA sequences. Mol Biol Evol. 2001; 18(11):1993-2009.

Miya M, Friedman M, Satoh TP, Takeshima H, Sado T, Iwasa K et al. Evolutionary origin of the Scombridae (tunas and mackerels): members of a Paleogene adaptive radiation with 14 other pelagic fish families. PLoS One. 2013; 8(9): e73535.

Molina JI. Sagio sulla storia naturale del Chile. Lib. 4. The Geographical, Natural and Civil History of Chili. Irving’s English translation. 1782.

Miller MA, Pfeiffer W, Schwartz T. Creating the CIPRES Science Gateway for inference of large phylogenetic trees in Proceedings of the Gateway Computing Environments Workshop (GCE), 14 Nov. 2010, New Orleans, LA; p.1-8.

Muizon de C, Gayet M, Lavenu A, Marsall LG, Sigé B. Late Cretaceous vertebrates including mammals, from Tiupampa, southcentral Bolivia. Geobios. 1983; 16:774-53.

Mukai T, Sato C. Complete mitochondrial DNA sequences of two haplotypes of the smallmouth bass, Micropterus dolomieu, collected from nonindigenous populations in Japan Ichthyol Res. 2009; 56(2):204-07.

Musyl MK, Keenan CP. Population genetics and zoogeography of australian freshwater golden perch, Macquaria ambigua (Richardson 1845) (Teleostei: Percichthyidae), and electrophoretic identification of a new species from the lake eyre basin. Mar Freshw Res. 1992; 43(6):1585-601.

Near TJ, Dornbur A, Eytan RI, Keck BP, Kuhn KL, Smith WL, Kuhn KL, Moore JA et al. Phylogeny and tempo of diversification in the superradiation of spiny-rayed fishes. Proc Nat Acad Sci USA. 2012; 109(34):13698-703.

Nelson JS. Fishes of the world, third edition. New York (NY): John Wiley & Sons; 1994.

Nelson JS. Fishes of the world, fourth edition. Hoboken (NJ): John Wiley & Sons; 2006.

Nelson JS, Grande T, Wilson MVH. Fishes of the world, fifth edition. Hoboken (NJ): John Wiley & Sons; 2016.

Nock CJ, Elphinstone MS, Rowland SJ, Baverstock PR. Phylogenetics and revised taxonomy of the Australian freshwater cod genus, Maccullochella (Percichthyidae). Mar Freshw Res. 2010; 61(9):980-91.

Northcutt G. The phylogenetic distribution and innervation of craniata mechanoreceptive lateral lines. In: Coombs SP, Görner P, Münz H, editors. The mechanosensory lateral line. New York: Springer; 1989; p.17-78.
Park CE, Park GS, Kwak Y, Hong SJ, Khan AR, Jung BK et al. Complete mitochondrial genome of the endemic species Korean aucha perch Coreoperca herzi (Teleostei, Centracanthiformes, Sinipercaidae). Mitochondrial DNA. 2016; 27(5):3493-95. 

Pavlova A, Gan HM, Lee YP, Austin CM, Gilligan DM, Lintermans M et al. Purifying selection and genetic drift shaped Pleistocene evolution of the mitochondrial genome in an endangered Australian freshwater fish. Heredity. 2017; 118(5):466-76. 

Paxton JR, Hoese DF, Allen GR, Hanley JE. Zoological catalogue of Australia. Pisces. Petromyzodontidae to Carangidae. Canberra: Austral. Government Publishing Service. 1989. 

Pedroza V, Le Roux JP, Gutierrez NM, Vicencio VE. Stratigraphy, sedimentology, and geothermal reservoir potential of the volcanlastic Cura-Mallin succession at Lonquimay, Chile. J South Amer Earth Sci. 2017; 77:1-20. 

Pen LJ, Potter IC. The biology of the night fish, Bostockia porosa, in a south-western Australian river. Aust J Mar Freshwat Res. 1990; 41:627-45. 

Prosdocimi F, de Carvalho DC, de Almeida RN, Beheregayr LB. The complete mitochondrial genome of two recently derived species of the fish genus Nannopterus (Perciformes, Percichthyidae). Mol Biol Rep. 2012; 39(3):2767-72. 

Pusey BJ, Kennard MH. Guyu wujalwujalensis, a new genus and species (Pisces: Percichthidae) from north-eastern Queensland, Australia. Ichthyol Explor Freshwaters. 2001; 12(1):17-28. 

Pusey B, Keenan M, Artington AH. Freshwater fishes of north-eastern Australia. Collingwood: Csiro Pub; 2004. 

Quezada-Romegialli C, Guerrero CJ, Vélez D, Vila I. The complete mitochondrial genome of the endemic and threatened killifish Orestias ascostenensis Parenti, 1984 (Cyprinodontiformes, Cyprinodontidae) from the High Andes. Mitochondrial DNA Part A. 2016a; 27(4):2798-99. 

Quezada-Romegialli C, Guerrero CJ, Vélez D, Vila I. The complete mitochondrial genome of the killifish Orestias sp. (Cyprinodontiformes, Cyprinodontidae) from the high Andean range. Mitochondrial DNA Part A. 2016b; 27(4):2840-41. 

Quezada-Romegialli C, Vélez D, Docmac F, Harrod C. The complete mitochondrial genome of the rocky reef fish Cheilodactylus variegatus Valenciennes, 1833 (Teleostei: Cheilodactylidae). Mitochondrial DNA Part A. 2016c; 27(4):2359-60. 

Regan CT. A revision of the fishes of the genus Kuhlia. Proc Zool Soc London. 1913; pt 3:374-81. 

Regan CT. The Perciform Genera Gymnapogon and Nannatherina. Copeia. 1940; 1940(3):173. 

Richardson J. Fishes. In: Adams A, editor. The zoology of the voyage of H. M. S. Samaran; under the command of Captain Sir Edward Belcher, during the years 1843-1846. Reeve & Benham, London. 1848; p.1-28. 

Ringuelet R, Arámburu R, Alonso de Arámburu A. Los peces argentinos de agua dulce. La Plata: Comisión de Investigación Científica. 1967. 

Roberts CD. Comparative morphology of spined scales and their phylogenetic significance in the Teleostei. Bull Mar Sci. 1993; 52:60-113. 

Rubilar A. Diversidad iictológica en depósitos continentales mio-cenos de la Formación Cura-Mallín, Chile (37-39ºS): implicancias paleogeográficas. Rev Geol Chile. 1994; 21(1):3-29. 

Rubilar A, Abad E. Percichthys sylvaiae sp. nov. del Terciario de los Andes sur-centrales de Chile (Pisces. Perciformes, Percichthyidae). Rev Geol Chile. 1990; 17(2):197-204. 

Ruzzante DN, Walde SJ, Cussac VE, Dalebout ML, Seibert J et al. Phylogeography of the Percichthyidae (Pisces) in Patagonia: roles of orogeny, glaciation, and volcanism. Mol Ecol. 2006; 15:2949-68. 

Sancianco MD, Carpenter KE, Betancur-R. R. Phylogenetic placement of enigmatic percomorph families (Teleostei: Percomorphaceae). Mol Phylogenet Evol. 2016; 94:565-76. 

Sabaj MH. 2016. Standard symbolic codes for institutional resource collections in herpetology and ichthyology: an online reference. Version 6.5 (16 August 2016). Electronically accessible at http://www.asih.org/, American Society of Ichthyologists and Herpetologists, Washington, DC. 

Schaeffer B. An Eocene fossil serranid from Patagonia. Amer Mus Novitates. 1947; 1331:1-9. 

Schultze H-P. Morphologische und histologische Untersuchungen an den Schuppen mesozoischer Actinopterygier (Übergang von Ganoid- zu Rundschuppen). Neues Jb Geol Paliäont, Abh. 1966: 126:232-312. 

Schultze H-P. Nomenclature and homologization of cranial bones in actinopterygians. In: Arratia G, Schultze H-P, Wilson MVH, editors. Mesozoic Fishes 4 - Homology and Phylogeny. München: Verlag Dr. F. Pfeil, 2008: p.23-48. 

Scott TD. The marine and fresh water fishes of South Australia. South Australian branch of the British Science guild. 1962; 1-338. 

Setiamarga DHE, Miya M, Yamanoue Y, Mabuchi K, Satoth TP, Inoue JG et al. Interrelationships of Atherinomorpha (me-dakas, flyingfishes, killifishes, silversides, and their relatives): The first evidence based on whole mitogenome sequences. Mol Phylogenet Evol. 2008;49(2):598-605. 

Smith CL. Hermaphroditism in some serranid fishes from Bermuda. Pap Michigan Acad Sci Arts Lett. 1959. 44:111-18. 

Smith WL, Craig MT. Casting the percomorph net widely: the importance of broad taxonomic sampling in the search for the placement of serranid and percid fishes. Copeia. 2007; 1:35-55. 

Stamatakis A. RAxML version 8: A tool for phylogenetic analysis and post-analysis of large phylogenies. Bioinformatics. 2014; 30(9):1312-13. 

Steindachner F. Über die fische von Port Jackson in Australien. 1866; Ann Kais Akad Wiss Wien, Math-Naturwiss Kl v. 3(7):50-54. [Abstract of Steindachner 1866. English translation in Ann Mag Nat Hist (Series 3) 17:317-20.] 

Stiassny ML. The phyletic status of the family Cichlidae (Pisces. Perciformes): a comparative anatomical Investigation. Netherlands J Zool. 1981; 31(2):275-314. 

Swofford DL. PAUP*: Phylogenetic Analysis Using Parsimony (* and other methods). Version 4.0 Beta. Sinauer Associates, Sunderland, Massachusetts. 2000.
Trnski T, Hay AC, Fielder DS. Larval development of estuary perch (*Macquaria colonorum*) and Australian bass (*M. novemaculata*) (Perciformes: Percichthyidae), and comments on their life history. Fish Bull. 2005; 103(1):183-94.

Unmack PJ, Hammer MP, Adams M, Dowling TE. A Phylogenetic analysis of pygmy perches (Teleostei: Percichthyidae) with an assessment of the major historical influences on aquatic biogeography in Southern Australia. Syst Biol. 2011; 60(6):797-812.

Unmack PJ, Hammer MP, Adams M, Johnson JB, Dowling TE. The role of continental shelf width in determining freshwater phylogeographic patterns in south-eastern Australian pygmy perches (Teleostei: Percichthyidae). Mol Ecol. 2013; 22(6):1683-99.

Unmack PJ, Sandoval-Castillo J, Hammer MP, Adams M, Raadik TA, Beheregaray LB. Genome-wide SNPs resolve a key conflict between sequence and allozyme data to confirm another threatened candidate species of river blackfishes (Teleostei: Percichthyidae: *Gadopsis*). Mol Phy Evol. 2017;109, 415-420. DOI: 10.1016/j.ympev.2017.02.013

Van Der Laan R, Eschmeyer WN, Fricke R. Family-group names of recent fishes. Zootaxa. 2014; 3882(1):1-230.

Vega RM, Viozzi G. The cephalic lateral line system of temperate perches (Perciformes: Percichthyidae) from Argentinean Patagonia. Zoologia. 2016; e20160025. DOI: 10.1590/S1984-4689zoo-20160025

Wang A, Sun Y, Wu C. Characteristics and phylogenetic analysis of the complete mitochondrial genome of *Cheilodactylus quadricornis* (Perciformes, Cheilodactylidae). Mitochondrial DNA Part A DNA Mapping, Seq Anal. 2016; 27(6):4444-46.

Winterbotten R. A descriptive synonymy of the striated muscles of the Teleostei. Proc Acad Nat Sci Philadelphia. 1974; 125:225-317.

Woodburne MO, Zinsmeister WJ. The first land mammal from Antarctica and its biogeographic implications. J Paleont. 1984; 58:913-48.

Wyman SK, Jansen RK, Boore JL. Automatic annotation of organelar genomes with DOGMA. Bioinformatics. 2004; 20(17):3252-55.

Yagishita N, Miya M, Yamanoue Y, Shirai SM, Nakayama K, Suzuki N *et al*. Mitogenomic evaluation of the unique facial nerve pattern as a phylogenetic marker within the perciform fishes (Teleostei: Percomorpha). Mol Phy Evol. 2009; 53(1):258-66.