UNIVERSIDADE DE SÃO PAULO FACULDADE DE FILOSOFIA, CIÊNCIAS E LETRAS DE RIBEIRÃO PRETO PROGRAMA DE PÓS-GRADUAÇÃO EM BIOLOGIA COMPARADA

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João Pedro Trevisan dos Santos

Dissertação apresentada à Faculdade de Filosofia, Ciências e Letras de Ribeirão Preto da Universidade de São Paulo, como parte das exigências para obtenção do título de Mestre em Ciências, no Programa de Pós-Graduação em Biologia Comparada.

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Orientador: Prof. Dr. Flávio Alicino Bockmann

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Trevisan, João Pedro

Taxonomic revision of subgenus Awaous (Chonophorus) (Lichtenstein, 1822) and phylogenetic placement within "Stenogobius lineage" (Gobioidei: Gobiidae).

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"I choose to see the beauty in this world." Dolores Abernatti, Westworld.

"I want a third pill [...], a pill that would enable me to perceive, not the reality behind the illusion, but the reality in illusion itself." Slavoj Žižek, The pervert's guide to cinema.

RESUMO

SANTOS, João Pedro Trevisan dos. **Revisão taxonômica do subgênero** *Awaous* (*Chonophorus*) (Lichtenstein, 1822) e relações filogenéticas dentro da "*Stenogobius* lineage" (Gobioidei: Gobiidae). 2020. Dissertação (Mestrado em Ciências) – Faculdade de Filosofia, Ciências e Letras de Ribeirão Preto, Universidade de São Paulo, 2020.

Gobiidae atualmente é tida como uma das mais diversas famílias de peixes, por isso, apesar de amplamente estudada, ainda apresenta muitas lacunas de conhecimento. Nessa família encontra-se Awaous que é diagnosticado por apresentar papilas sobre grande parte da estrutura das brânquias. Esse gênero é atualmente dividido em três subgêneros, sendo eles Awaous, Chonophorus e Euctenogobius. O subgênero Awaous (Chonophorus) apresentaria três espécies nominais, Awaous (Chonophorus) banana, Awaous (Chonophorus) lateristriga e Awaous (Chonophorus) tajasica. Infelizmente as características diagnósticas apresentavam grande sobreposição o que dificultava o entendimento da real diversidade do subgênero. Assim um trabalho de revisão taxonômica foi empreendido. O trabalho de revisão contou com uma vasta análise de caracteres como contagem de raios e escamas, análise dos padrões de escamação em diferentes regiões do corpo, análise dos padrões dos poros do canal sensorial cefálico, das linhas de neuromastos superficiais cefálicas e, pela primeira vez, das papilas orais. Os resultados mostraram quatro espécies nominais, sendo uma delas Awaous (Chonophorus) transandeanus, considerada um sinônimo atualmente. Além disso a posição filogenética de Awaous sempre foi alvo de intenso debate. Inicialmente o gênero foi considerado proximamente relacionado à subfamília Sicydiinae, posteriormente membro de Gobionellinae e atualmente, com o advento de metodologia genética, Awaous foi novamente considerado próximo a Sicydiinae. Assim, uma análise filogenética baseada em morfologia externa, sistema sensorial, osteologia e musculatura foi implementada. Além de contar com uma nova proposta de homologia para as linhas de neuromastos superficiais, a presente dissertação é a primeira tentativa de incluir caracteres miológicos. Ficou demonstrado que Awaous seria grupo irmão de Stenogobius, proximamente relacionado a Sicydiinae. Assim a subfamília Sicydiinae é proposta abarcando o clado Awaous e Stenogobius e os demais gêneros atualmente alocados em Sicydiinae. O clado formado por Awaous e Stenogobius foi nomeado tribo Stenogobini e o clado formado pelos demais gêneros atualmente alocados em Sicydiinae foi chamado tribo Sicydiini. Além disso, o estudo das relações filogenéticas entre as espécies de Awaous mostrou que o suporte para a divisão desse gênero em subgêneros é muito fraco, sugerindo que a divisão de Awaous em três subgêneros pode não ser a mais adequada.

Palavras-chave: Taxonomia. Filogenia. Morfologia.

ABSTRACT

SANTOS, João Pedro Trevisan dos. **Taxonomic revision of subgenus** *Awaous (Chonophorus)* (Lichtenstein, 1822) and phylogenetic placement within "*Stenogobius* lineage" (Gobioidei: Gobiidae). 2020. Dissertação (Mestrado em Ciências) – Faculdade de Filosofia, Ciências e Letras de Ribeirão Preto, Universidade de São Paulo, 2020.

Gobiidae is considered one of the most diverse families of fish, therefore, despite being widely studied, it still has many knowledge gaps. In this family is found Awaous which is diagnosed by the presence of papillae over much of the gill structure. This genus is currently divided into three subgenera, namely Awaous, Chonophorus and Euctenogobius. The subgenus Awaous (Chonophorus) would present three nominal species, Awaous (Chonophorus) banana, Awaous (Chonophorus) lateristriga and Awaous (Chonophorus) tajasica. Unfortunately, the diagnostic characteristics overlap extensively, which made it difficult to understand the real diversity of the subgenera. Thus, a taxonomic revision was implemented. The revision work was based on several characteristics such as ray and scale count, analysis of scale pattern in different regions of the body, analysis of pore patterns of the cephalic sensory canal, cephalic superficial neuromast lines and, for the first time, oral papillae. The results revealed four nominal species, one of them being Awaous (Chonophorus) transandeanus, currently considered a synonym. Moreover, the phylogenetic position of Awaous has always been the subject of intense debate. Initially the genus was considered closely related to the subfamily Sicydiinae, later a member of Gobionellinae and now, with the advent of genetic methodology, Awaous was once again considered close to Sicydiinae. Thus, a phylogenetic analysis based on external morphology, sensory system, osteology and musculature was implemented. Besides proposing new homology for the superficial neuromasts lines, this dissertation is the first attempt to include myological characters. It was demonstrated that Awaous is the sister group of Stenogobius, closely related to Sicydiinae. Thus, the Sicydiinae Subfamily is proposed encompassing Awaous, Stenogobius and the other genera currently allocated in Sicydiinae. The clade formed by Awaous and Stenogobius was named tribe Stenogobini and the clade formed by genera currently allocated in Sicydiinae was called tribe Sicydiini. In addition, the study of phylogenetic relationships among Awaous species revealed that the support for the division of this genus into subgenera is very weak, suggesting that the division of Awaous into three subgenera may not be the most appropriate.

Keywords: Taxonomy. Phylogeny. Morphology.

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1. TAXONOMY

1.1. INTRODUCTION

Currently the family Gobiidae comprises 258 genera and 1.873 species distributed throughout the tropical zone (ESCHMEYER *et al.*, 2019. Diagnostic features for this family are five branchiostegal rays, expanded and medially-placed ventral processes on ceratobranchial 5 and a complex base on the dorsal hemitrich of pelvic-fin rays (GILL; MOOI, 2012).

Recently it was suggested that this family would be divided into two separate families, Gobiidae and Gobionellidae (THACKER, 2009). This division was adopted by some authors (NELSON *et al.*, 2016; PEZOLD, 2011; THACKER, 2013; 2015), but the nomenclature may be inacurate. According to Gill and Mooi (2012), the names Oxudercidae, Amblyopina and Trypauchenina would predated Gobionellidae.

Herein the family Gobiidae is adopted *sensu* Gill and Mooi (2012) and, following (PEZOLD, 1993), divided into five subfamilies: Oxudercinae, Amblyopinae, Sicydiinae, Gobiinae and Gobionellinae.

The gobionelline genus *Awaous* Valenciennes, 1837, the main focus of this dissertation has pantropical distribution (PARENTI; THOMAS, 1998). It is distinguished by the presence of sensory papillae over much of the gill structure (**Figure 1**) (WATSON, 1992). *Awaous* comprises 21 presumably valid species of which *Awaous* (*Awaous*) ocellaris Broussonet, 1782 is the type species. According to Watson (1992), the junior synonyms for *Awaous* are *Platygobius* Bleeker, 1874; *Trichopharynx* Ogilby, 1898; *Suiboga* Pinto, 1960 and *Chiramenu* Rao, 1971. Watson (1992) also proposed that *Awaous* should be divided in three subgenera: *Awaous* Valenciennes, 1837; *Euctenogobius* Gill, 1859 and *Chonophorus* Poey, 1860.

WATSON (1992) brought together the species of *Awaous* (*Awaous*) in two groups. The *Awaous ocellaris* group has scales in the opercular and pre-opercular regions which are absent in the *Awaous nigripinnis* Valenciennes, 1837 group.

WATSON (1992) diagnosed the subgenus *Awaous* (*Chonophorus*) by the presence of a complete posterior oculoscapular canal between the pores "H" and "K" [*vs.* incomplete in *Awaous* (*Awaous*)], presence of well-developed sensory papillae over much of the lateral surface of the body [*vs.* poorly developed or absent in *Awaous* (*Awaous*)], caudal fin with two or three longitudinal rows of sensory papillae extending over the entire length of the fin [*vs.*

usually absent in *Awaous* (*Awaous*)], body shape slender [*vs.* usually robust in *Awaous* (*Awaous*)], absence of a dark spot over the posterior margin of the first dorsal fin [*vs.* conspicuous in most species of *Awaous* (*Awaous*)], sexual dichromatism absent [*vs.* usually present in *Awaous* (*Awaous*), male usually darker than the female] and color pattern usually cream or tan color with a series of irregular streaks or crescentic shaped markings and two to five brownish oblique bars [*vs.* color pattern varying between white, gray, green or tan with brown or black sports appearing on the lateral face of the body in *Awaous* (*Awaous*)].



Figure 1 – Papillae over the gill structure of *Awaous (Chonophorus) tajasica* (Lichtenstein, 1822). Exemplar previously stained with alcian blue and alizarin red (LIRP 1074, 93.9 mm CP).

Watson (1992) also postulated that *Awaous* (*Chonophorus*) can be distinguished from *Awaous* (*Euctenogobius*) by the presence of a complete posterior oculoscapular canal between the pores "H" and "K" [vs. incomplete in *Awaous* (*Euctenogobius*)], presence of well-developed sensory papillae over much of the lateral surface of the body [vs. poorly developed or absent in *Awaous* (*Euctenogobius*)], absence of sexual dimorphism [vs. present in *Awaous* (*Euctenogobius*), males presenting longer jaws, longer and higher fins and a larger body size when compared to females], and papillae inside the mouth and interior surface of the gill more conspicuous [vs. poorly developed in *Awaous* (*Euctenogobius*)]. Furthermore, the color pattern in *Awaous* (*Euctenogobius*) is characterized by a series of six to eight vertical bars reaching

from the base of the pectoral fin to the anterior margin of the caudal fin, and the first dorsal fin usually red or orange, very distinctive from the color pattern of *Awaous* (*Chonophorus*) (WATSON & HORSTHEMKE, 1995).

According to Watson (1996) *Awaous* (*Chonophorus*) comprises three valid species. (1) *Awaous* (*Chonophorus*) *Banana* (Valenciennes, 1837), occuring in the Atlantic coast from Florida to Trinidad and Tobago, occurring also on all Caribbean islands, and from Tamaulipas, Mexico until Caracas, Venezuela in the continental shelf. This species would also be distributed along the Pacific slope reaching from Baja California Sur and Sonora, Mexico to Tumbes in Peru. (2) *Awaous* (*Chonophorus*) *lateristriga* (Duméril, 1861) occurs on the African coast from Sierra Leone to the border between Angola and Namibia, also occurring in the Bioko island, Equatorial Guinea and (3) *Awaous* (*Chonophorus*) *tajasica* (Lichtenstein, 1822) distributed over the Brazilian coast from Piauí to Santa Catarina.

According to Watson (1996), *Awaous* (*Chonophorus*) *banana* (Valenciennes, 1837) has eight junior synonyms: *Gobius martinicus* Valenciennes, 1837, *Chonophorus bucculentus* Poey, 1860, *Gobius transandeanus* Günther, 1861, *Chonophorus contractus* Poey, 1861, *Gobius mexicanus* Günther, 1861, *Gobius dolichocephalus* Cope, 1867, *Awaous nelsoni* Evermann, 1898 and *Gobius (Awaous) guentheri* Regan, 1903. This species is distinguished by the presence of a duplicated pore "F" in the oculoscapular canal, scales in the longitudinal series ranging from 57 to 86 and scales in the pre-dorsal region ranging from 0 to 57.

Awaous (Chonophorus) lateristriga (Duméril, 1861) would present Gobius (aeneofuscus) guineenses var. Peters 1876 and Gobius bustamantei Greef, 1882 as junior synonyms. This species would be distinguished by the presence of a single pore "F" in the oculoscapular canal, scales in the longitudinal series reaching from 54 to 66 (usually 59 to 63), scales in the transversal series reaching from 13 to 20 (usually 17 to 18) and scales in the predorsal region reaching from 0 to 35, always cycloid. Pre-dorsal region would never be entire scaled in this species (WATSON, 1996).

Awaous (*Chonophorus*) *tajasica* (Lichtenstein, 1822) would have as junior synonyms *Euctenogobius latus* O'Shaughnessy, 1875 and *Suiboga travassosi* Pinto, 1960. This species can be distinguished by the presence of a single pore "F" in the oculoscapular canal, scales in the longitudinal series reaching from 57 to 70 (usually 61 to 66), scales in the transversal series reaching from 14 to 21 (usually 16 to 18), pre dorsal scales reaching from 2 to 39. The pre-dorsal region would present naked spots but never entirely naked (WATSON, 1996).

Watson (1996) proposed *Gobius transandeanus* Günther, 1861 as junior synonym of *Awaous* (*Chonophorus*) *banana*. However, name *Awaous* (*Chonophorus*) *transandeanus* is currently considered as valid by some authors (BUSSING, 2002; ESCHMEYER et al., 2018). The distribution of *Awaous* (*Chonophorus*) *transandeanus* (Günther 1861) would reach from Costa Rica to Peru in the pacific slope (BUSSING, 2002). This species would be distinguished by the presence of larger scales, scales in the transversal series reaching from 16 to 19 and scales in the longitudinal series reaching from 56 to 61.

In spite of Watson (1996) efforts the taxonomy of the subgenus remains uncertain, some of the diagnostic features are still not entirely sufficient to precisely identify the species within *Awaous (Chonophorus)*. For example, the diagnostic scale counts for *Awaous (Chonophorus)* tajasica and *Awaous (Chonophorus) lateristriga* show a nearly complete overlap. Since both species present a single pore "F" in the oculoscapular canal, the difference between them would be the fact that the pre-dorsal region would be never completely naked in *Awaous (Chonophorus) tajasica* and never fully scaled in *Awaous (Chonophorus) lateristriga*. Such diagnostic features frequently lead to problems in the identification of exemplars.

Another interesting aspect of species within *Awaous* is the huge distribution area occupied by them, probably related to the amphidromous habit. According to Myers (1949) amphidromous species are "diadromous fishes whose migration from fresh water to the sea [...] is not for the purpose of breeding". In *Awaous* this migration has trophic reasons. Adults lay their eggs in freshwater, and, after the eclosion, the larvae are carried to the sea where they remain as part of the plankton. After that the larvae return to freshwater, where they will reside during the adult phase (RADTKE *et al.*, 1988). There are four main factors influencing the dispersion of amphidromous species, the time spent in the sea, the capacity of active dispersal, geographic barriers and the influence of ocean currents (ROCHA *et al.*, 2005).

Despite the amphidromous habit, some distribution areas assigned to some *Awaous* species extent beyond the limits of the ocean currents and geographical barriers proposed in the literature. As an example, it is very unlikely that *Awaous* (*Chonophorus*) *banana* would occur in both Atlantic and Pacific slopes of the American continent.

Another aspect of *Awaous* (*Chonophorus*) distribution remain in occurrence registers far away from the proposed distribution area for the species. *Awaous* (*Chonophorus*) *tajasica* was recently reported in North America (BERRA, 2002) and even in the Baja California, Mexico (RUIZ-CAMPOS, 2012; RUIZ-CAMPOS *et al.*, 1993; 2002), despite occurring originally in the Brazilian coast reaching from Maranhão to Rio Grande do Sul (TREVISAN, 2016).

In face of this scenario a taxonomic revision became extremely important, not only for stablishing diagnostic features and the occurrence areas for the species but also for help in the phylogenetic study of the group, explored in the second chapter of this dissertation.

1.2. OBJECTIVES

- Diagnose the species within *Awaous* (*Chonophorus*), comparing them with similar forms, assigning names to previously undescribed new species;
- Establish a complete list of synonyms for all recognized forms among *Awaous* (*Chonophorus*);
- Delimit the occurrence areas for the species within Awaous (Chonophorus).

1.3. MATERIAL AND METHODS

The species concept adopted in this dissertation follow Nelson and Platnick (1981), which define species as "the smallest detected samples of self-perpetuating organisms that have unique sets of characters".

1.3.1. Material examined

The examined material was obtained in scientific collections. The main criteria adopted for choosing the material was the geographic one. Specimens were selected through specialized browsers such as SpeciesLink (<u>http://splink.cria.org.br/</u>) for the Brazilian collections and Fishnet2 (<u>http://fishnet2.net</u>) for the international ones.

List of examined material:

Awaous (Chonophorus) banana (Atlantic slope):

NHM 1856.4.17: 41-42: 2 alc: 131.5 – 143.6 mm SL. Mexico. **Syntypes** of *Gobius mexicanus* designated by Günther (1861): 61. No information about Atlantic or Pacific slope. **SU** 47636:

1 alc. 145.8 mm SL. Mexico, San Luis Potossi, Tamazunchale, rio Moctezuma, Panuco river basin. 1952. MCZ 31220: 1 alc. 153.5 mm SL. Holotype of Chonophorus contractus designated by Poey (1861): 424. MCZ 13330: 1 alc. 241 mm SL. Cuba. Syntype of Chonophorus bucculentus designated by Poey (1860): 275. MCZ 13379: 1 alc. 219 mm SL. Cuba. Syntype of Chonophorus bucculentus designated by Poey (1860): 275. MCZ 13380: 1 alc. 234 mm SL. Cuba. Syntype of Chonophorus bucculentus designated by Poey (1860): 275. MCZ 13375: 1 alc. 165 mm SL. Cuba. NMNH 4772: 1 alc. 214 mm SL. Cuba. NMNH 4774: 1 alc. 210 mm SL. Cuba. ANSP 88598: 2 alc. 112.6 – 139 mm SL. Cuba, Santiago de Cuba, rio del aqueduto, San Boniato. 1938. MCZ 31220: 1 alc. 153.5 mm SL. Cuba. 1861. ANSP 64613: 1 alc. 147.3 mm SL. Guatemala, el Rancho, Motagua river. 1935. NMNH 134681: 23 alc. 145,8 – 72,3 mm SL. Guatemala, Zacapa, Chimalapa river in Cabanas, 23 miles west from Zacapa. 1946. ANSP 85774: 4 alc. 73.6 – 77.6 mm SL. Haiti, Port-au-Prince. 1936. ANSP 10819: 1 alc. 153.4 mm SL, Dominican Republic, Santo Domingo, West Indies. Year not informed. MNHN A- 1265: 1 alc. 98.6 mm SL. Dominican Republic, Santo Domingo. 1837. Lectotype designated by Watson (1996): 3. MNHN A-1359: 1 alc. 71.8 mm SL. Dominican Republic, Santo Domingo. 1837. Paralectotype designated by Watson (1996): 3. MNHN A-1266: 1 alc. 118.8 mm SL. Martinica. Year not informed. Syntype of Gobius martinicus designated by Valenciennes (1837): 105. UCR 1352-8: 10 alc. 61.8 – 94.9 mm SL. Costa Rica, Limón, Hone creek, 6 km west of Puerto Viejo. 1981. UCR 210-7: 7 alc. 64.9 – 93.1 mm SL. Costa Rica, Limón, río Suárez 1 km south of Cahuita at road crossing to Puerto Viejo. 1967. UCR 1144-6: 4 alc. 56.6 – 108.9 mm SL. Costa Rica, Limón, río Cocolis, 3.5 km southeast of Shiroles, on Bratsi-Shiroles road. 1977. UCR 1299-6: 7 alc. 129.6 – 61 mm SL. Costa Rica, río Cocolis, 3.5 km southeast of Shiroles, on Bratsi-Shiroles road. 1979. UCR 279-6: 7 alc. 108 – 50 mm SL. Costa Rica, Limón, inlet of río Sixaola, slightly upstream of Isla Grande. 1968. ANSP 163759: 1 alc. 42.2 mm SL. Costa Rica, Limon, Kelly creek at beach, Cauhita. 1988. CAS 219379: 2 alc. 135 – 125.4 mm SL. Trinidad and Tobago, river mouth in the Little Englishman bay. 2001. AMNH 264747: 1 alc. 51.3 mm SL. Panama. 2003. AMNH 243507: 1 alc. 51.3 mm SL. Venezuela, Falcon, mouth of La Pava River, below a road bridge, 30 meters from the sea. 2007.

Awaous (Chonophorus) banana (Pacific slope):

NMNH 48836: 1 alc. 66.5 mm SL. Mexico, Sinaloa, Rosario, Rosario river. 1897. Holotype of Awaous nelsoni designated by Evermann (1898): 2. NMNH 48837: 3 alc. 68.7 – 61.7 mm SL. Mexico, Sinaloa, Rosário, Rosário river. 1897. Paratype (cotype) of Awaous nelsoni designated by Evermann (1898): 2. NMNH 221109: 3 alc. 81.5 – 58.5 mm SL. Mexico, Sinaloa, Rosário, Rosário river. 1897. Paratype of Awaous nelsoni designado por Evermann (1898): 2. CAS 54365: 2 alc. 67.9 – 54.4 mm SL. Mexico, Sinaloa, vila Union, Presidio river, Presidio river basin, 14 miles south of Mazatlan on the road to Durango. 1952. NMNH 37172: 1 alc. 83.2 mm SL. Mexico, Presidio river, northwest Mexico. 1885. NMNH 102266: 1 alc. 83.8 mm SL. Mexico, Matias Romero, Oaxaca, Malotenga river, tributary of the Coatzalcoalcos four miles southeast of Matias Romero. NMNH 30741: 1 alc. 86.6 mm SL. Mexico, Baja California, Saint Lucas cape. 1882. NMNH 30931: 1 alc. 91.9 mm SL. Mexico, Baja California, Lapaz port, San José. NMNH 114395: 1 alc. 105.8 mm SL. Guatemala, Patulul, Coyolate river five miles southwest of Patulul. 1947. UCR 184-3: 7 alc. 97.8 – 52 mm SL. Nicaragua, León, rio 50 km west of Managua, Highway 12 Managua-León. 1967. UCR 121-3: 8 alc. 112 - 55.7 mm SL. Costa Rica, Puntarenas, rio Agujas, 3 Km from the coast on Tárcoles-Jacó road. 1967. UCR 101-14: 5 alc. 68.8 – 54.9 mm SL. Costa Rica, Puntarenas, rio Nuevo, 12 km east of the río Claro village at Interamerican Highway. 1967. UCR 69-3: 8 alc. 141.7 - 58.2 mm SL. Costa Rica, Puntarenas, río Tamarindo, on road 12 to León. 1966. AMNH 264771: 1 alc. 53.2 mm SL. Panama, Chiriquí, canal close to Raya island. 2003. Mzusp 66632: 3 alc. 58.1 – 52.3. Panamá, Chepo, rio Mamoni, província de Panamá. 1965. NMNH 339912: 2 alc. 73.7 – 71.0 mm SL. Colombia, Choco, Creek of rio Parado, C. 10 Min. Helicopter Flight from Village of Parado. 1967. NMNH 120215: 1 alc. 57.1 mm SL. Colombia, rio D'agua, Buenaventura. 1943. NMNH 292679: 3 of 7 alc. 100.2 – 67.9 mm SL. Colombia, Choco, Creek into rio Jurado, C. 5 Min Heli-Flight Downstream Fr. Mountains. 1967. NHM 1860.6.16: 135-136: 2 alc. 84.8 – 86.3 mm SL. West Ecuador. Syntypes of *Gobius transandeanus* designated by Günther (1861): 62. NHM 1860.6: 16: 133-134: 2 alc. 102.4 – 108.5 mm SL. West Ecuador. Syntypes of *Gobius (Awaous) Guenteri* designated by Regan (1903): 629. NMNH 288040: 2 alc. 89.9 – 87.2 mm SL. Ecuador, Esmeraldas, Rio Bogota, Estero Sabalera a 600 m. Cerea Al Campamento La Chiquita Del Mag, Carretera a Ricaurte. 1987. NMNH 167717: 2 alc. 61.7 – 60 mm SL. Ecuador, waterfall close to Calima river. 1956.

Awaous (Chonophorus) lateristriga:

NMNH 292655: 3 alc. 72.5 – 68.7 mm SL. Sierra Leone, Foya Village, Tabe river, 16 mi. Southeast of Bo. 1962. **NMNH** 179697: 2 alc. 81.7 - 74.6 mm SL. Liberia, 2 miles east of Messurado river mouth. 1953. **SU** 63040: 3 alc. 60.9 - 51.1 mm SL. Gana, Amedica, volta R. 1963. **NMNM** 292667: 3 alc. 59 - 58.9 mm SL. Gana, Aimaso river. 1970. **NMNH** 295449: 3 alc. 93.4 – 88.7 mm SL. Togo, Mono river 36 km. Due E. of Ayengre. 1969. **SU** 15955: 2 alc. 95.8 – 82.1 mm SL. Cameroon, Biafra bay. 1940. **SU** 40391: 2 alc. 84.6 - 83.8 mm SL. Cameroon, brackish stream emptying into ocean, Mbode, 10 mi. south from Batangaon coast of Cameroon. 1940. **MNHN** 6228-1: 1 alc. 87.5 mm SL. Gabon. Year not informed. **Lectotype** designated by Watson (1996): 10. **MNHN** 1996-301: 1 alc. 73 mm SL. Gabon. Year not informed. **Paralectotype** designated by Watson (1996): 10. **AMNH** 238340: 4 alc. 63.5 – 53.2 mm SL. Democratic Republic of the Cong, main channel of Congo river, upstream of Boma. 2005. **AMNH** 263636: 2 alc. 52.2 – 50 mm SL. Democratic Republic of the Cong, main channel of Congo river, upstream of Boma. 2005. **AMNH** 263636: 2 alc. 52.2 – 50 mm SL. Democratic Republic of the Congo, Congo river, Boma region. 2014. **CAS** 214397: 1 alc. 50.2 mm SL. Sao Tome and Principe, Sao Tome, Agua Azeitona, below hwy. bridge. 2001.

Awaous (Chonophorus) tajasica:

MNRJ 44321: 3 alc. 91.4 – 73.9 mm SL. Ceará, Icó, Rio Salgado. 1945. ANSP 84176: 2 alc. 141.2 – 100.7 mm SL. Ceará, Fortaleza. 1937. ANSP 84174: 1 alc. 92.4 mm SL. Ceará, Choró river. 1937. UFPB 10028: 1 alc. 68.7 mm SL. Ceará, Itapipoca, riacho inominado, afluente do Rio Cruxati. 2014. ANSP 84175: 1 alc. 131.8 mm SL. Ceará, Russas, Rio Jaguaribe. 1936. Neotype designated by Watson (1996): 14. MZUSP 45041: 1 alc. 77.4 mm SL. Rio Grande do Norte, Tibau do Sul, Riacho do Galhardo. 1992. UFPB 4104: 1 alc. 73.4 mm SL. Paraíba, Itabaiana, Rio Paraíba do Norte. 1998. UFPB 4151: 1 alc. 118.8 mm SL. Paraíba, Rio Paraíba do Norte, PB - 408. 1998. UFPB 9359: 1 alc. 103 mm SL. Paraíba, Alhandra, rio Cupissura. 2013. UFPB 9360: 1 alc. 104.3 mm SL. Paraíba, Alhandra, rio Cupissura. 2013. UFPB 9360: 1 alc. 104.3 mm SL. Paraíba, Alhandra, rio Cupissura. 2013. UFPB 4525: 2 alc. 145.7 – 119.6 mm SL. Paraíba, Areia, Rio Angelim, bacia do Rio Mamanguape. 1999. MCP 30931: 1 alc. 95.7 mm SL. Alagoas, São Miguel dos Campos, Rio Barreiro na estrada BR 101 entre Pilar/São Miguel dos Campos, afluente do Rio Sumauma, Lagoa Mamguaba. 2002. UFPB 3430: 1 alc. 66.4 mm SL. Alagoas, Maceió, Complexo Estuarino Mundaú-Manguaba. 1988. MZUSP 66634: 1 alc. 62 mm SL. Alagoas, Maceió, Rio

dos Remédios. 1988. **MZUSP** 66637: 7 alc. 123 – 99.5 mm SL. Alagoas, Maceió, Lagoa de Mundaú. 1985. **MZUSP** 51745: 1 alc. 112.4 mm SL. Alagoas, Penedo, Rio São Francisco no porto da balsa. 1997. **UFRGS** 17055: 1 alc. 122.6 mm SL. Sergipe, Muribeca, Rio Ladim, na BR-101 junto à ponte no km 28, afluente do baixo Rio Vaza Barris. 2012. **UFRGS** 17089: 2 alc. 98.3 – 97.3 mm SL. Sergipe, Itaporanga d'ajuda, Rio Banhado na estrada BR-101, junto à ponte. 2012.

NHM 1862.11.23: 42: 1 alc. 125 mm SL. South America; Brazil; Bahia. Holotype Euctenogobius latus designated by O'Shaughnessy (1875): 146. MNRJ 6196: 1 alc. 175.3 mm SL. Bahia, Salvador, Rio Pituaçu. Comissão do Museu Nacional e do Instituto de Saúde Pública do Estado da Bahia. 1951. Holotype Suiboga tavassosi designated by Pinto (1959) 218: 1. MNRJ 22941: 2 alc. 90.2 – 71.5 mm SL. Bahia, Itagimirim, Rio limoeiro, drenagem do Rio Jequitinhonha, BR 101 a montante do Rio Itagimirim. 2001. MCP 17853: 2 alc. 169 – 95.8 mm SL. Bahia, Teixeira de Freitas, rio Itanhém (costeiro), no corredor iniciando na estrada entre Teixeira Freitas e Medeiros Neto, a 17 km da BR-101. 1995. ANSP 174254: 1 alc. 107.4 mm SL. Brazil, Bahia, rio Caraiva, approx. 500 m W of highway BR 101 in Monte Pascoal. Year not informed. UNT 9498: 1 alc. 106.1 mm SL. Bahia, Gongogi, rio Gongogi. 2009. UNT 10418: 1 alc. 117 mm SL. Bahia, Ilhéus, Castelo novo, rio Almada. 2011. UNT 9259: 3 alc. 134.5 – 91.2. Bahia, Ilhéus, Castelo novo, rio Almada. 2009. MZUSP 111241: 1 alc. 127.3 mm SL. Bahia, Nilo Peçanha, Rio das Almas, dez quilômetros de Nilo Peçanha na estrada, corredeiras do Rio das Almas. Year not informed. MZUSP 66626: 2 alc. 97 – 58.4 mm SL. Espírito Santo, Linhares. Rio Doce. 2005. MZUSP 51710: 1 alc. 51.4 mm SL. Espírito Santo, Linhares, Rio Doce, margem direita da praia de areia abaixo da ponte da BR-101. 1997. MCP 42069: 1 alc. 110.1 mm SL. Espírito Santo, Linhares, rio Pequeno. 2002. MZUSP 66627: 2 alc. 92.3 – 68.1 mm SL. Espírito Santo, Santa Leopoldina, rio Santa Maria da Vitória. 1965. MNRJ 41842: 1 alc. 149.9 mm SL. Espírito Santo, Santa Teresa, rio Santa Maria do Rio Doce, bacia do rio Doce, na cachoeira do Rudio. 2013. MNRJ 8566: 3 alc. 90.8 - 58.1 mm SL. Espírito Santo, Santa Tereza. 1942. MNRJ 37630: 1 alc. 82.2 mm SL. Espírito Santo, Baixo Guandu, rio Mutum Preto no terço médio, entre o povoado de Alto Mutum. 2010. MNRJ 38982: 2 alc. 109.6 – 80.8 mm SL. Espírito Santo, Pau gigante, rio Taquarussú. 1940. ANSP 174255: 1 alc. 132.8 mm SL. Brazil, Espírito Santo, Itapemirim river at bridge on highway BR 101 approx. 12 km SW of Rio Novo do Sul. Year not informed. MNRJ 46587: 1 alc. 109.4 mm SL. Minas Gerais, Além Paraíba, Rio Paraíba do Sul, bacia do Rio Paraíba do Sul. 2015. MNRJ 17104: 1 alc. 58.1 mm SL. Minas Gerais, Além Paraíba, Rio Paraíba do Sul. 1990. MNRJ 17850: 3 alc. 153.6 – 116.7 mm SL. Minas Gerais, Cataguases, Rio Novo, afluente da margem direita do Rio Pomba, afluente da margem esquerda do Rio Paraíba do Sul. 1989. MNRJ 14771 1 alc. 136.6. Minas Gerais, Cataguases, Rio Novo, afluente da margem direita do Rio Pomba e afluente da margem esquerda do Rio Paraíba do Sul, até 8 Km a montante da foz. 1989. MZUSP 10319: 1 alc. 121.6 mm SL. Rio de Janeiro, São João da Barra. 1964. MZUSP 100849: 1 alc. 149.3 mm SL. Rio de Janeiro, Trajano de Morais. Margem esquerda do Rio grande na fazenda São Manuel, antes da desembocadura do Córrego do Macaco. 2008. MZUSP 66623: 1 alc. 92.5 mm SL. Rio de Janeiro, São Fidélis. Rio Paraíba do Sul. 1965. MZUSP 66635: 2 alc. 101.6 -92.5 mm SL. Rio de Janeiro, São Fidélis, Córrego pedra d'água. 1965. MZUSP 121468: 1 alc. 60 mm SL. Rio de Janeiro, conceição de Macabu, Rio Aduelas, afluentes do rio São Pedro, na Fazenda Sossego. Bacia do Rio Macaé. Year not informed. MZUSP 26842: 2 alc. 90.9 – 87 mm SL. Rio de Janeiro. Cabeceira do Rio Guapiaçu, Cachoeira de Macacu. 1979. MNRJ 131580: 3 alc. 136.9 – 174.1 mm SL. Rio de Janeiro, Casemiro de Abreu, Rio Macaé, Figueira Branca, Casemiro de Abreu. 2017. MNRJ 48675: 6 alc. 126.6 – 156.4 mm SL. Rio de Janeiro, Macaé, Lagoa de Cabiúnas, Macaé. 1982. LIRP 6848: 1 alc. 116.8 mm SL. Rio de Janeiro, Bom Jesus do Itabapoana, Rio Itabapoana. 2008. LIRP 567: 3 alc. 50.4 – 39.6 mm SL. Rio de Janeiro, Parati, Rio Muricana, faz. Muricana, Perequê-Açu. 1995. MZUSP 107461: 2 alc. 59.9 - 58.8 mm SL. São Paulo, Ubatuba, Riacho do Canto da Paciência, núcleo Picinguaba, Parque estadual da serra do mar. 2002. LIRP 1045: 4 alc. 63.5 – 37.4 mm SL. São Paulo, Ubatuba, Rio da Fazenda, núcleo Picinguaba. 1997. LIRP 1030: 1 alc. 57.5 mm SL. São Paulo, Ubatuba, Rio Picinguaba. 2000. LIRP 1022: 1 alc. 67.1 mm SL. São Paulo, Ubatuba, Rio da Fazenda, Parque Estadual da Serra do Mar - Núcleo Picinguaba. 1998. MZUSP 66628: 1 alc. 62.6 mm SL. São Paulo, Ubatuba, córrego do lado esquerdo da Praia do Perequê-Mirim. 1975. MZUSP 111188: 1 alc. 107.5 mm SL. São Paulo, Ubatuba, cachoeira do Rio Promirim. Km 30, BR-101. 2012. MZUSP 66629: 2 alc. 88.6 – 87.8 mm SL. São Paulo, Ubatuba Rio Indaiá, junto a estrada rio Santos. 1973. LIRP 1074: 14 alc. 94.7 - 51.5 mm SL. São Paulo, Ubatuba, Rio Indaiá. 1984. LIRP 543: 11 alc. 45.4 – 28.4 mm SL. São Paulo, Ubatuba, Rio Indaiá. 1988. LIRP 7687: 5 alc. 88.2 – 66.4 mm SL. São Paulo, Ubatuba, Rio Itamambuca, sob a ponte da BR-101. 2010. LIRP: 5745 3 alc: 100.5 – 74 mm SL. São Paulo, São Sebastiao, Rio Paúba. 2004. UFRGS 10192: 1 alc. 76.2 mm SL. São Paulo, Ilha Bela, Riacho indo para a praia do Castelhano, próximo ao centro. 2008. MNRJ 40907: 1 alc. 67.2 mm SL. Paraná, Paranaguá, rio Colônia Pereira (bacia do Garaguacu). 2012. MNRJ 40856: 3 alc. 101.7 – 80.4 mm SL. Paraná, Morretes, Rio Sagrado, bacia do Nhundiaquara, a montante do rio Pitanga, em estrada secundaria, continuação da BR-408. 2012. MZUSP 111193: 1 alc. 103 mm SL. Santa Catarina, Florianópolis, ponte Hiperbom. Agosto de 2010. MNRJ 41220: 1 alc. 145.7 mm SL. Santa Catarina, Jacinto Machado, Rio da Pedra, bacia do Araranguá, pontilhão de concreto, cerca de 10 Km do início da estrada dos cânions. 2012. MNRJ 40942: 1 alc. 121.1 mm SL. Santa Catarina, Joinville, Rio Pirabeiraba, bacia do Palmital, BR-101, entre Garuva e Joinville. Outubro de 2012. LIRP 480: 4 alc. 106.7 – 47.1 mm SL. Santa Catarina, Itapema, Rio Perequê. 1988. UFRGS 21377: 1 alc. 99 mm SL. Santa Catarina, Tubarão, Rio do Pouso, afluente direto do Rio Tubarão, na margem esquerda. 2016. UFRGS 21507: 1 alc. 81.1 mm SL. Santa Catarina, Luiz Alves, pequeno afluente do Rio Luiz Alves. 2016. MCP 15266: 1 alc. 129.7 mm SL. Rio Grande do Sul, Cidreira, Arroio desaguando diretamente no mar, Praia do Pinhal. 1991.

Awaous (Euctenogobius) flavus (Valenciennes, 1837):

MZUSP 66633: 1 alc. 84 mm SL. Brasil, Amapá, perto de Santana, Rio Amazonas. MPEG 1223: 2 alc. 55.4 – 59 mm SL. Brasil, Pará, Salvaterra, Praia de Jubim, mangue. 1982. MPEG 3775: 3 alc. 25 – 49.2 mm SL. Brasil, Pará, Icoroaci, bahia de Guajará. 1995. MPEG 3788: 2 alc. 24.3 – 27.3 mm SL. Brasil, Pará, Icoroaci, bahia de Guajará. Year not informed. MPEG 4029: 1 alc. 32.2 mm SL. Brasil, Pará, Rio Amazonas, furos-estuário. 1994. MPEG 4031: 1 alc. 33,1 mm SL. Brasil, Pará, Icoroaci, bahia de Guajará. 1995. MPEG 4034: 1 alc. 59.5 mm SL. Brasil, Pará, Rio Amazonas, furos-estuário. 1994. MPEG 4038: 2 alc. 55.1 – 56 mm SL. Brasil, Pará, Rio Amazonas, furos-estuário. 1994. MPEG 4038: 2 alc. 60.1 – 59.3 mm SL. Brasil, Pará, Belém, Bahia de Marajó. Year not informed.

Awaous (Awaous) commersonii (Schneider in Bloch & Schneider, 1801):

NMNH 19983: 1 alc. 128.6 mm SL. Mautitius. Year not informed.

Awaous (Awaous) ocellaris (Broussonet, 1782):

ANSP 95521: 3 alc. 135.6 – 59,7 mm SL. Solomon Islands, British Solomon Islands, Guadalcanal Island, Poha River. 1953. **NMNS** 64842: 1 alc. 46.5 mm SL. Solomon Islands, Guadalcanal Island, Honiara. Year not informed.

1.3.2. Morphometrics

Morphometric data were acquired with a caliper with a 0,1 mm precision under a stereomicroscope LEICA MZ16-DFC295 available in Laboratório de Ictiologia de Ribeirão Preto (LIRP) and a Zeiss SteREO Discovery.V12 stereomicroscope with attached Zeiss Axio-Cam HRc digital camera and Z-stack software. Measurements details are expressed in the **Table 1** and **Figure 2**.

Twenty four measurements were taken on all 278 exemplars of *Awaous* (*Chonophorus*). All measurements were converted to a ratio of the Standard length, except for measurements of regions of the head which were converted to a ratio of the head length. Certain body regions of some exemplars were poorly preserved, thus the measurements were not taken in these regions.

The measurements of type specimens are presented separately in order to increase the comparative analysis. Measurements of individuals of the same species collected in different biogeographical regions (*sensu* SPALDING *et al.*, 2007) were also compared separately in order to check the hypothesis of different species in different marine provinces.

The distribution of *Awaous* (*Chonophorus*) *banana* in the Atlantic slope encompasses only the biographical province of the "Tropical Northwestern Atlantic". On the Pacific slope the distribution encompasses the biogeographical regions of the "Warm Temperate Northeast Pacific" and "Tropical East Pacific", the distribution of *Awaous* (*Chonophorus*) *lateristriga* comprises the provinces of "West African Transition" and "Gulf of Guinea" and the distribution of *Awaous* (*Chonophorus*) *tajasica* encompasses the biogeographic regions of "Tropical Southwestern Atlantic" and "Warm Temperate Southwestern Atlantic". The boundaries of the provinces are presented in the map below (**Figure 3**).

Measurement	Abbreviation	Description
Total length	TL	From anteromedial margin of the mesethmoid to tip of caudal fin
Standard length	SL	From anteromedial margin of the mesethmoid to base of caudal fin

Table 1 – Details of the measurements.

Measurement	Abbreviation	Description
Head length	HL	From anteromedial margin of the mesethmoid to posterior margin of the opercle
Pre-dorsal distance	PD	From anteromedial margin of the mesethmoid to anterior margin of the first dorsal fin
Preopercular	POD	From anteromedial margin of the mesethmoid to
distance		posterior margin of the preopercular bone
Mandibular length	ML	From anteromedial margin of the dentary to posterior margin of the angular bone
Inter-opercular distance	ID	From posterior margin of each opercle
Interorbital distance	IOD	Horizontal distance between dorsal tip of each eye
Orbital diameter	OD	Horizontal distance between anterior and
		posterior margin of the eye
Distance between	DN	Distance between the anterior nasal openings
the nares	DIN	
Snout length	SNI	From anteromedial margin of the mesethmoid to
	SILL	anteromedial margin of the eye
Preanal distance	PA	From anteromedial margin of the dentary to
D 1 1 1 1	DU	urogenital opening
Body height	BH	On anterior margin of the second dorsal fin.
Caudal peduncle	CPL	From anteroventral region of the ventral most
length		anterior procurrent ray of the caudal fin to
Caudal neduncle		
height	СРН	From base of the procurrent rays of the caudal
neight		1111
First dorsal fin	FDF	From anterior margin of the anterior fin ray to
length		posterior margin of the posterior fin ray
Second dorsal fin	SDF	From anterior margin of the anterior fin ray to
length		posterior margin of the posterior fin ray
Anal fin length	AF CF	From anterior margin of the anterior fin ray to
		posterior margin of the posterior fin ray
caudal fin length		From anterior margin of the caudal fin rays to
	PCF	Erom anterior margin of the pectoral fin rous to
Pectoral fin length		posterior tip of the pectoral fin

Measurement	Abbreviation	Description
Pelvic fin length	PLF	From anterior margin of the frenum to posterior margin of the connective pelvic fin membrane
Pelvic fin frenum length	PFFL	From anterior margin to posterior margin of the pelvic fin frenum
Distance between pelvic fin spines	DPFS	Distance between the spines of the pelvic fin



Figure 2 – Details of the measurements. Illustration extracted from Steindachner (1911). Abbreviations follow Table 1.



Figure 3 – Marine biogeographical regions according to Spalding *et al.* (2007). Number 11: "Warm Temperate Northeast Pacific", number 12: "Tropical Northwestern Atlantic", number 14: "Tropical Southwestern Atlantic", number 16: "West African Transition", number 17: "Gulf of Guinea", number 43: "Tropical East Pacific" and number 47: "Warm Temperate Southwestern Atlantic". Other regions were not mentioned in the text, thus were not detailed here.

1.3.3. Meristic

Fin rays were categorized on the basis of ossification and segmentation. Spines are represented in capital roman numbers, segmented but not branched rays are represented in lower case roman numbers, and branched rays are represented in arabic numerals following Akihito (1984). The most posterior ray of the second dorsal and anal fin is divided in two in a condition called *split to the base*. Akihito (1984) considered this condition representing only one ray, but, since they were completely split, in this dissertation, they were considered two independent rays.

Scale counts in transverse series follow Akihito (1984). Scale counts in dorsal margin, ventral margin and circum-peduncular series follow Caires (2012).

The pre-dorsal region of the species examined has an irregular disposition, thus scale counts were not taken in this region. A detailed study of the scale pattern was performed and is available in the next topic of this dissertation.

The scale count in the longitudinal series proposed by Akihito (1984) includes scales in pre-dorsal region, thus scale count in this series was here performed starting in the region of the vertical traced in the anterior margin of the first dorsal fin. Scale counts in the transversal and

longitudinal series show an interesting variation, thus was stablished a comparative analysis of these counts in the different biogeographical provinces.

The scale counts of type specimens are presented separately in order to increase the comparative analysis. Some exemplars presented regions of the body poorly preserved, thus the counts were not taken in these regions.

1.3.4. Scale pattern

Previous studies with gobies demonstrate that some regions of the body of these fishes presents different scale patterns (DAWSON, 1967; CHEN; SHAO, 1996; HASTINGS; FINDLEY, 2015; WATSON, 1991), sometimes presenting different types of scales in distinct regions of the body. This information can be useful in a taxonomic context. Herein the scale pattern was analyzed in the chest region, pre-dorsal and anterior region of pectoral fin.

Scale pattern in the chest region was discriminated in three categories: chest region fully scaled, partially scaled and naked. Partially scaled pattern was stablished when the scales were absent in the region between the pelvic spines (**Figure 4 A, B** and **C**).



Figure 4 – Ventral view of *Awaous (Chonophorus)* illustrating the scale pattern in the chest region. A: fully scaled; B: partially scaled; C: naked.

Scale pattern in the pre-dorsal region also presented three distinctive arrangements: fully scaled, partially scaled and poorly scaled. The Partially scaled pattern was stablished when the scales were present only in half of the pre-dorsal region, poorly scaled pattern was considered when scales present a triangular arrangement not covering entirely the posterior half of pre-

dorsal region (Figure 5 A, B and C). Some individuals present the scales in the median region of the pre-dorsal region absent, thus this pattern was also discriminated (Figure 6 A B and C).



Figure 5 – Dorsal view of *Awaous* (*Chonophorus*) illustrating the pre-dorsal region scale pattern. A: fully scaled; B: partially scaled; C: poorly scaled.



Figure 6 – Dorsal view of *Awaous* (*Chonophorus*) illustrating the scale pattern variation in the median region of the pre-dorsal region. **A**: poorly scaled with an interrupted median region; **B**: poorly scaled with a naked median region; **C**: fully scaled with an interrupted median region.

1.3.5. Oral papillae

An interesting feature of the species within *Awaous* (*Chonophorus*) is the presence of oral papillae. Initially the abundance of these papillae was measured in the region of post dental membrane, basihyal, vomer, presphenoid, cheeks, posterior region of the palate and gills. Subsequently a detailed study was implemented on the parasphenoid region and posterior region of the palate, the most informative ones. In the parasphenoid region the format was discriminated in conic or digitiform, conic ones being categorized as single or branched (**Figure 7 A, B** and **C**). The abundance and distribution of lines in this region were also examined. In the posterior region of the palate the papillae were always conical, thus were discriminated as single or branched, when branched could be abundant or sparse (**Figure 8 A, B e C**).

In some exemplars the papillae were poorly preserved, thus the papillae pattern was not considered in these specimens.



Figure 7 – Ventral view of the palate of *Awaous* (*Chonophorus*) illustrating the format observed in the papillae on the parasphenoid region. A: digitiform papillae; B: single conical papillae; C: branched conical papillae. Arrow points to anterior region.



Figure 8 – Ventral view of the palate of *Awaous* (*Chonophorus*) illustrating the pattern observed on the posterior region of the palate. **A**: single sparse papillae; **B**: branched sparse papillae; **C**: branched abundant papillae. Arrow points to anterior region.

1.3.6. Cephalic sensory system pores

The nomenclature adopted for the cephalic sensory system pores and canals follow Akihito (1984) (**Figure 9**). The oculoscapular canal between pores "H" and "K" was examined in order to check if the species of *Awaous* (*Chonophorus*) have a complete oculoscapular canal or not. In addition, the state of the pore "F" of the oculoscapular canal was categorized throughout single or branched (WATSON, 1996).



Figure 9 – Exemplar of Awaous (Awaous) ocellaris illustrating the nomenclature adopted for the pores of the oculoscapular canal (sensu AKIHITO, 1984) (NMNS 67320, 76.7 mm SL).

1.3.7. Superficial neuromast lines

The nomenclature adopted for the superficial neuromast lines in the opercular region follows Sanzo (1911). Sanzo (1911) adopted two different nomenclatures for the lines in the infra-orbital region. Letters were used to name lines in a longitudinal disposition (**Figure 10**), while numbers were adopted to name lines in a transversal orientation (**Figure 11**).

Sanzo's (1911) nomenclature presents some limitations, especially because it treats longitudinal and transversal lines distinctively. The author comments that his intention was to name lines based on innervation pattern and not only on position. Thus, herein, the nomenclature of Sanzo (1911) was adopted but with some adjustments based on the innervation pattern found in the literature and some examined exemplars. The reasons for adopting a new nomenclature and the new nomenclature proposal are detailed in the result section.


Figure 10 – *Bathygobius soporator*, illustrating the longitudinal pattern of superficial neuromast lines. Capital letters represent the pore nomenclature *sensu* Akihito (1984), small letters represent the nomenclature *sensu* Sanzo (1911), line *ot*: opercular transversal, line *os*: opercular superior, line *oi*: opercular inferior. AN: anterior nasal opening, PN: posterior nasal opening (**LIRP** 1414, 80.8 mm SL).



Figure 11 – *Gobionellus oceanicus*, illustrating the transversal pattern of superficial neuromast lines. Capital letters represent the pore nomenclature *sensu* Akihito (1984), numbers represent the nomenclature *sensu* Sanzo (1911), *ot*: opercular transversal line, *os*: opercular superior line, *oi*: opercular inferior line. AN: anterior nasal opening, PN: posterior nasal opening (**MZUSP** 66005, 132.5 mm SL).

1.4. RESULTS

1.4.1. Type specimens

Before presenting the results, it is necessary to introduce some important information about some type specimens.

Only one of the syntypes of *Gobius martinicus* Valenciennes, 1837, was found in the collection. Despite a clear mention of the lot **a-1327** in the catalog of type specimens of the **MNHN**, the specimen was not found.

The type specimens of *Chonophorus bucculentus* Poey, 1860 shows an interesting history. Presumably the lots containing type specimens are MCZ 13330, MCZ 13379, MCZ 13380. The lots MCZ 13375, NMNH 4772 e NMNH 4774 were collected by the same author in the same place and date but do not figure in the type series. These lots were also analyzed in order to check if they could be included in the type series.

The original description suggests that Poey looked at more than one individual of *Chonophorus bucculentus*, at least one male and one female '**Nous avons dans l'île une autre** espèce qui diffère, dans les deux sexes, de celle que M. Valenciennes a décrite, par une tête très large et des joues renflées [...]'.

Poey (1860) also identified some of the collected individuals as *Awaous banana*. The main difference between the species would be the volume of the cheeks, much broader in the proposed one.

Poey (1860) affirmed that he had one exemplar with 7 inches (178 mm) and one with 8 inches (203 mm) of *Awaous* (*Chonophorus*) banana "[...] qui est d'un cinquième de la longueur de la tête dans un individu de cinq pouces, et d'un septième dans un de sept pouces. J'ai cru reconnaître cette espèce parmi nos poisons d'eau douce: mon individu de sept pouces a l'oeil d'un septième, et celui de huit pouces l'a d'un huitième [...].

None of the exemplars has 178 mm of total length but the smallest individual is the **MCZ** 13375 (207 mm TL), and this exemplar was probably assigned to *Awaous banana* by the author. The exemplar in the jar **NMNH** 4774 has the smallest cheek size so it is probably the other exemplar identified as *Awaous (Chonophorus) banana*.

Poey (1860) provided a complete analysis of one individual with 265 mm "[...] ce qu'il me reste a en diré est pris chez un individu de 265 millimètres [...]." The individual with the

total length closest to this value is **NMNH** 4772 (267 mm TL), currently not considered one of the syntypes. The author also mentioned that the largest examined individual would have 300 mm in total length "[...] **Les plus grands individus sont de 300 mili** [...]", the one closest to this measure is **MCZ** 13330 (305 mm TL). The lot **MCZ** 13380 (282 mm CT) is the only remaining jar with a female exemplar, so it is also probably part of the type series.

It was not possible to confirm if the lot MCZ 13379 belongs to the type series. In addition, the notes in the collection catalog are questionable. Despite the inscription of "type" in the label of the lot MCZ 13379, this information was not present in the collection catalog. Furthermore, the lot MCZ 13375 presents a "type" inscription in the catalog book, but this mark was not found in the label.

In face of this scenario, it was not possible to confirm if the lot MCZ 13379 belong to the type series, and accordingly it was not considered a type specimen here.

1.4.2. Morphometrics

The following tables demonstrate in details the measurements taken.

Awaous (Chonophorus) banana	Measurements	Maximum	Minimum	Mean	Ν
(Atlantic)	SL	188.7	50.0	95.9	73
	PD	39.6	32.2	36.9	73
	POD	81.4	65.3	74.9	73
	ML	73.3	26.9	55.4	72
HL	ID	75.9	38.3	56.4	72
	IOD	19.5	6.4	11.1	73
	OD	24.8	13.9	19.1	72
	DN	21.3	11.8	15.5	70
	SNL	44.3	26.9	36.3	73
	HL	30.0	23.4	26.9	73
	TL	127.0	119.2	123.4	73
	PA	57.3	47.7	51.7	71
	BH	19.2	13.8	15.9	73
	CPL	20.7	12.2	15.5	68
	СРН	11.2	8.0	9.3	73
SL	FDF	14.8	10.7	12.5	67
	SDF	28.0	20.0	25.4	72
	AF	26.5	20.9	23.4	71
	CF	27.6	19.9	24.3	71
	PCF	26.7	19.7	23.4	70
	PLF	22.0	6.3	18.8	70
SL	PFFL	6.8	2.6	4.9	71
	DPFS	4.2	1.7	2.6	70

Table 2 – Measurements taken in exemplars of Awaous (Chonophorus) banana collected in the Atlantic slope.

Gobius banana (lectotype)	Measurements	Values
MNHN A- 1265	SL	98.6
	PD	37.3
	POD	70.9
	ML	64.2
HL	ID	36.6
	IOD	7.5
	OD	20.8
	DN	11.3
	SNL	31.3
	HL	26.9
	TL	
	PA	58
	BH	14.1
	CPL	14.8
	СРН	9.6
SL	FDF	10.2
	SDF	29
	AF	23.3
	CF	
	PCF	23.6
	PLF	17
	PFFL	3.3
	DPFS	

 Table 3 – Measurements taken on the lectotype of Gobius banana. Measurements in bold diverge from Table 2.



Figure 12 – Lateral view of the lectotype of Gobius banana (MNHN A- 1265, 98.6 mm SL), courtesy of MNHN.

Gobius banana (paralectotype)	Measurements	Values
MNHN A- 1359	SL	71.8
	PD	40.9
	POD	65.5
	ML	54.3
HL	ID	32.5
	IOD	
	OD	
	DN	
	SNL	36
	HL	27.4
	TL	123.1
	PA	55.4
	BH	13.5
	CPL	12.7
	СРН	7.4
SL	FDF	9.5
	SDF	22.4
	AF	18.7
	CF	21
	PCF	21
	PLF	20.3
	PFFL	3.9
	DPFS	1.9

Table 4 – Measurements taken on the paralectotype of *Gobius banana*. Measurements in bold diverge from **Table 2**.



Figure 13 – Lateral view of the paralectotype of *Gobius banana* (MNHN A- 1359, 71.8 mm SL), courtesy of MNHN.

Gobius martinicus (syntype)	Measurements	Values
MNHN A-1266	SL	118.8
	PD	37.3
	POD	70.8
	ML	61.5
HL	ID	61.2
	IOD	12.4
	OD	15.8
	DN	15.2
	SNL	37.6
	HL	27.1
	TL	121
	PA	52.4
	BH	15.4
	CPL	13.2
	СРН	9.3
SL	FDF	12.7
	SDF	25.8
	AF	23.9
	CF	21.5
	PCF	22.3
	PLF	16.6
	PFFL	4.4
	DPFS	2.3

Table 5 – Measurements taken on the syntype of *Gobius martinicus*.



Figure 14 – Lateral view of the syntype of *Gobius martinicus* (MNHN A-1266, 118.8 mm SL), courtesy of MNHN.

Chonophorus contractus (holotype)	Measurements	Values
MCZ 31220	SL	153.5
	PD	38.1
	POD	78.8
	ML	67.3
HL	ID	59.6
	IOD	17.5
	OD	21.2
	DN	15
	SNL	37.7
	HL	26.1
	TL	123.8
	PA	52.9
	BH	15.7
	CPL	13.9
	СРН	9.6
SL	FDF	11.3
	SDF	22.7
	AF	23.1
	CF	24.7
	PCF	23.3
	PLF	18.8
	PFFL	4.6
	DPFS	1.8

 Table 6 – Measurements taken on the holotype of Chonophorus contractus.



Figure 15 – Lateral view of the holotype of *Chonophorus contractus* (MCZ 31220, 153.5 mm SL), photo taken by Sandra Raredon at NMNH.

Chonophorus bucculentus (syntype)	Measurements V	
MCZ 13330	SL	241
	PD	38.8
	POD	81.5
	ML	66.1
HL	ID	66.4
	IOD	21.2
	OD	12
	DN	19.9
	SNL	37.1
	HL	28.8
	TL	125.3
	PA	55.5
	BH	17.9
	CPL	12.7
	СРН	10.6
SL	FDF	11.9
	SDF	25.6
	AF	24.6
	CF	24.1
	PCF	24.9
	PLF	19.3
	PFFL	6.3
	DPFS	3.3

Table 7 – Measurements taken on one of the syntypes of *Chonophorus bucculentus*. Measurements in bold divergefrom **Table 2**.



Figure 16 – Lateral view of one of the syntypes of *Chonophorus bucculentus* (MCZ 13330, 241 mm SL), photo taken by Sandra Raredon at NMNH.

Chonophorus bucculentus (syntype)	Measurements	Values
MCZ 13380	SL	234
	PD	36
	POD	75
	ML	58.1
HL	ID	67.3
	IOD	18.3
	OD	12.5
	DN	16.2
	SNL	40
	HL	26.6
	TL	118.8
	РА	55
	BH	17.3
	CPL	12.6
	СРН	9.9
SL	FDF	10.7
	SDF	24.3
	AF	21.6
	CF	21.6
	PCF	22
	PLF	16.1
	PFFL	4.8
	DPFS	3.3

Table 8 – Measurements taken on one of the syntypes of *Chonophorus bucculentus*. Measurements in bold divergefrom Table 2.



Figure 17 – Lateral view of one of the syntypes of *Chonophorus bucculentus* (MCZ 13380, 234 mm SL), photo taken by Sandra Raredon at NMNH.

Chonophorus bucculentus (syntype)	Measurements	Values
NMNH 4772	SL	214
	PD	38.6
	POD	83.7
	ML	65.4
HL	ID	66.6
	IOD	17
	OD	15.2
	DN	22.1
	SNL	42.3
	HL	28.9
	TL	123.4
	PA	53.7
	BH	18.5
	CPL	12.3
	СРН	11.5
SL	FDF	11.7
	SDF	24.7
	AF	23.8
	CF	23
	PCF	21.8
	PLF	19.6
	PFFL	4.6
	DPFS	3

 Table 9 – Measurements taken on one of the syntypes of Chonophorus bucculentus. Measurements in bold diverge from Table 2.

Gobius mexicanus (syntype)	Measurements	Values
NHM 1856.4.17.41	SL	143.6
	PD	36.6
	POD	73.7
	ML	54.8
HL	ID	54
	IOD	10.4
	OD	17.8
	DN	15.9
	SNL	37.5
	HL	25.4
	TL	127.4
	PA	53.5
	BH	16.8
	CPL	14.5
	СРН	9.5
SL	FDF	11.5
	SDF	25.1
	AF	23.2
	CF	21.7
	PCF	20.1
	PLF	15.1
	PFFL	3.5
	DPFS	2.8

 Table 10 – Measurements taken on one of the syntypes of Gobius mexicanus. Measurements in bold diverge from Table 2.



Figure 18 – Lateral view of one of the syntypes of *Gobius mexicanus* (NHM 1856.4.17.41, 143.6 mm SL), courtesy of NHM.

Gobius mexicanus (syntype)	Measurements	Values
NHM 1856.4.17.42	SL	131.5
	PD	36
	POD	
	ML	68.8
HL	ID	58.7
	IOD	10.4
	OD	16.5
	DN	17.1
	SNL	32.1
	HL	24.9
	TL	122.4
	PA	53.3
	BH	18.5
	CPL	14.8
	СРН	10.2
SL	FDF	12.8
	SDF	27.1
	AF	23.3
	CF	22.7
	PCF	23.4
	PLF	16.3
	PFFL	4.5
	DPFS	2.3

Table 11 – Measurements taken on one of the syntypes of Gobius mexicanus. Measurements in bold diverge from**Table 2.** Blank spaces represent damaged regions.



Figure 19 - Lateral view of one of the syntypes of *Gobius mexicanus* (NHM 1856.4.17.42, 131.5 mm SL), courtesy of NHM.

Awaous (Chonophorus) banana	Measurements	Maximum	Minimum	Mean	Ν
(Pacific)	SL	141.7	52	76.3	47
	PD	40	34	36.6	47
	POD	84.1	20.8	74.6	47
	ML	68.9	16.4	57.2	47
HL	ID	84.4	15.8	54.6	47
	IOD	17.5	3.7	10.6	47
	OD	25.2	5.7	20.5	47
	DN	20.4	4.4	15.4	47
	SNL	45.3	10.8	35.2	47
	HL	100	23	28.1	47
	TL	127.7	119.1	123.7	46
	PA	56.2	47.4	51.4	44
	BH	17.8	14.2	15.8	47
	CPL	18.7	13	15.1	40
	СРН	10	7.8	9.1	47
SL	FDF	16.1	11.1	12.6	44
	SDF	27.9	23.2	26	46
	AF	26.4	21.4	23.8	43
	CF	26.6	19.8	24	39
	PCF	25.8	19.2	23.5	46
	PLF	21.4	15.1	19	47
	PFFL	6.4	2.4	4.7	44
	DPFS	3.7	1.6	2.4	47

Table 12 – Measurements taken in exemplars of Awaous (Chonophorus) banana collected in the pacific slope.

Warm Temperate Northeast	Measurements	Maximum	Minimum	Mean	Ν
Pacific	SL	91.9	54.4	76.8	5
	PD	37.1	35.7	36.5	5
	POD	77.1	71.9	74.3	5
	ML	63.7	54	57	5
HL	ID	56.1	51.9	53.4	5
	IOD	13.1	8.6	10.7	5
	OD	21.5	17.1	19.2	5
	DN	17.8	11.5	15.3	5
	SNL	35.9	28.3	32.6	5
	HL	26.7	24.7	25.7	5
	TL	124.4	120.3	122.9	4
	PA	51.8	50.4	51.2	3
	BH	16.9	14.4	15.6	5
	CPL	14.4	13.2	13.9	4
	СРН	10	8.1	9	5
SL	FDF	16.1	12	13.4	5
	SDF	26.6	24.5	25.4	5
	AF	24.7	22.4	23.5	5
	CF	23.7	22.3	23	4
	PCF	24.4	19.2	21.7	5
	PLF	19.3	15.1	18	5
	PFFL	5.6	2.4	3.8	4
	DPFS	3.3	1.8	2.5	5

Table 13 – Measurements taken in exemplars of *Awaous (Chonophorus) banana* collected in the pacific slope occurring on the biogeographical province of "Warm Temperate Northeast Pacific" (*sensu SPALDING et al.* 2007).

Tranical Fast Desifie	Measurements	Maximum	Minimum	Mean	Ν
Hopical Last I achie	SL	141.7	52	77.8	27
	PD	37.9	34.2	36.2	27
	POD	84.1	68.8	76.6	27
	ML	68.9	43.1	58.7	27
HL	ID	84.4	49.5	56.8	27
	IOD	17.5	6.7	10.9	27
	OD	24.6	14.9	20.7	27
	DN	18	11.9	15.5	27
	SNL	45.3	24.4	36	27
	HL	29	23	26.1	27
	TL	126.5	119.3	123.5	27
	PA	54.1	47.6	50.9	26
	BH	17.8	14.5	15.9	27
	CPL	17.4	14.1	15	21
	CPH	10	8	9.2	27
SL	FDF	13.8	11.1	12.4	24
	SDF	27.9	25.2	26.5	26
	AF	26.4	22.9	24.3	23
	CF	26.5	19.8	24	22
	PCF	24.9	20.9	23.5	26
	PLF	21.4	16.4	18.9	27
	PFFL	6.4	3.7	4.9	26
	DPFS	2.9	1.7	2.2	27

Table 14 – Measurements taken in exemplars of Awaous (Chonophorus) banana collected in the pacific slope occurring on the biogeographical province of "Tropical East Pacific" (sensu SPALDING et al. 2007).

Gobius transandeanus (syntype)	Measurements	Values
NHM 1860.6.16.135	SL	86.3
	PD	35.9
	POD	73
	ML	62.8
HL	ID	46.5
	IOD	11.1
	OD	21.7
	DN	17.3
	SNL	33.6
	HL	26.2
	TL	121.2
	PA	53.5
	BH	<u>13.6</u>
	CPL	16.1
	СРН	7.9
SL	FDF	12.2
	SDF	25
	AF	22.4
	CF	21.3
	PCF	22.2
	PLF	18.1
	PFFL	3.2
	DPFS	1.7

Table 15 – Measurements taken on one of the syntypes of *Gobius transandeanus*. Measurements in bold divergefrom **Table 12** and values underlined in bold diverge from **Table 2** and **12**.



Figure 20 – Lateral view of one of the syntypes of *Awaous transandeanus* (NHM 1860.6.16.135, 86.3 mm SL), courtesy of NHM.

Awaous transandeanus (syntype)	Measurements	Values
NHM 1860.6.16.136	SL	84.8
	PD	36.1
	POD	72.2
	ML	54.2
HL	ID	43.6
	IOD	8.8
	OD	19.8
	DN	15.4
	SNL	37.9
	HL	26.8
	TL	<u>112.6</u>
	PA	<u>47.3</u>
	BH	14.3
	CPL	14.9
	СРН	8.4
SL	FDF	12.3
	SDF	25.8
	AF	22.5
	CF	<u>18.3</u>
	PCF	22.9
	PLF	20
	PFFL	5.8
	DPFS	1.7

Table 17 – Measurements taken on one of the syntypes of *Gobius transandeanus*. Values underlined in bold diverge from **Table 2** and **12**.



Figure 21 – Lateral view of one of the syntypes of *Gobius transandeanus* (NHM 1860.6.16.136, 84.8 mm SL), courtesy of NHM.

Awaous nelsoni (holotype)	Measurements	
NMNH 48836	SL	66
	PD	37.9
	POD	77.1
	ML	56
HL	ID	52
	IOD	11.4
	OD	24
	DN	14.9
	SNL	32
	HL	26.5
	TL	
	PA	46.4
	BH	15
	CPL	
	СРН	9.5
SL	FDF	12.4
	SDF	26.8
	AF	
	CF	
	PCF	19.1
	PLF	18.5
	PFFL	5.2
	DPFS	2.6

Table 18 – Measurements taken on the holotype of Awaous nelsoni. Measurements in bold diverge from Table**12.** Blank spaces represent damaged regions.



Figure 22 – Lateral view of the holotype of *Awaous nelsoni* (**NMNH** 48836, 66.0 mm SL), photo taken by Sandra Raredon at **NMNH**.

Gobius (Awaous) guentheri (syntype)	Measurements	Values
NHM 1860.6.16.133	SL	108.5
	PD	33.5
	POD	80.7
	ML	69.1
HL	ID	59.6
	IOD	11.6
	OD	18.6
	DN	17.5
	SNL	40
	HL	26.3
	TL	120.9
	PA	54.1
	BH	<u>13.1</u>
	CPL	13.6
	СРН	8.7
SL	FDF	11.7
	SDF	26.6
	AF	24
	CF	24.7
	PCF	23.4
	PLF	18.2
	PFFL	3.1
	DPFS	2.5

Table 19 – Measurements taken on one of the syntypes of Gobius (Awaous) guentheri, species currentlyconsidered a junior synonym of Awaous (Chonophorus) banana. Measurements in bold diverge from Table 12and values underlined in bold diverge from Table 2 and 12.



Figure 23 – Lateral view of one of the syntypes of *Gobius (Awaous) guentheri* (NHM 1860.6.16.133, 108.5 mm SL), courtesy of NHM.

Gobius (Awaous) guentheri (syntype)	Measurements	Values
NHM 1860.6.16.134	SL	102.4
	PD	35.2
	POD	80.7
	ML	63.4
HL	ID	55.9
	IOD	14.5
	OD	20
	DN	18.3
	SNL	39
	HL	28.3
	TL	125
	PA	53
	BH	14.6
	CPL	14
	СРН	9.6
SL	FDF	11.5
	SDF	26.4
	AF	24.5
	CF	25.4
	PCF	20.2
	PLF	20.1
	PFFL	5.8
	DPFS	1.3

Table 20 – Measurements taken on one of the syntypes of *Gobius (Awaous) guentheri*. Measurements in bold diverge from Table 12.



Figure 24 – Lateral view of one of the syntypes of *Gobius (Awaous) guentheri* (NHM 1860.6.16.134, 102.4 mm SL), courtesy of NHM.

Awaous (Chonophorus) lateristriga	Measurements	Maximum	Minimum	Mean	Ν
	SL	95.8	50.2	69.9	27
	PD	39	34.1	36.4	27
	POD	81.7	71.2	76.2	27
	ML	65.4	43.1	57.3	25
HL	ID	76.7	48	57.1	27
	IOD	11.9	6.1	8.2	27
	OD	26.2	15.6	21.8	27
	DN	20.4	10.6	14.2	27
	SNL	43.7	27.3	33.2	26
	HL	29	24	26.3	27
	TL	123.5	116	120.8	23
	PA	56.8	48.6	53	25
	BH	16.6	13.8	15.3	27
	CPL	15.9	10.3	13.7	26
	CPH	10.1	7.4	8.8	27
SL	FDF	13.7	10.3	12.4	23
	SDF	27.6	23.9	25.4	23
	AF	26.5	20	23.3	24
	CF	24.5	17.1	21.5	23
	PCF	25.7	20.8	22.7	26
	PLF	22.2	15.7	19	25
	PFFL	6.3	3.5	4.8	27
	DPFS	3.1	1.5	2.2	27

 Table 21 – Measurements taken in exemplars of Awaous (Chonophorus) lateristriga.

West African Transition	Measurements	Maximum	Minimum	Mean	Ν
west Affican Transition	SL	95.8	50.2	69.8	24
	PD	37.9	34.1	36.2	24
	POD	81.7	71.2	76.4	24
	ML	65.4	43.1	56.4	22
HL	ID	76.7	48	57.7	24
	IOD	11.9	6.1	8.2	24
	OD	26.2	18.1	22	24
	DN	20.4	10.6	14.3	24
	SNL	43.7	27.3	33.3	23
	HL	29	24	26.2	24
	TL	123.5	116	120.8	20
	PA	55.6	48.6	52.7	22
	BH	16.6	13.8	15.3	24
	CPL	15.9	10.3	13.7	23
	СРН	10.1	7.4	8.8	24
SL	FDF	13.7	10.3	12.3	20
	SDF	27.6	24.5	25.5	20
	AF	26.5	21	23.5	21
	CF	24.5	17.1	21.5	20
	PCF	24.7	20.8	22.5	23
	PLF	22.2	15.7	18.9	22
	PFFL	6.3	3.5	4.8	24
	DPFS	3.1	1.5	2.3	24

Table 22 – Measurements taken in exemplars of *Awaous (Chonophorus) lateristriga* collected in the biogeographical province of "West African Transition" (*sensu* SPALDING *et al.*, 2007).

	Measurements	Values	Ν
Gull of Guinea	SL	50.2	1
	PD	37.3	1
	POD	77.5	1
	ML	63.4	1
HL	ID	50	1
	IOD	9.9	1
	OD	21.8	1
	DN	13.4	1
	SNL	32.4	1
	HL	28.3	1
	TL	121.7	1
	PA	56.8	1
	BH	15.9	1
	CPL	15.1	1
	СРН	8.8	1
SL	FDF	12.5	1
	SDF	24.1	1
	AF	22.7	1
	CF	22.7	1
	PCF	25.7	1
	PLF	19.5	1
	PFFL	6.2	1
	DPFS	2.4	1

Table 23 – Measurements taken in exemplars of *Awaous (Chonophorus) lateristriga* collected in the biogeographical province of "Gulf of Guinea" (*sensu* SPALDING *et al.*, 2007). Measurements in bold diverge from **Table 22**.

Gobius lateristriga (lectotype)	Measurements	Values
MNHN- 6228-1	SL	87.5
	PD	39
	POD	73.4
	ML	63.1
HL	ID	54.5
	IOD	9
	OD	15.6
	DN	13.1
	SNL	33.6
	HL	27.9
	TL	121
	РА	55.4
	BH	15.7
	CPL	12.8
	СРН	9.3
SL	FDF	13
	SDF	23.9
	AF	20
	CF	21.6
	PCF	24.7
	PLF	19.3
	PFFL	4.5
	DDES	17

Table 24 – Measurements taken on the lectotype of *Gobius lateristriga*. Measurements in bold diverge from **Table 21**.



Figure 25 – Lateral view of the lectotype of *Gobius lateristriga* (MNHN 6228-1, 87.5 mm SL), courtesy of MNHN.

Gobius lateristriga (paralectotype)	Measurements	Values
MNHN- 1996-301	SL	73
	PD	36.2
	POD	72.6
	ML	62.9
HL	ID	51.8
	IOD	6.6
	OD	21.3
	DN	12.7
	SNL	29.9
	HL	27
	TL	119.5
	PA	53.7
	BH	16.4
	CPL	12.6
	СРН	9
SL	FDF	13
	SDF	25.2
	AF	22.9
	CF	22.1
	PCF	22.3
	PLF	19.2
	PFFL	4.1
	DPFS	1.6

Table 25 – Measurements taken on the paralectotype of *Gobius lateristriga*. Measurements in bold diverge from**Table 21**.

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Figure 26 – Lateral view of the paralectotype of *Gobius lateristriga* (MNHN 1996-301, 73.0 mm SL), courtesy of MNHN.

Awaous (Chonophorus) taiasica	Measurements	Maximum	Minimum	Mean	Ν
Awaous (Chonophorus) iajasica	SL	169	51.4	91.5	101
	PD	39.7	32.8	36.2	101
	POD	86.5	71	78.6	98
	ML	85.3	48.8	61.6	77
HL	ID	81.3	43.4	59.6	101
	IOD	20.2	6	10.2	102
	OD	28.4	14.8	20.5	100
	DN	23.9	11.1	15.4	98
	SNL	44.3	29.9	37.1	97
	HL	30.1	21.9	25.6	102
	TL	126.3	115.4	121.8	86
	PA	72.9	37.2	51.3	66
	BH	21.3	11.5	14.7	96
	CPL	17.8	11.6	13.9	84
	CPH	13.3	7.5	9.3	98
SL	FDF	18.8	9.3	12.5	93
	SDF	36	23	25.8	100
	AF	31.2	20.8	23.9	100
	CF	28.9	18.5	22.8	92
	PCF	28	17.1	22.7	95
	PLF	22.1	10.1	18.1	86
	PFFL	5.9	2.5	4.3	69
	DPFS	4.2	1.4	2.3	90

 Table 26 – Measurements taken in exemplars of Awaous (Chonophorus) tajasica.

Warm Tamparata Southwastorn Atlantia	Measurements	Maximum	Minimum	Mean	Ν
warm Temperate Southwestern Atlantic	SL	145.7	51.5	78.8	47
	PD	37.9	33.7	35.8	46
	POD	85.9	71	78.4	45
	ML	85.3	48.8	61	37
HL	ID	70.7	43.4	55.4	46
	IOD	16.4	6	9.1	47
	OD	25.5	14.8	21.1	47
	DN	19.4	11.1	14.5	47
	SNL	42.9	30.7	36.7	46
	HL	28.9	21.9	25.3	47
	TL	126.3	118.8	122.1	43
	PA	55	37.2	50.7	29
	BH	16.3	11.9	13.9	44
	CPL	17.8	11.6	13.9	43
	СРН	10.3	7.5	8.7	44
SL	FDF	14.5	9.3	12.1	46
	SDF	28.4	23	25.4	47
	AF	25.7	20.8	23.6	46
	CF	26.4	19.6	22.9	45
	PCF	25.8	17.1	22.4	43
	PLF	22.1	15.1	18.8	35
	PFFL	5.8	2.5	4.4	33
	DPFS	4.2	1.4	2.2	37

Table 27 – Measurements taken in exemplars of Awaous (Chonophorus) tajasica collected in the biogeographical province of "Warm Temperate Southwestern Atlantic" (sensu SPALDING et al., 2007).

Tranical Southwastern Atlantic	Measurements	Maximum	Minimum	Mean	Ν
Topical Southwestern Atlantic	SL	169	51.4	102.2	55
	PD	39.7	32.8	36.6	56
	POD	86.5	72	78.6	54
	ML	75.9	53	62.1	41
HL	ID	81.3	47.3	63	56
	IOD	20.2	6.2	11	56
	OD	28.4	14.8	20	54
	DN	23.9	11.5	16.3	52
	SNL	44.3	29.9	37.5	52
	HL	30.1	22.4	25.8	56
	TL	125	115.4	121.6	44
	PA	72.9	48.6	51.8	38
	BH	21.3	11.5	15.3	53
	CPL	16.5	12	14	42
	СРН	13.3	7.8	9.7	55
SL	FDF	18.8	10.6	13	48
	SDF	36	24.1	26.2	54
	AF	31.2	21.1	24.2	55
	CF	28.9	18.5	22.7	48
	PCF	28	19.7	22.9	53
	PLF	21.9	10.1	17.6	52
	PFFL	5.9	3.1	4.2	37
	DPFS	3.9	1.4	2.3	54

Table 28 – Measurements taken in exemplars of Awaous (Chonophorus) tajasica collected in the biogeographical province of "Tropical Southwestern Atlantic" (sensu SPALDING et al., 2007).

Gobius tajasica (neotype)	Measurements	Values
ANSP 84175	SL	131.8
	PD	39
	POD	81.3
	ML	52.6
HL	ID	67.6
	IOD	11.9
	OD	16.1
	DN	18.5
	SNL	38.7
	HL	30.1
	TL	124.4
	PA	50.8
	BH	17.1
	CPL	12.5
	СРН	10.5
SL	FDF	13.5
	SDF	25.8
	AF	24.1
	CF	21.2
	PCF	25.3
	PLF	17.6
	PFFL	4.1
	DPFS	2.7

Table 29 – Measurements taken on the neotype of Gobius tajasica.



Figure 27 – lateral view of the neotype of *Gobius tajasica* (ANSP 84175: 1 alc. 131.8 mm SL), photo taken by Sandra Raredon.

Euctenogobius latus (holotype)	Measurements	Values
NHM 1862.11.23.42	SL	125
	PD	38.2
	POD	85.3
	ML	68.6
HL	ID	55.1
	IOD	12.7
	OD	19.5
	DN	18.4
	SNL	39.5
	HL	28.3
	TL	119.2
	PA	50.7
	BH	13.8
	CPL	12.4
	СРН	9
SL	FDF	11.1
	SDF	24.8
	AF	23.2
	CF	23.2
	PCF	24.3
	PLF	17.8
	PFFL	3.2
	DPFS	2.3

 Table 30 – Measurements taken on the holotype of Euctenogobius latus.



Figure 28 – Lateral view of the holotype of *Euctenogobius latus* (NHM 1862.11.23.42, 125 mm SL), courtesy of NHM.

Suiboga travassosi (holotype)	Measurements	Values
MNRJ 6196	SL	<u>175.3</u>
	PD	37.3
	POD	84.9
	ML	65.3
HL	ID	58.7
	IOD	16.3
	OD	<u>14.3</u>
	DN	<u>20</u>
	SNL	40.7
	HL	28.3
	TL	<u>129.8</u>
	PA	48.2
	BH	14.3
	CPL	12.2
	СРН	<u>10.7</u>
SL	FDF	11.5
	SDF	23.6
	AF	22.5
	CF	22.2
	PCF	23.6
	PLF	17.2
	PFFL	5.7
	DPFS	2

 Table 31 – Measurements taken on the holotype of Suiboga travassosi. Measurements underlined in bold diverge from Table 26, Measurements underlined diverge from Table 27 e Measurements in bold diverge from Table 28.



Figure 29 – Pictures of the holotype of *Suiboga travassosi* (MNRJ 6196, 175.3 mm SL), extracted from the original article (PINTO, 1960). 1: dorsal view of the head; 2: ventral view of the head.

1.4.3. Fin ray counts

Almost all individuals of *Awaous* examined presented the same fin ray count, with rare exceptions (**Table 32**).

Species	Fist dorsal	Second dorsal	Anal	Pectoral	Pelvic
A. (Chonophorus) banana (Atlantic)	VI (75)	I + 10 (2) I + 11 (72)	I + 10 (2) I + 11 (71)	14 + i (6) 15 + i (68) 16 + i (1)	II + 10 (75)
A. (Chonophorus) banana (Pacific)	VI (56)	I + 11 (53)	I + 11 (53)	14 +i (7) 15 + i (47) 16 + i (1)	II + 10 (56)
A. (Chonophorus) lateristriga	VI (30)	I + 11 (30)	I + 11 (25)	14 + i (3) 15 + i (25) 16 + i (1)	II + 10 (33)
A. (Chonophorus) tajasica	V (1) VI (117)	I + 10 (3) I + 11 (117)	I + 10 (4) I + 11 (109)	14 + i (16) 15 + i (112) 16 + i (2)	II + 10 (121)

Table 32 – Fin ray counts in exemplars of Awaous (Chonophorus). Numbers in parenthesis represent the examined individuals.

Table 33 – Most common values of fin ray counts in Awaous (Chonophorus).

		Fin ray cou	nt	
Fist dorsal	Second dorsal	Anal	Pectoral	Pelvic
VI	I + 11	I + 11	15 + i	II + 10

1.4.4. Scale counts

Scale count in dorsal margin, ventral margin and circum-peduncular region are presented in Table 34.

Table 34 – Scale count in dorsal margin, ventral margin and circum-peduncular region. Numbers in parenthesisrepresent the examined individuals.

	Scale count		
Species	circum-peduncular	dorsal margin	ventral margin
A. (Chonophorus) banana (Atlantic)	19 - 30 (83)	10-19 (83)	10-17 (83)
A. (Chonophorus) banana (Pacific)	19 – 25 (54)	10 - 15 (54)	9 - 15 (54)
A. (Chonophorus) lateristriga	17 – 21 (40)	9 - 14 (40)	9 - 13 (40)
A. (Chonophorus) tajasica	14 – 23 (121)	7 – 13 (121)	8 - 14 (121)

Table 35 – Scale count in dorsal margin, ventral margin and circum-peduncular region of the examined type specimens.

Scale count in type specimens				
Exemplar	circum- peduncular	dorsal margin	ventral margin	
MNHN A- 1265 (lectotype) Gobius banana	25	12	14	
MNHN A- 1359 (paralectotype) Gobius banana	21	17	14	
MNHN A-1266 (syntype) Gobius martinicus	26	11	11	
MCZ 31220 (holotype) Chonophorus contractus	26	14	13	

Scale count in type specimens				
Exemplar	circum- peduncular	dorsal margin	ventral margin	
MCZ 13330 (syntype) Chonophorus	25	11	13	
bucculentus	23	11	15	
MCZ 13380 (syntype) Chonophorus	25	14	13	
bucculentus	23	11	15	
NMNH 4772 (syntype)	26	11	11	
Chonophorus bucculentus	20	11	11	
NHM 1856.4.17.41 (syntype)	26	16	15	
Gobius mexicanus	20	10	15	
NHM 1856.4.17.42 (syntype)	26	15	13	
Gobius mexicanus	20	15	15	
NHM 1860.6.16.135 (syntype)	21	14	12	
Awaous transandeanus	21	17	12	
NHM 1860.6.16.136 (syntype)	21	13	11	
Awaous transandeanus	21	15	11	
NMNH 48836 (holotype) Awaous	23	13		
nelsoni	23	15		
NHM 1860.6.16.133 (syntype)	22	12	13	
Gobius (Awaous) guentheri		12	15	
NHM 1860.6.16.134 (syntype)	25	13	12	
Gobius (Awaous) guentheri	23	15	12	
MNHN- 6228-1 (lectotype) Gobius	10	12	12	
lateristriga	19	12	12	
MNHN- 1996-301 (paralectotype)	18	10	10	
Gobius lateristriga	10	10	10	
ANSP 84175 (neotype) Gobius	20	10	10	
tajasica	20	10	10	
NHM 1862.11.23.42 (holotype)	20	11	10	
Euctenogobius latus	20	11	12	
MNRJ 6196 (holotype) Suiboga	21	0	10	
travassosi	Δ1	7	12	

1.4.5. Scale count in longitudinal series

Scale counts in longitudinal series are presented in **Table 36**. The scale counts in *Awaous (Chonophorus) tajasica* have two separated ranges of high frequency, thus an analysis in the different biogeographical regions was performed (**Figure 30**). An analysis of the scale counts in the longitudinal series in *Awaous (Chonophorus) banana* occurring on both slopes was also implemented (**Figure 31**).

Table 36 – Scale counts in longitudinal series. Numbers in parenthesis represent the examined individuals.

Scale counts in longitudinal series				
Species	Range	Mode		
A. (Chonophorus) banana (Atlantic)	49 - 68 (83)	53 - 63 (76)		
A. (Chonophorus) banana (Pacific)	50 - 60 (54)	50 - 55 (46)		
A. (Chonophorus) lateristriga	46 - 55 (40)	50 - 53 (30)		
A. (Chonophorus) tajasica	34 - 58 (121)	37 - 41 (39) and 48 - 55 (48)		

Table 37 – Scale counts in longitudinal series of the examined type specimen.

Longitudinal series of the examined type specimen			
Exemplar	Longitudinal		
MNHN A- 1265 (lectotype) Gobius banana	54		
MNHN A- 1359 (paralectotype) Gobius banana	56		
MNHN A-1266 (syntype) Gobius martinicus	56		
MCZ 31220 (holotype) Chonophorus contractus	58		
MCZ 13330 (syntype) Chonophorus bucculentus	55		
MCZ 13380 (syntype) Chonophorus bucculentus	56		
NMNH 4772 (syntype) Chonophorus bucculentus	54		
NHM 1856.4.17.41 (syntype) Gobius mexicanus	64		
NHM 1856.4.17.42 (syntype) Gobius mexicanus	66		
NHM 1860.6.16.135 (syntype) Awaous transandeanus	54		
NHM 1860.6.16.136 (syntype) Awaous transandeanus	52		
NMNH 48836 (holotype) Awaous nelsoni	51		
NHM 1860.6.16.133 (syntype) Gobius (Awaous) guentheri	53		
NHM 1860.6.16.134 (syntype) Gobius (Awaous) guentheri	52		
Longitudinal series of the examined type specimen			
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Exemplar	Longitudinal		
MNHN- 6228-1 (lectotype) Gobius lateristriga	53		
MNHN- 1996-301 (paralectotype) Gobius lateristriga	50		
ANSP 84175 (neotype) Gobius tajasica	49		
NHM 1862.11.23.42 (holotype) Euctenogobius latus	45		
MNRJ 6196 (holotype) Suiboga travassosi	49		



Figure 30 – Scale counts in the longitudinal series in *Awaous (Chonophorus) tajasica* comparing individuals collected in both biogeographical provinces (*sensu* SPALDING *et al.*, 2007) cited before.



Figure 31 – Scale counts in the longitudinal series of Awaous (Chonophorus) banana collected in the Atlantic and Pacific slopes.

1.4.6. Scale count in transversal series

Scale counts in transverse series are presented in Table 38.

Table 38 – Scale counts in transversal series. Values in bold diverge from the range presented by other species.Numbers in parenthesis represent the examined individuals.

Scale counts in transversal series					
Species	Range	Mode			
A. (Chonophorus) banana	16.28 (80)	20, 24 (67)			
(Atlantic)	10-28 (80)	20-24 (07)			
A. (Chonophorus) banana	16 22 (49)	17 20 (41)			
(Pacific)	10-25 (48)	17-20 (41)			

Scale counts in transversal series					
Species	Range	Mode			
A. (Chonophorus) lateristriga	15-22 (38)	17-19 (35)			
A. (Chonophorus) tajasica	13-19 (129)	14-18 (122)			

Table 39 – Scale count in transverse series of the examined type specimens. Values in bolddiverge from other Awaous (Chonophorus) species.

Scale count in transversal series of type specimens	b
Exemplar	Transversal
MNHN A- 1265 (lectotype) Gobius banana	23
MNHN A- 1359 (paralectotype) Gobius banana	20
MNHN A-1266 (syntype) Gobius martinicus	21
MCZ 31220 (holotype) Chonophorus contractus	22
MCZ 13330 (syntype) Chonophorus bucculentus	24
MCZ 13380 (syntype) Chonophorus bucculentus	20
NMNH 4772 (syntype) Chonophorus bucculentus	22
NHM 1856.4.17.41 (syntype) Gobius mexicanus	26
NHM 1856.4.17.42 (syntype) Gobius mexicanus	26
NHM 1860.6.16.135 (syntype) Awaous transandeanus	20
NHM 1860.6.16.136 (syntype) Awaous transandeanus	18
NMNH 48836 (holotype) Awaous nelsoni	20
NHM 1860.6.16.133 (syntype) Gobius (Awaous) guentheri	19
NHM 1860.6.16.134 (syntype) Gobius (Awaous) guentheri	19
MNHN- 6228-1 (lectotype) Gobius lateristriga	17
MNHN- 1996-301 (paralectotype) Gobius lateristriga	16
ANSP 84175 (neotype) Gobius tajasica	18
NHM 1862.11.23.42 (holotype) Euctenogobius latus	19
MNRJ 6196 (holotype) Suiboga travassosi	19

		Aw	aous	(Cho	noph	orus) ban	ana	(Atlar	ntic)	
16	17	18		20	21	22	23	24	25	26	28
	17			20	21	22	23	24	25	26	
	17			20	21	22	23	24	25	26	
				20	21	22	23	24			
				20	21	22	23	24			
				20	21	22	23	24			
				20	21	22	23	24			
				20	21	22	23	24			
				20	21	22	23	24			
				20	21		23	24			
				20	21		23				
				20	21		23				
				20	21		23				
					21		23				
					21		23				
							23				
							23				
							23				
							23				
							23				
							23				
		Aи	vaous	c (Ch	onop	horus	:) bar	ıana	(Pac	ific)	
16	17	18	19	20	21	22	23				
16	17	18	19	20		22	23				
	17	18	19	20							
	17	18	19	20							
	17	18	19	20							
	17	18	19								
	17	18	19								
	17	18									
	17	18									
	17	18									
	17	18									
	17	18									
		18									
		18									
		18									
		18									
		18									

Figure 32 – Comparative analysis of scale counts in transversal series of *Awaous (Chonophorus) banana* occurring in the Atlantic and Pacific slopes.

1.4.7. Chest region scales

The scale pattern in the chest region is presented in **Table 40**. Values in bold will be discussed in details.

Table 40 – Scale pattern in chest region. Numbers in parenthesis represent the examined individuals.

Scale pattern in chest region						
Species	Naked	Partially scaled	Fully scaled			
Awaous (Chonophorus) banana (Atlantic)	24% (17)	9% (6)	67% (47)			
Awaous (Chonophorus) banana (Pacific)	28% (9)		72% (23)			
Awaous (Chonophorus) lateristriga	77% (30)		23% (9)			
Awaous (Chonophorus) tajasica	76% (79)	14% (15)	10% (10)			

Table 41 – Scale pattern in chest region of the type specimens examined.

Scale pattern in chest region in the type specimens				
Exemplar	chest			
MNHN A- 1265 (lectotype) Gobius banana	Fully scaled			
MNHN A- 1359 (paralectotype) Gobius banana	Fully scaled			
MNHN A-1266 (syntype) Gobius martinicus	Fully scaled			
MCZ 31220 (holotype) Chonophorus contractus	Fully scaled			
MCZ 13330 (syntype) Chonophorus bucculentus	Fully scaled			
MCZ 13380 (syntype) Chonophorus bucculentus	Fully scaled			
NMNH 4772 (syntype) Chonophorus bucculentus	Fully scaled			
NHM 1856.4.17.41 (syntype) Gobius mexicanus	Fully scaled			
NHM 1856.4.17.42 (syntype) Gobius mexicanus	Fully scaled			
NHM 1860.6.16.135 (syntype) Awaous transandeanus	Fully scaled			
NHM 1860.6.16.136 (syntype) Awaous transandeanus	Fully scaled			
NMNH 48836 (holotype) Awaous nelsoni	Fully scaled			
NHM 1860.6.16.133 (syntype) Gobius (Awaous) guentheri	Fully scaled			
NHM 1860.6.16.134 (syntype) Gobius (Awaous) guentheri	Fully scaled			

Scale pattern in chest region in the type specimens					
Exemplar	chest				
MNHN- 6228-1 (lectotype) Gobius lateristriga	Partially scaled				
MNHN- 1996-301 (paralectotype) Gobius lateristriga	Naked				
ANSP 84175 (neotype) Gobius tajasica	Naked				
NHM 1862.11.23.42 (holotype) Euctenogobius latus	Partially scaled				
MNRJ 6196 (holotype) Suiboga travassosi	Naked				

1.4.8. Pre-dorsal region scales

The scale pattern in the pre-dorsal region presented a high variation in the examined individuals, the results are presented in **Table 42**.

Table 42 – Scale pattern in the pre-dorsal region of Awaous (Chonophorus). Numbers in parenthesis represent th
examined individuals. C: complete median region; I: interrupted median region e N: naked median region.

Pre-dorsal region						
Spacing	Poorly scaled			Partially scaled	Fully scaled	
Species	Complete	Ι	Ν		С	Ι
A. (Chonophorus) banana (Atlantic)	6% (4)		2%(1)	2%(1)	71% (46)	20% (13)
A. (Chonophorus) banana (Pacific)	6% (3)				80% (41)	14% (7)
A. (Chonophorus) lateristriga	33% (12)				56% (20)	11% (4)
A. (Chonophorus) tajasica	17% (18)	11% (11)	13 % (13)	4% (4)	41% (42)	15 % (15)

Table 43 – Scale pattern in chest region of the type specimens examined.

Scale pattern in the pre-dorsal region of type spe	ecimens
Exemplar	Pre-dorsal
MNHN A- 1265 (lectotype) Gobius banana	Fully scaled
MNHN A- 1359 (paralectotype) Gobius banana	Fully scaled
MNHN A-1266 (syntype) Gobius martinicus	Fully scaled
MCZ 31220 (holotype) Chonophorus contractus	Fully scaled

Scale pattern in the pre-dorsal region of type specimens					
Exemplar	Pre-dorsal				
MCZ 13330 (syntype) Chonophorus bucculentus	Fully scaled				
MCZ 13380 (syntype) Chonophorus bucculentus	Fully scaled				
NMNH 4772 (syntype) Chonophorus bucculentus	Fully scaled				
NHM 1856.4.17.41 (syntype) Gobius mexicanus	Fully scaled				
NHM 1856.4.17.42 (syntype) Gobius mexicanus	Fully scaled				
NHM 1860.6.16.135 (syntype) Awaous transandeanus	Fully scaled				
NHM 1860.6.16.136 (syntype) Awaous transandeanus	Fully scaled				
NMNH 48836 (holotype) Awaous nelsoni	Fully scaled				
NHM 1860.6.16.133 (syntype) Gobius (Awaous) guentheri	Fully scaled				
NHM 1860.6.16.134 (syntype) Gobius (Awaous) guentheri	Fully scaled				
MNHN- 6228-1 (lectotype) Gobius lateristriga	Fully scaled				
MNHN- 1996-301 (paralectotype) Gobius lateristriga	Fully scaled				
ANSP 84175 (neotype) Gobius tajasica	Fully scaled				
NHM 1862.11.23.42 (holotype) Euctenogobius latus	Fully scaled				
MNRJ 6196 (holotype) Suiboga travassosi	Inconclusive				

1.4.9. Pectoral fin base scales

Some of the analyzed type specimens have the base of the pectoral fin covered with scales. Thus, an investigation of the scale pattern in this region was performed. Results can be seen in **Table 44** and **45**.

Table 44 – Scales in the base of pectoral fin of Awaous (Chonophorus). Numbers in parenthesis represent	the
examined individuals.	

Base of pectoral fin					
Species	Naked	Fully scaled			
Awaous (Chonophorus) banana (Atlantic)	74% (52)	26% (18)			
Awaous (Chonophorus) banana (Pacific)	97% (30)	3% (1)			
Awaous (Chonophorus) lateristriga	100% (41)				
Awaous (Chonophorus) tajasica	98% (107)	2% (2)			

Table 45 – Scale pattern in the base of pectoral fin of examined type specimens. Values in bold diverge from expected.

Base of pectoral fin of type specimens					
Exemplar	Scales				
MNHN A- 1265 (lectotype) Gobius banana	Absent				
MNHN A- 1359 (paralectotype) Gobius banana	Absent				
MNHN A-1266 (syntype) Gobius martinicus	Present				
MCZ 31220 (holotype) Chonophorus contractus	Present				
MCZ 13330 (syntype) Chonophorus bucculentus	Present				
MCZ 13380 (syntype) Chonophorus bucculentus	Present				
NMNH 4772 (syntype) Chonophorus bucculentus	Present				
NHM 1856.4.17.41 (syntype) Gobius mexicanus	Present				
NHM 1856.4.17.42 (syntype) Gobius mexicanus	Present				
NHM 1860.6.16.135 (syntype) Awaous transandeanus	Present				
NHM 1860.6.16.136 (syntype) Awaous transandeanus	Absent				
NMNH 48836 (holotype) Awaous nelsoni	Present				
NHM 1860.6.16.133 (syntype) Gobius (Awaous) guentheri	Absent				
NHM 1860.6.16.134 (syntype) Gobius (Awaous) guentheri	Absent				
MNHN- 6228-1 (lectotype) Gobius lateristriga	Absent				
MNHN- 1996-301 (paralectotype) Gobius lateristriga	Absent				
ANSP 84175 (neotype) Gobius tajasica	Absent				
NHM 1862.11.23.42 (holotype) Euctenogobius latus	Absent				

Base of pectoral fin of type specimens	
Exemplar	Scales
MNRJ 6196 (holotype) Suiboga travassosi	Absent

1.4.10. Oral papillae

Papillae in the post-dental membrane, basihyal, vomer, cheeks and gills present the same abundance and morphology in all examined exemplars. On the other hand, papillae in the parasphenoid region presented a variation in the morphology, abundance and disposition in *Awaous (Chonophorus)*, results are presented in **Table 46** and **47**. Papillae in the posterior region of the palate were always conic in all analyzed individuals, thus, in this region, only the abundance and presence of ramification were examined. Results are presented in **Table 48**. An analysis of the correlation between papillae in both regions were conducted (*e.g.* exemplars with branched papillae in the parasphenoid region presenting always branched papillae in the posterior region of the palate), but no correlation was found.

Table 46 – Abundance of the papillae in the parasphenoid region of *Awaous* (*Chonophorus*). Numbers in parenthesis represent the examined individuals.

Abundance of	f the papillae in th	ne parasphenoid region	ı
Species	Abundant	Sparse	Absent
A. (Chonophorus) banana (Atlantic)	16% (10)	76% (48)	8% (5)
A. (Chonophorus) banana (Pacific)	21% (11)	71% (37)	8% (4)
A. (Chonophorus) lateristriga	36% (13)	58% (21)	7% (2)
A. (Chonophorus) tajasica	56% (58)	42% (43)	2% (2)

Table 47 – Abundance of the papillae in the parasphenoid region of examined type specimens. Values in bold diverge from expected.

Abundance of papillae in the parasphenoid region				
Exemplar	Papillae			
MNHN A- 1265 (lectotype) Gobius banana	Absent			
MNHN A- 1359 (paralectotype) Gobius banana	Absent			
MNHN A-1266 (syntype) Gobius martinicus	Abundant			
MCZ 31220 (holotype) Chonophorus contractus	Sparse			
MCZ 13330 (syntype) Chonophorus bucculentus	Abundant			
MCZ 13380 (syntype) Chonophorus bucculentus	Sparse			
NMNH 4772 (syntype) Chonophorus bucculentus	Sparse			
NHM 1856.4.17.41 (syntype) Gobius mexicanus	Sparse			
NHM 1856.4.17.42 (syntype) Gobius mexicanus	Sparse			
NHM 1860.6.16.135 (syntype) Awaous transandeanus	Sparse			
NHM 1860.6.16.136 (syntype) Awaous transandeanus	Sparse			
NMNH 48836 (holotype) Awaous nelsoni	Absent			
NHM 1860.6.16.133 (syntype) Gobius (Awaous) guentheri	Absent			
NHM 1860.6.16.134 (syntype) Gobius (Awaous) guentheri	Sparse			
MNHN- 6228-1 (lectotype) Gobius lateristriga	Abundant			
MNHN- 1996-301 (paralectotype) Gobius lateristriga	Abundant			
ANSP 84175 (neotype) Gobius tajasica	Abundant			
NHM 1862.11.23.42 (holotype) Euctenogobius latus	Sparse			
MNRJ 6196 (holotype) Suiboga travassosi	Sparse			

Table	$48\ -$	Disposition,	morphology	and	ramification	of	papillae	in	the	parasphenoid	region	of	Awaous
(Chone	ophori	<i>us</i>). Numbers	in parenthesis	repr	esent the exar	nine	ed individ	lual	ls.				

Papillae in parasphenoid region							
о ·	lin	es	Morph	ology	Ramification		
Species	One	Several	Digitiform	Conical	Single	Branched	
A. (Chonophorus) banana (Atlantic)	83% (45)	17% (9)	32% (18)	68% (38)	64% (36)	36% (20)	
A. (Chonophorus) banana (Pacific)	91% (43)	9% (4)	38% (18)	62% (29)	68% (32)	32% (15)	
A. (Chonophorus) lateristriga	100% (30)			100% (30)	63% (19)	37% (11)	
A. (Chonophorus) tajasica	83% (85)	17% (17)	6% (6)	94% (90)	66% (64)	34% (33)	

Papillae in parasphenoid region				
Exemplar	Lines	Morphology	Ramification	
MNHN A- 1265 (lectotype)	Absont	Inapplicable	Inapplicable	
Gobius banana	Absent	mappileable	mappicable	
MNHN A- 1359				
(paralectotype) Gobius	Absent	Inapplicable	Inapplicable	
banana				
MNHN A-1266 (syntype)	Two lines	Conio	Single	
Gobius martinicus	I wo miles	Conic	Single	
MCZ 31220 (holotype)	One line	Conio	Single	
Chonophorus contractus	One line	Conic	Single	
MCZ 13330 (syntype)	One line	Conie	01.	
Chonophorus bucculentus	One line	Conic	Single	
MCZ 13380 (syntype)	On a line	Comio	Single	
Chonophorus bucculentus	One line	Conic	Single	
NMNH 4772 (syntype)	On a line	Comio	Single	
Chonophorus bucculentus	One line	Conic	Single	
NHM 1856.4.17.41 (syntype)	T	Conie	01.	
Gobius mexicanus	Inconclusive	Conic	Single	
NHM 1856.4.17.42 (syntype)	T	Conie	01.	
Gobius mexicanus	Inconclusive	Conic	Single	
NHM 1860.6.16.135 (syntype)	Inconclusivo	Conio	Single	
Awaous transandeanus	Inconclusive	Conic	Single	
NHM 1860.6.16.136 (syntype)	Inconclusivo	Conio	Single	
Awaous transandeanus	meonerusive	Come	Single	
NMNH 48836 (holotype)	Abcont	Inonnliaghla	Inonalizable	
Awaous nelsoni	Absent	mappicable	mappicable	
NHM 1860.6.16.133 (syntype)	A b com 4	Inanaliashia	Incombachle	
Gobius (Awaous) guentheri	Adsent	inapplicable	паррпсабіе	
NHM 1860.6.16.134 (syntype)	On a line	Caria	Circala	
Gobius (Awaous) guentheri	One line	Conic	Single	

 $\label{eq:table 49-Disposition, morphology and ramification of papillae in the parasphenoid region of type specimens. Values in bold diverge from expected.$

Papillae in parasphenoid region					
Exemplar	Lines	Morphology	Ramification		
MNHN- 6228-1 (lectotype)	One line	Conic	Branchad		
Gobius lateristriga	One fine	Come	Drancheu		
MNHN- 1996-301					
(paralectotype) Gobius	One line	Conic	Single		
lateristriga					
ANSP 84175 (neotype)	Onalina	Conio	Duonahad		
Gobius tajasica	One nine	Conic	Drancheu		
NHM 1862.11.23.42					
(holotype) Euctenogobius	Two lines	Conic	Branched		
latus					
MNRJ 6196 (holotype)	One line	Carrie	01.		
Suiboga travassosi	One line	Conic	Single		

Table 50 – Abundance and ramification of papillae in the posterior region of the palate in *Awaous (Chonophorus)*. Numbers in parenthesis represent the examined individuals.

Papillae in the posterior region of the palate							
Spacing	Abundance		Ramif	Alegant			
Species	Abundant	Sparse	Branched	Single	Absent		
A. (Chonophorus)	200/ (10)		0(0/ (21)	1.40 (. (5)	70/ (2)		
banana (Atlantic)	28% (10)	72% (26)	86% (31)	14% (5)	7% (3)		
A. (Chonophorus)							
banana (Pacific)	17% (5)	83% (24)	75% (21)	25%(7)	7% (2)		
A (Chonophorus)							
A. (Chonophorus)	32% (10)	68% (21)	25% (7)	75% (21)	7% (2)		
lateristriga							
A. (Chonophorus)							
tajasica	89% (85)	11% (10)	92% (71)	8% (6)	2%(2)		

Papillae in the posterior region of the palate						
Exemplar	Abundance	Ramification				
MNHN A- 1265 (lectotype) Gobius	Absont	Absont				
banana	Absent	Absent				
MNHN A- 1359 (paralectotype)	Absont	Absont				
Gobius banana	Absent	Absent				
MNHN A-1266 (syntype) Gobius	Sporse	Branched				
martinicus	Sparse	Dranched				
MCZ 31220 (holotype)	Sparse	Dranahad				
Chonophorus contractus		Diancheu				
MCZ 13330 (syntype)	Sparse	Dranahad				
Chonophorus bucculentus		Diancheu				
MCZ 13380 (syntype)	Sparse	Dranahad				
Chonophorus bucculentus		Diancheu				
NMNH 4772 (syntype)	Sparse	Dranahad				
Chonophorus bucculentus		Diancheu				
NHM 1856.4.17.41 (syntype)	Sparse	Dronahad				
Gobius mexicanus		Diancheu				
NHM 1856.4.17.42 (syntype)	Sparse	Dranahad				
Gobius mexicanus		Diancheu				
NHM 1860.6.16.135 (syntype)	Sparse	Dranahad				
Awaous transandeanus		Dranched				
NHM 1860.6.16.136 (syntype)	Sparse	Dranahad				
Awaous transandeanus		Dranched				
NMNH 48836 (holotype) Awaous	Abcont	Abcont				
nelsoni	Absent	Absent				
NHM 1860.6.16.133 (syntype)	Sparse	Dronchad				
Gobius (Awaous) guentheri		Branched				
NHM 1860.6.16.134 (syntype)	Sparse	Duon ch - 1				
Gobius (Awaous) guentheri	Branched					

Table 51 – Abundance and ramification of papillae in the posterior region of the palate in examined type specimens.

Papillae in the posterior region of the palate				
Exemplar Abundance Ramification				
MNHN- 6228-1 (lectotype) Gobius	Sparse	Single		
lateristriga		Single		
MNHN- 1996-301 (paralectotype)	Sparse	Single		
Gobius lateristriga		Single		
ANSP 84175 (neotype) Gobius	Abundant	Branched		
tajasica	Toundant	Draitened		
NHM 1862.11.23.42 (holotype)	Abundant	Branched		
Euctenogobius latus	Toundant	Branchea		
MNRJ 6196 (holotype) Suiboga	Sparse	Branched		
travassosi	Spuide	Dranonou		

1.4.11. Cephalic sensory system pores

The oculoscapular canal is considered complete between pores "H" and "K" in *Awaous* (*Chonophorus*) (WATSON, 1996). Despite some rare exceptions this condition is confirmed herein (**Table 52**) and (**Figure 33**).



Figure 33 – Awaous (Chonophorus) lateristriga (NMNH 292655, 100.5 mm SL).

The presence of pore "J" was variable among *Awaous* (*Chonophorus*) species. The majority of individuals of *Awaous* (*Chonophorus*) *tajasica* and *A*. (*Chonophorus*) *lateristriga* presented this pore, having three pores in the posterior region of oculoscapular canal. In *Awaous* (*Chonophorus*) *banana* this pore was absent in half of the individuals collected in both slopes, resulting in two pores present in the posterior region of oculoscapular canal.

 Table 52 – Pores in posterior region of the oculoscapular canal in Awaous (Chonophorus). Numbers in parenthesis represent the examined individuals.

Pores in posterior region of oculoscapular canal				
Species	Two pores	Three pores	Four pores	Interrupted canal
A. (Chonophorus)	45% (30)	50% (32)	3%(2)	
banana (Atlantic)	4370 (30)	30 /0 (32)	370(2)	
A. (Chonophorus)	110/ (22)	57% (76)	10/(2)	
banana (Pacific)	44% (22)	32 /0 (20)	470 (2)	
A. (Chonophorus)	(7.0/ (19)	150/(4)		100/ (5)
lateristriga	07 70 (10)	1370 (4)		1976 (3)
A. (Chonophorus)	90% (46)	10% (5)		
tajasica				

T 11 53 D	•		•	C .1	1	1	1 *	• •		•
Table 53 – Pc	res in	nosterior i	equon (ot the	oculosca	nular	canal II	i examined	twne sn	ecimens
Table 35 TC	nes m	posteriori	logion v	or the	ocurosca	pulai	canar n	i examined	type sp	connents.

Pores in posterior region of oculoscapular canal		
Exemplar	Observed state	
MNHN A- 1265 (lectotype) Gobius banana	Two pores	
MNHN A- 1359 (paralectotype) Gobius	Two moreos	
banana	I wo pores	
MNHN A-1266 (syntype) Gobius	Τ	
martinicus	I wo pores	
MCZ 31220 (holotype) Chonophorus	T	
contractus	I wo pores	
MCZ 13330 (syntype) Chonophorus	T	
bucculentus	I wo pores	
MCZ 13380 (syntype) Chonophorus	T	
bucculentus	1 wo pores	

Pores in posterior region of oculoscapular canal		
Exemplar	Observed state	
NMNH 4772 (syntype) Chonophorus	Two pores	
bucculentus		
NHM 1856.4.17.41 (syntype) Gobius	Three nores	
mexicanus	Three pores	
NHM 1856.4.17.42 (syntype) Gobius	Three nores	
mexicanus	Three pores	
NHM 1860.6.16.135 (syntype) Awaous	Two pores	
transandeanus	1 wo poles	
NHM 1860.6.16.136 (syntype) Awaous	Two pores	
transandeanus	1 wo poles	
NMNH 48836 (holotype) Awaous nelsoni	Two pores	
NHM 1860.6.16.133 (syntype) Gobius	Three nores	
(Awaous) guentheri	Three pores	
NHM 1860.6.16.134 (syntype) Gobius	Two pores	
(Awaous) guentheri	1 wo pores	
MNHN- 6228-1 (lectotype) Gobius	Two pores	
lateristriga	1 wo poles	
MNHN- 1996-301 (paralectotype) Gobius	Two pores	
lateristriga	i wo pores	
ANSP 84175 (neotype) Gobius tajasica	Two pores	
NHM 1862.11.23.42 (holotype)	Two nores	
Euctenogobius latus	i wo pores	
MNRJ 6196 (holotype) Suiboga travassosi	Inconclusive	

Awaous (Chonophorus) lateristriga and Awaous (Chonophorus) tajasica presented a single pore "F" of the oculoscapular canal, while in Awaous (Chonophorus) banana this pore is presented branched in individuals collected on both slopes (**Table 54**).

State of ramification of pore "F"		
Species	pore	e "F"
	Single	Branched
Awaous (Chonophorus) banana (Atlantic)	7% (5)	93% (69)
Awaous (Chonophorus) banana (Pacific)	31% (17)	69% (37)
Awaous (Chonophorus) lateristriga	90% (27)	10% (3)
Awaous (Chonophorus) tajasica	100% (104)	

Table 54 – State of ramification of pore "F" in *Awaous (Chonophorus)*. Numbers in parenthesis represent the examined individuals.

Table 55 – State of ramification of pore "F" in the examined type specimens. Values in bold diverge from expected.

State of ramification of pore "F"		
Exemplar	Pore "F"	
MNHN A- 1265 (lectotype) Gobius banana	Branched	
MNHN A- 1359 (paralectotype) Gobius		
banana	Branched	
MNHN A-1266 (syntype) Gobius	Single (right side)	
martinicus	Single (right side)	
MCZ 31220 (holotype) Chonophorus	Provohod	
contractus	Branched	
MCZ 13330 (syntype) Chonophorus	Branched	
bucculentus	Branched	
MCZ 13380 (syntype) Chonophorus	Branched	
bucculentus	Branched	
NMNH 4772 (syntype) Chonophorus	Branched	
bucculentus	Dianched	
NHM 1856.4.17.41 (syntype) Gobius	Branched	
mexicanus	Dianched	
NHM 1856.4.17.42 (syntype) Gobius	Branched	
mexicanus	Dianched	
NHM 1860.6.16.135 (syntype) Awaous	Branched	
transandeanus	Draitened	

State of ramification of pore "F"			
Exemplar	Pore "F"		
NHM 1860.6.16.136 (syntype) Awaous	Branched		
transandeanus	Dianched		
NMNH 48836 (holotype) Awaous nelsoni	Branched		
NHM 1860.6.16.133 (syntype) Gobius	Propohod		
(Awaous) guentheri	Diancheu		
NHM 1860.6.16.134 (syntype) Gobius	Propohod		
(Awaous) guentheri	Diancheu		
MNHN- 6228-1 (lectotype) Gobius	Single		
lateristriga	Single		
MNHN- 1996-301 (paralectotype) Gobius	Single		
lateristriga	Single		
ANSP 84175 (neotype) Gobius tajasica	Single		
NHM 1862.11.23.42 (holotype)	Single		
Euctenogobius latus	Single		
MNRJ 6196 (holotype) Suiboga travassosi	Single		

1.4.12. Superficial neuromast lines

To understand the homology of the superficial neuromast lines it is necessary to clarify the relationships between the lines and the nerves associated with them. In addition, a comparative analysis encompassing the lines and nerves throughout the lineages of Gobioidei can support homology statements.

Currently Rhyacichthyidae is considered the basal family within Gobioidei (MILLER, 1973). A recent work demonstrated that *Rhyacichthys*, member of this family, presents only lines *b* and *d* (*sensu* SANZO, 1911) (ASAOKA *et. al*, 2014).

Wongrat and Miller (1991) performed a description of the innervation pattern in exemplars of Odontobutidae, Butidae and Eleotridae finding an interesting associated pattern between lines and nerves. However, they decided to keep the established Sanzo (1911) nomenclature. After that, Asaoka *et al.* (2011) described the innervation pattern in *Odontobutis obscurus* (Temminck & Schlegel, 1845), again without changing the nomenclature.

Both papers provide interesting information concerning the homology of the lines, particularly helping in the understanding of the homology between transverse and longitudinal lines, neglected in the currently nomenclature. The knowledge obtained by these anatomical works were used to better represent the homology of the lines. Thus, herein, the nomenclature of Sanzo (1911) was adopted, with some necessary small adjustments, explained below.

In the following text, the region closest to the origin of the nerve is treated as **branch**, the intermediary region is treated as **portion** and the most distal region is called **segment**. Since Odontobutidae also figures in the base of ramification of Gobioidei, *Odontobutis obscurus* was taken as a starting point to understand of the homology of the lines.

A closer look in the innervation pattern of *Odontobutis obscurus* reveals that the *line a* (*sensu* SANZO, 1911) is actually innervated by two different branches of the buccal ramus. The **anterior region** of the *line a* is innervated by the **anterior segment** of the **posterior portion** of the **second branch** of the buccal ramus of trigeminus nerve, while the **posterior region** is innervated by the **third branch** of the buccal ramus of trigeminus nerve. Thus, the **anterior region** of *line a* (*sensu* SANZO, 1911) will be treated as a_2 , since *line a1* already figures in the current nomenclature.

In conclusion, the adopted nomenclature considers the *line a* as the one innervated by the **third branch** of the buccal ramus of trigeminus nerve, *line a1* innervated by **posterior segment** of the **posterior portion** of the **second branch** of the buccal ramus of trigeminus nerve and a_2 line innervated by the **anterior segment** of the **posterior portion** of the **second branch** of the **buccal ramus** of trigeminus nerve (**Figure 34** and **35**).

The *line c* is innervated by three different portions. The portions were called c_3 , c_4 and c_5 following the antero-posterior orientation. Lines c_1 and c_2 already figure in the Sanzo (1911) nomenclature. *Line c3* is associated with the **anterior segment** of the **posterior portion** of the **first branch** of the buccal ramus of trigeminus nerve, *line c4* is associated with the **posterior segment** of the **posterior portion** of the **first branch** of the buccal ramus of trigeminus nerve, *line c4* is associated with the **posterior segment** of the **posterior portion** of the **first branch** of the buccal ramus of trigeminus nerve and c_5 is associated to the **anterior portion** of the **second branch** of the buccal ramus of trigeminus nerve (**Figure 34** and **35**).

The pattern observed in *Odontobutis obscurus* was then compared to that observed in *Perccottus glenii* Dybowski, 1877, another representative of Odontobutidae (WONGRAT; MILLER, 1991). In this species the differentiation between a_1 and a_2 lines was not possible (**Figures 36** and **37**).



Figure 34 – Disposition of the superficial neuromast lines and the nerves in *Odontobutis obscurus* adapted from Asaoka *et al* (2011). Lines in purple: *line a*, lines in light blue: *line a*₁, lines in orange: a_2 line, lines in dark blue: c_3 , lines in green: c_4 , lines in red: c_5 . BR: buccal ramus of trigeminus nerve, MR: mandibular ramus of trigeminus nerve.



Figure 35 – Disposition of the superficial neuromast lines in *Odontobutis obscurus* adapted from Asaoka *et al* (2011). Lines in purple: *line a*, lines in light blue: *line a*₁, lines in orange: a_2 line, lines in dark blue: c_3 , lines in green: c_4 , lines in red: c_5 . AN: anterior nasal opening, PN: posterior nasal opening. Other letters represent the nomenclature proposed by Sanzo (1911).



Figure 36 – Disposition of the superficial neuromast lines and the nerves in *Perccottus glenii* adapted from Wongrat and Miller (1991). Lines in purple: *line a*, lines in light blue: *line a*, lines in orange: a_2 line, lines in dark blue: c_3 , lines in green: c_4 , lines in red: c_5 . BR: buccal ramus of trigeminus nerve, MR: mandibular ramus of trigeminus nerve.



Figure 37 – Disposition of the superficial neuromast lines in *Perccottus glenii* adapted from Wongrat e Miller (1991). Lines in purple: *line a*, lines in light blue: *line a*₁, lines in orange: a_2 line, lines in dark blue: c_3 , lines in green: c_4 , lines in red: c_5 . Other letters represent the nomenclature proposed by Sanzo (1911).

Lastly the pattern was applied to species of *Oxyeleotris* Bleeker, 1874 at in the base of diversification of Gobioidei (Figures 38 and 39).



Figure 38 – Disposition of the superficial neuromast lines and the nerves in *Oxyeleotris marmorata* (Bleeker, 1852) adapted from Wongrat e Miller (1991). Lines in purple: *line a*, lines in light blue: *line a*₁, lines in orange: a_2 line, lines in dark blue: c_3 , lines in green: c_4 , lines in red: c_5 . BR: buccal ramus of trigeminus nerve, MR: mandibular ramus of trigeminus nerve.



Figure 39 – Disposition of the superficial neuromast lines in *Oxyeleotris marmorata* (Bleeker, 1852) adapted from Wongrat e Miller (1991). Lines in purple: *line a*, lines in light blue: *line a*₁, lines in orange: a_2 line, lines in dark blue: c_3 , lines in green: c_4 , lines in red: c_5 . Other letters represent the nomenclature proposed by Sanzo (1911).

An analysis of the correlation between lines and nerves in gobies and eleotrids is being prepared to determine if the pattern found here can be observed in these families. However, some exemplars of *Awaous* (*Chonophorus*) *tajasica* were prepared following the protocol for nerve staining developed by Esguícero and Bockmann (*in prep.*) and a preliminary analysis suggests that the pattern can be observed in gobiid species. The disposition of lines in *Awaous* (*Chonophorus*) *tajasica* can be observed above (**Figure 43**).

Exemplars of *Awaous* (*Chonophorus*) present a very conservative pattern in the disposition of superficial neuromasts lines, thus it was not possible to distinguish species based on the disposition of these lines.



Figure 43 – Disposition of the superficial neuromast lines in *Awaous (Chonophorus) tajasica*, demonstrating the pattern observed in *Awaous (Chonophorus)* (**LIRP** 5745, 100.5 mm SL). Lines in purple: *line a*, lines in light blue: *line a*₁, lines in orange: a_2 line, lines in dark blue: c_3 , lines in green: c_4 , lines in red: c_5 .

In spite of the extremely conservative pattern observed in *Awaous* (*Chonophorus*) there are some differences when compared to the pattern presented by Watson (1996: fig.7) (**Figure 44**).

In the illustration (**Figure 44**) the line d (sensu SANZO, 1991) is absent. The posterior portion of *line c3* is much more inclined anteriorly, *line c4* is segmented in several diagonal lines much more dorsally expanded, *line a1* is much more posterior. In addition, the *line a* has two anterior branches, not observed in the examined exemplars. Since the author did not identified the represented exemplar it is not possible to confront the image with the original specimen.



Figure 44 – Disposition of the superficial neuromast lines in Awaous (Chonophorus) tajasica (according to WATSON, 1996: p. 13, fig.7).

1.5. DISCUSSION

1.5.1. Morphometric data

An analysis of the morphometric data indicates that the body shape is extremely conservative in *Awaous* (*Chonophorus*). In spite of all additional measurements taken, the proportion of the measurements remain extremely similar in all examined species.

All exemplars of *Awaous* (*Chonophorus*) *banana* collected in the Atlantic slope belong to the same biogeographical province, thus a comparative analysis was not possible. Since exemplars collected in the Pacific slope belonged to different biogeographical provinces the comparative analysis was performed, however the measurements were extremely superposed making impossible to separate species. In addition, the measurements taken in exemplars occurring in the Atlantic and Pacific slope demonstrate a complete overlap, also making impossible the establishment of new species.

The comparative analysis between the biogeographical provinces in *Awaous* (*Chonophorus*) *tajasica* also revealed a complete overlap, not allowing differentiation of species. The preanal distance and second dorsal fin length in the examined *A*. (*Chonophorus*) *lateristriga* occurring in the biogeographical province of "Gulf of Guinea" diverge from other exemplars collected in the biogeographical province of "West African Transition", however it is possible that this variation may be related to the poor sample allied with the small size of the analyzed exemplar collected in the "Gulf of Guinea" province.

The lectotype MNHN A- 1265 of *Gobius banana* presented the distance between the nares, preanal distance and second dorsal fin length diverging from the range observed in individuals of the same species. In addition, the paralectotype MNHN A- 1359 presented the pre-dorsal length, the inter-opercular distance, caudal peduncle height and first dorsal fin length also diverging from the expected. No other measurements diverged in those exemplars. It is relevant to say that both specimens are in a very poor state of conservation, the head shape was extremely affected by a degradation process throughout the years, especially in the paralectotype. As consequence, some measurements were not taken in the anterior region of both exemplars since it was impossible to establish reliable landmarks. Thus, the divergence in the measurements was considered an effect of the poor state of conservation of the exemplars.

Some measurement proportions of the exemplars of *Chonophorus bucculentus* diverge from the range found for *Awaous* (*Chonophorus*) *banana*, but the syntypes of this species present the largest standard length when compared to examined exemplars of *A*. (*Chonophorus*) *banana*, which it may explain the variation.

The syntype of *Gobius mexicanus* (NHM 1856.4.17.41) presented a larger ratio in total and standard length when compared to *Awaous* (*Chonophorus*) *banana*. However, all other morphological features of this specimen agreed with the species cited above. This difference was them considered a variation within *A*. (*Chonophorus*) *banana*.

Body and caudal peduncle depths diverge between the syntype NHM 1860.6.16.135 of *Awaous transandeanus* and the other specimens of *Awaous (Chonophorus) banana* analyzed. In addition, the total length, pre-anal distance, and caudal fin length varied between the syntype NHM 1860.6.16.136 of *Awaous transandeanus* and the other specimens of *Awaous (Chonophorus) banana* occurring in the Pacific slope. No measurements varied in both syntypes at the same time and other characteristics agreed with the pattern found in the specimens occurring in the Pacific Ocean. Thus, that divergence was considered a variation.

The syntype NHM 1860.6.16.133 of *Gobius guentheri* presented the pre-dorsal and mandibular lengths diverging from other specimens of *Awaous* (*Chonophorus*) *banana* collected in the pacific slope. Also, the body depth varied among specimens occurring in both slopes. In addition, proportions of the pre-dorsal distance and distance between pelvic fin spines varied between the syntype NHM 1860.6.16.134 of *Gobius guentheri* and the individuals of *Awaous* (*Chonophorus*) *banana* collected in the Pacific Ocean. No measurement proportions varied in both syntypes at the same time and the other characteristics agreed with the

morphology found in other specimens of *Awaous* (*Chonophorus*) *banana* from the Pacific slope. Thus, such a divergence was also considered a variation.

The proportions of the orbital diameter and total length of the holotype of *Suiboga travassosi* MNRJ 6196 (**Table 29**) diverge from the range found for *A*. (*Chonophorus*) *tajasica* (**Table 24**). Furthermore, the proportions of the preanal distance and length of the second dorsal-fin of *Suiboga travassosi* diverge from the range found for *A*. (*Chonophorus*) *tajasica* occurring in the biogeographical province of "Tropical Southwestern Atlantic". In addition, the proportions of the distance between nares and the caudal peduncle depth of this specimen diverge from the range observed in the biogeographical province of the "Warm Temperate Southwestern Atlantic". This was the largest examined specimen. Besides, the eyes were found in a poor state of conservation, remaining almost completely sunken in the cranium. Furthermore, some body parts of this specimen were deformed during the fixation process, including the anterior portion of the head. Thus, the observed variation may be associated with the large size allied with the poor state of conservation of the holotype of *Suiboga travassosi*.

1.5.2. Meristic Data

Fin-ray counts were extremely conserved among *Awaous (Chonophorus)* species, showing almost complete overlapping so that no diagnostic character was extracted from these counts. Scale counts in dorsal margin, ventral margin and circum-peduncular region also presented a wide overlap in all examined specimens.

In spite of some overlap, the scale counts in longitudinal region was very informative. Specimens of *Awaous (Chonophorus) banana* collected in the Pacific slope presented less scales in the longitudinal region when compared to specimens collected in the Atlantic slope (**Table 35**).

The found range for *A*. (*Chonophorus*) *tajasica* presented two different curves (**Table 35**), which could indicate the presence of two distinct species. However, a comparative analysis of the scale counts in the different biogeographical provinces revealed two different ranges in both provinces, not indicating allopatric species. The morphology of all examined exemplars is extremely similar. In addition, the scale count in transversal series presented a huge overlap. Moreover, the scale count in the longitudinal series follow a different methodology, which could probably explain the results observed in *A*. (*Chonophorus*) *tajasica*. In face of this

scenario the final decision was to consider the divergence in the scale count in the longitudinal region of *Awaous (Chonophorus) tajasica* as a variation of the species.

Scale count in the transversal region was also very informative. The range presented by *Awaous (Chonophorus) banana* collected in the Atlantic slope, in spite of a small overlap, diverge from all other examined specimens, including specimens of *Awaous (Chonophorus) banana* collected in the Pacific slope (**Table 37**). A closer look reveals that the overlap is caused only by a minority of specimens (**Figure 32**). Results found in this dissertation are very similar to the ones obtained by Bussing (2002), which reinforces the accuracy of the information presented herein.

Since specimens of *Awaous* (*Chonophorus*) banana occurring in the Pacific slope differ from the ones collected in the Atlantic slope by scale counts in transversal and longitudinal regions, the Pacific ones are here proposed as belonging to another species. The name *Awaous transandeanus* (Günther, 1861) had already been proposed and will be adopted here to refer to the forms occurring in the Pacific Ocean. In addition, the type specimens of the species *Awaous nelsoni* Evermann, 1898 and *Gobius* (*Awaous*) guentheri Regan, 1903 presented the scale count in transversal and longitudinal regions congruent with those ranges found for *Awaous* (*Chonophorus*) transandeanus. As a result, these names will be considered junior synonyms of *Awaous transandeanus* (Günther, 1861) which has the nomenclatural priority.

1.5.3. Chest region scales

Awaous (Chonophorus) banana and A. (Chonophorus) transandeanus presented the base of the pelvic fin covered with scales while in A. (Chonophorus) tajasica and A. (Chonophorus) lateristriga the scales in this region are frequently absent (**Table 39**). Scale pattern in this region permit to differ the Caribbean and Pacific species from the others. Also, it could indicate that the Brazilian species may be closer related to the African one. See chapter II for further discussion.

1.5.4. Pre-dorsal region scales

Despite there is a huge variation in the disposition of scales in the pre-dorsal region, it was not possible to segregate species based on this characteristic. All examined species presented the majority of individuals exhibiting the pre-dorsal region fully scaled or fully scaled with an interruption at the median region (**Table 41**).

1.5.5. Pectoral fin base scales

Scales in the base of pectoral region are frequently absent in *Awaous (Chonophorus)*. However, one fourth of analyzed specimens of *Awaous (Chonophorus) banana* presented scales in this region (**Table 43**). Scales in this region were also observed in the syntype MNHN A-1266 of *Gobius Martinicus*, all syntypes of *Chonophorus bucculentus*, all syntypes of *Gobius mexicanus* and holotype NMNH 48836 of *Chonophorus contractus*. Furthermore, scales in this region are present in one of the syntypes of *Awaous (Chonophorus) transandeanus* (NHM 1860.6.16.135) and in the holotype NMNH 48836 of *Awaous nelsoni*.

The presence of scales in the base of pectoral fin was rare in all examined species, thus it was also considered a variation.

1.5.6. Oral papillae

The arrangement of the papillae in the post-dental membrane, palatine region, region between gills, vomer and tongue was extremely conserved in species belonging to *Awaous* (*Chonophorus*).

The papillae in parasphenoid region are usually sparse in the subgenus cited above. However, more than a half of specimens of *Awaous* (*Chonophorus*) *tajasica* presented abundant papillae in this region (**Table 45**). In addition, *Awaous* (*Chonophorus*) frequently present conic papillae in the parasphenoid region. However, one third of examined individuals assigned to *A*. (*Chonophorus*) *banana* and *Awaous* (*Chonophorus*) *transandeanus* presented digitiform papillae in the parasphenoid region (**Table 47**). Since the variation was only found in a fraction of the exemplars, they were not considered diagnostic features themselves, but this variation can be considered part of the set of diagnostic features for the species (*sensu* NELSON; PLATNICK, 1981).

In the lectotype MNHN A- 1265 and paralectotype MNHN A- 1359 of *Gobius banana*, the holotype NMNH 48836 of *Awaous nelsoni* and the syntype 1860.6.16.133 of *Gobius (Awaous) guentheri* the papillae were absent in the parasphenoid region, which may be explained by the poor state of conservation of these exemplars. Furthermore, the syntype

MNHN A-1266 of *Gobius martinicus*, the syntype MCZ 13330 of *Chonophorus bucculentus*, the lectotype MNHN- 6228-1 and the paralectotype MNHN- 1996-301 of *Gobius lateristriga* presented abundant papillae in this region, which considered a variation for the species.

Awaous (Chonophorus) tajasica presented abundant papillae in the posterior region of the palate diverging from all other examined species (**Table 49**). The sparse papillae in the posterior region of the palate in the holotype of *Suiboga travassosi* was considered a variation. Moreover, A. (Chonophorus) lateristriga presented single papillae in this region contrasting with the branched ones presented by other analyzed species. Variations cited above were present in the majority of individuals, thus they were considered diagnostic characters for Awaous (Chonophorus) lateristriga and Awaous (Chonophorus) tajasica.

1.5.7. Cephalic sensory system

Only a small sample of *A*. (*Chonophorus*) lateristriga and *A*. (*Chonophorus*) tajasica presented the pore "J" in the posterior oculoscapular canal while half of individuals of *A*. (*Chonophorus*) banana and *A*. (*Chonophorus*) transandeanus presented the cited pore (**Table 51**). This variation was also not considered diagnostic itself, but figure in the diagnostic set of characters as an auxiliary character.

In *A*. (*Chonophorus*) *lateristriga* and *A*. (*Chonophorus*) *tajasica* the pore "F" was single in almost all examined specimens while in *A*. (*Chonophorus*) *banana* and *A*. (*Chonophorus*) *transandeanus* this pore is usually branched. The state of pore "F" was also considered a diagnostic feature.

1.5.8. Species of Awaous (Chonophorus)

Characters cited above allowed to conclude that *Awaous* (*Chonophorus*) includes four valid species: *Awaous* (*Chonophorus*) banana, *Awaous* (*Chonophorus*) lateristriga, *Awaous* (*Chonophorus*) tajasica, and *Awaous* (*Chonophorus*) transandeanus. Since the morphology of these species is extremely conserved, a general description of the morphology of *Awaous* (*Chonophorus*) is presented below.

General description of morphology of Awaous (Chonophorus):

Species of *Awaous* (*Chonophorus*) present an elongated body with body height decreasing posteriorly, cylindric body in the pre-dorsal region, gradually tapering posteriorly. Lateral profile convex in the anterior region, gradually becoming almost vertical in the posterior region, caudal peduncle lower and more compressed than anterior region of the body. In dorsal view, the pre-dorsal region has a convex shape. They have an ellipsoid-shaped protuberance in the center of this region, extending from the anterior region of the first ray of the first dorsal fin to the median region of the supraoccipital bone. Pre-dorsal region usually fully scaled with cycloid scales, scales in this region smaller than scales in lateral surface of the body. Scales in chest region also cycloid, resembling scales in pre-dorsal region. Body covered with ctenoid scales with the same size along body length.

Head length greater than width, depressed, conical or round head depending on the degree of development of the *retromalaris* portion of the *adductor mandibulae* muscle, males presenting a round head shape and females presenting a conical one.

Lateral eyes, dorsal margin of orbits slightly exceeding the top of the head, ventral margin partially covered by cheeks. Anterior and posterior nostrils are next to each other, distance being minor than the distance between the two adjacent nostrils. Subterminal mouth. Lips fleshy and prominent. Interior of the mouth filled with oral papillae, mainly in the vomer region, post-dental membrane, parasphenoid, posterior region of the palate, cheeks, tongue, gill arches and gills.

Five branchiostegal rays, first, second, third and fourth branchiostegal rays associated with the anterior ceratohyal. Fifth ray associated with posterior ceratohyal. Branchiostegal membrane not attached to the posterior border of the operculum and isthmus region, adhering to the isthmus only in the posterior region of the inferior border of the operculum.

Pelvic fins are fused in an oval-shaped adhesive disc by a connective membrane. The two spines are associated with a frenum. Pelvic fins with five branched rays, the fifth ray being fused the connective membrane. Earlier branched rays are smaller in size and usually appear hidden by the frenum in ventral view, ray size gradually increases anteroposteriorly.

Triangular first dorsal fin, dorsally rounded, with 6 spines. Membrane between the spines not reaching the dorsal end of the spines resulting in a serrated conformation. It originates posteriorly to the pelvic fin, not reaching the second dorsal fin. Second dorsal fin in a rectangular shape, membrane between the rays reaching the dorsal end of them. Usually having one spine and eleven branched rays, the most posterior two fin rays have the same implantation

base, being separated since the base. It originates in the same vertical as the anal fin, posterior region not reaching the base of the caudal fin rays.

Lanceolate Pectoral Fins. Presenting one segmented but not branched fin ray in the most ventral region and 14 to 16 branched fin rays.

Anal fin with the same shape as the second dorsal fin and the same fin ray count, two posterior most rays also divided from its base. Truncated caudal fin with symmetrical lobes. Consisting of six branched rays in the upper lobe and six to seven in the lower lobe.

Incomplete lateral line ending in the posterior margin of the head. Anterior oculoscapular canal presenting pores A, B, C, D, F, G, H, K and L, pore D being the only unpaired one. Preopercular canal presenting pores M, N and O.

Color pattern in ethanol: Background of the body Yellowish or olivaceous with brownish bars and spots. Presenting two conspicuous parallel bars in the lateral side of the snout region, between the eyes and the upper lip. Anterior bar originating in the anterior region of the eye and posterior bar in the ventral region of the eyes, both reaching the dorsal margin of the upper lip. Cheeks with two slightly descending horizontal stripes present in the operculum region. Trunk region with three semicircular stripes. Anterior bar with origin slightly posterior to pore "F" of the oculoscapular canal reaching the base of the pectoral fin. Intermediate bar originating from the dorsal midline of the body near the posterior margin of the operculum and reaching the anterior third of the pectoral fin, partially overlapped by pectoral fin rays in lateral view. Posterior bar originating from the dorsal region of the body slightly posterior to the beginning of the pectoral fin, reaching the posterior third of this fin, also partially covered by the pectoral fin in lateral view. Juvenile specimens presenting, in addition to the semicircleshaped bars, three other vertical bars along the length of the body which shape gradually being posteriorly replaced by an irregular one. Dorsal region of the body with a series of small round spots that, due to their proximity, may form small irregular blotches. Circular blot in the base of the caudal fin rays extending posteriorly over the rays, covering one tenth of its length. Dorsal fin membrane colored by interrupted brownish horizontal bars and small spots, also brownish in color. Hyaline anal fin. Yellowish pelvic fin with. Caudal fin with a series of equidistant semicircular bars along its length, sometimes intertwining in the median region.

Ecology: Species within *Awaous* (*Chonophorus*) present a medium size, adult specimen reaching from 5 to 16 cm in standard length, usually found in river bottoms. They are considered omnivorous, but algae represent more than half of their gastric content (SABINO; CASTRO, 1991). Feeding strategies includes grazing, with separation of food items in the oral cavity

(SABINO; CASTRO, 1991). Species are usually found in rivers, but occasionally some specimens are collected in brackish water from intermittent streams during the dry season, being recorded in flooded fields and margin of rivers and streams (WATSON, 1996). They are considered amphidromous, habit characterized by migration between freshwater and saltwater for reasons other than reproductive (MYERS, 1949). In the case of *Awaous (Chonophorus)* species this migration would occur for trophic reasons: adults lay their eggs in the rivers and, after hatching, the larvae are passively carried to saltwater where they remain as part of the plankton before returning to freshwater, where they stay during the adult phase (RADTKE *et al.*, 1988).

Awaous (Chonophorus) banana (Valenciennes, 1837)

Gobius martinicus Valenciennes, 1837 Chonophorus bucculentus Poey, 1860 Chonophorus contractus Poey, 1861 Gobius mexicanus Günther, 1861 Gobius dolichocephalus Cope, 1867







Figure 45 – Awaous (Chonophorus) banana. A: lateral view, B: dorsal view, C: ventral view (UCR 1352-8: 88.4 mm SL).

Diagnosis: Awaous (Chonophorus) banana differs from Awaous (Chonophorus) lateristriga and Awaous (Chonophorus) tajasica by presenting the chest region fully scaled and the pore "F" of the oculoscapular canal branched [vs. chest region naked and the pore "F" of the oculoscapular canal single in Awaous (Chonophorus) lateristriga and Awaous (Chonophorus) tajasica]. Also, it differs from Awaous (Chonophorus) transandeanus by presenting scale count in longitudinal series varying from 49 to 68 (mode from 53 to 63) [vs. 50 – 60 (mode from 50 to 55 in Awaous (Chonophorus) transandeanus] and scale count in transversal series varying from 16 – 28 (mode from 20 to 24) [vs. 16 – 23 (mode from 17 to 20) in Awaous (Chonophorus) transandeanus].

Distribution: from northern Florida occurring on all Caribbean islands including Trinidad and Tobago, in the continental shelf occurs from Tamaulipas, Mexico, to Caracas, in Venezuela.



Figure 46 – Distribution map of Awaous (Chonophorus) banana.

Awaous (Chonophorus) lateristriga (Duméril, 1861) Gobius (aeneofuscus) guineenses var. Peters, 1876 (WATSON, 1996).

Gobius bustamantei Greeff, 1882 (WATSON, 1996).



Figure 47 – *Awaous (Chonophorus) lateristriga*. A: lateral view, B: dorsal view, C: ventral view (USNM 292655: 72.5 mm SL).

Diagnosis: Awaous (Chonophorus) lateristriga differs from Awaous (Chonophorus) banana and Awaous (Chonophorus) transandeanus by presenting the chest region naked and the pore "F" of the oculoscapular canal single [vs. chest fully scaled and pore "F" of the oculoscapular canal branched in Awaous (Chonophorus) banana and Awaous (Chonophorus) transandeanus]. Also, it differs from Awaous (Chonophorus) tajasica by presenting single and sparse oral papillae in the posterior region of the palate [vs. oral papillae in the posterior region of the palate [vs. oral papillae].

Distribution: *Awaous (Chonophorus) lateristriga* occurs from Sierra Leone to the border between Angola e Namibia, occurring also in Bioko Island, Equatorial Guinea.



Figure 48 – Distribution map of Awaous (Chonophorus) lateristriga.
Awaous (Chonophorus) tajasica (Lichtenstein, 1822)

Suiboga travassosi Pinto, 1960

Euctenogobius latus O'Shaughnessy, 1875



Figure 49 – Awaous (Chonophorus) tajasica. A: lateral view, B: dorsal view, C: ventral view (UNT 9259, 134.5 mm SL).

Diagnosis: Awaous (Chonophorus) tajasica differs from Awaous (Chonophorus) banana and Awaous (Chonophorus) transandeanus by presenting the chest region naked and a pore "F" of the oculoscapular canal single [vs. chest fully scaled and pore "F" of the oculoscapular canal branched in Awaous (Chonophorus) banana and Awaous (Chonophorus) transandeanus]. Also, it differs from Awaous (Chonophorus) lateristriga by presenting branched and abundant oral papillae in the posterior region of the palate (vs. oral papillae in the posterior region of the palate sparse and single in Awaous (Chonophorus) lateristriga).

Distribution: Awaous (Chonophorus) tajasica occurs from Rio Grande do Sul to Maranhão, Brazil.



Figure 50 – Distribution map of Awaous (Chonophorus) tajasica.

Awaous (Chonophorus) transandeanus

Awaous nelsoni Evermann, 1898 Gobius (Awaous) guentheri Regan, 1903



Figure 51 – *Awaous (Chonophorus) transandeanus*. A: lateral view, B: dorsal view, C: ventral view (UCR 121-3, 72.3 mm SL).

Diagnosis: Awaous (Chonophorus) transandeanus differs from Awaous (Chonophorus) lateristriga and Awaous (Chonophorus) tajasica by presenting the chest region fully scaled and the pore of the oculoscapular canal branched [vs. chest region naked and the pore "F" of the oculoscapular canal single in Awaous (Chonophorus) lateristriga and Awaous (Chonophorus) tajasica]. Also, it differs from Awaous (Chonophorus) banana by presenting scale count in longitudinal series varying from 50 – 60 (mode from 50 to 55) [vs. 49 – 68 (mode from 53 to 63) in Awaous (Chonophorus) banana) and scale count in transversal series varying from 16 – 23 (mode from 17 to 20) [vs. 16 – 28 (mode from 20 to 24) in Awaous (Chonophorus) banana].

Distribution: Pacific coast of America occurring from Baja California Sur and Sonora in Mexico to Tumbes, Peru.



Figure 52 – Distribution map of Awaous (Chonophorus) transandeanus.





Figure 53 – Distribution map for the species within Awaous (Chonophorus).

2. PHYLOGENETIC PLACEMENT

2.1. INTRODUCTION

Initially the genus *Gobius* Linnaeus, 1758 was described having seven nominal species. The genus was characterized by the presence of two pores of the cephalic sensory canal between the eyes very close to each other and two anterior pores also very close, four branchiostegal rays and pelvic fins fused in an oval shape with 12 rays. The type species, by original designation is *Gobius niger* Linnaeus, 1758.

Valenciennes (1837) devoted chapter 14 of his work to describe the family of the "Goboids." The family would present 9 genera, namely: *Apocryptes* Valenciennes, 1837, *Trypauchen* Valenciennes, 1837, *Amblyopus* Valenciennes, 1837, *Periophthalmus* Bloch & Schneider, 1801, *Boleophthalmus* Valenciennes, 1837, *Eleotris* Bloch & Schneider, 1801, *Gobioides* Lacepède, 1800, *Gobius* and *Sicydium* Valenciennes, 1837. He also suggested some genera that would be similar to "Goboid" such as *Platyptera* Cuvier, 1829 synonym of *Rhyacichthys* Boulenger, 1901. Although *Platyptera* was described before *Rhyacichthys*, this name was predated by *Platyptera* Meigen, 1803 in Diptera. Gobioids would present only the species *Gobioides broussonnetii*. Other gobioid species, described by Lacepède and Linnaeus, were considered synonyms and were considered members of *Amblyopus*. *Sicydium* would present four species characterized by having a jaw with numerous thin and flexible teeth and a row of stronger teeth implanted directly into the bone (VALENCIENNES, 1837).

Vallenciennes (1837) also stablished that *Gobius* would present two divisions, the *Gobius* of the Seas of Europe, with 19 species, and the foreign *Gobius*, with 79 species divided into eleven categories. Among the foreign *Gobius* was the "Lancettes" division, which would include *Gobius lanceolatus* (Bloch, 1783), currently a junior synonym of *Gobionellus oceanicus* (Pallas, 1770) (ESCHMEYER *et al.*, 2018), *Gobius bacalaus* (Valenciennes, 1837), another junior synonym of *Gobionellus oceanicus* (ESCHMEYER *et al.*, 2018), *Gobius bacalaus* (Valenciennes, 1837), another junior synonym of *Gobionellus oceanicus* (ESCHMEYER *et al.*, 2018), *Gobius brasiliensis* (Bloch & Schneider, 1801), a junior synonym of *Gobioides broussonnetii* Lacepède, 1800 (ESCHMEYER *et al.*, 2018) and *Gobius smaragdus* Valenciennes, 1837, currently dealt as *Ctenogobius smaragdus* (ESCHMEYER *et al.*, 2018). An "*Awaous* division" was also proposed, embracing *Gobius ocellaris* Broussonet, 1782, presently valid as *Awaous* (*Awaous*) *ocellaris* (ESCHMEYER *et al.*, 2018), *Gobius nigripinnis* Valenciennes, 1837, a junior synonym of *Awaous* (*Awaous*) *commersoni* (Schneider, 1801) (ESCHMEYER *et al.*, 2018), *Gobius nigripinnis* Valenciennes, 1837, a

2018), Gobius pallidus Valenciennes, 1837, valid as Awaous (Awaous) pallidus (ESCHMEYER et al., 2018), Gobius guamensis Valenciennes, 1837, valid as Awaous (Awaous) guamensis (ESCHMEYER et al., 2018), Gobius banana Valenciennes, 1837, valid as Awaous (Chonophorus) banana (ESCHMEYER et al., 2018) and Gobius martinicus Valenciennes, 1837, a junior synonym of Awaous (Chonophorus) banana (ESCHMEYER et al., 2018). This division was characterized by an elongated face due to the posterior position of the eyes.

Bleeker (1874) proposed a classification for the family gobioid (*sensu* VALENCIENNES, 1837), proposing several divisions for the subfamily Gobiiformes "Les groupes, dans la sous-famille des Gobiiformes, sont plus nombreux" (BLEEKER, 1874). The Latrunculini group which, among others, included *Evorthodus* Gill, 1859 and *Sicyopus* Gill, 1863. The Sicydiini group would be characterized by presenting "a mobile gum over the teeth", being dived in three divisions. The first division including only *Tridentiger* Gill, 1859, the second containing *Sicydium* Valenciennes, 1837, *Sicyopterus* Gill, 1860 and *Microsicydium* Bleeker, 1874, currently junior synonym of *Sicyopterus* (ESCHMEYER *et al.*, 2018) and the third presenting only *Lentipes* Günther, 1861.

In addition, Bleeker (1874) proposed the Gobiini group with five subgroups. The Eugobii subgroup would have seven divisions named from "a" to "g" characterized by having "jaw teeth decreasing in size along the maxillary length". Within Eugobii *Awaous* Valenciennes, 1837 was grouped with *Rhinogobius* Gill, 1859 (division "d") both not grouped with *Stenogobius* Bleeker, 1874 since the last one had no teeth in the external series (division "a"). *Euctenogobius* Gill, 1859 was placed in the division "g" of the Eugobii subgroup along with *Oxyurichthys* Bleeker, 1857.

Furthermore, Bleeker (1874) proposed Gobionelli, another subgroup of Gobiini. This division have *Gobionellus* and *Synechogobius* Gill, 1859, currently a junior synonym of *Acanthogobius* Gill, 1859 (ESCHMEYER *et al.*, 2018). This was the first mention to the subfamily Gobionellinae (LARSON, 2001).

Regan (1911) listed a number of characteristics for Gobiidae, then treated in familial rank, dividing it in two subfamilies. The subfamily Gobiinae would present two divisions. The first one containing *Awaous*, *Gobionellus*, *Oxyurichthys* and *Stenogobius*, among others, and the second one containing *Gobioides*, *Taenioides*, *Trypauchen* Valenciennes, 1837, and *Trypauchenichthys* Bleeker, 1860.

Koumans (1931) proposed the subfamily Sicydiaphine resulting from the union between the Sicydiini and Latrunculini subgroups proposed by Bleeker (1874). This subfamily would be characterized by its elongated body, not very wide gill openings, except in *Aphia* Risso, 1827, wide isthmus, second dorsal fin not elongated, united pelvic fins, labial teeth on the lower lip, a row of simple teeth on the jaw, posterior rows sometimes covered by the gum, elongated head and naked snout and cheeks. In addition to included in this subfamily *Aphia*, a current member of Gobiinae (PEZOLD, 1993), and *Gobiopterus* Bleeker, 1874and *Evorthodus*, the last two genera currently included in Gobionellinae (PEZOLD, 1993).

Miller (1973) described the osteology of *Rhyacichthys* and placed it in a separate family, Rhyacichthidae, a basal clade of the suborder Gobioidei. Miller (1973) also proposed to include more than 20 genera in the subfamily Gobionellinae, encompassing *Gobioides*, *Gobionellus*, *Oxyurichthys* and *Stenogobius*, among others. Unfortunately, *Awaous* was not treated in this publication. This subfamily would be characterized by the presence of "two epural bones; fanhypurals separate; no endopterygoid; five branchiostegal rays; no upper postcleithrum, or supratemporals; scapula minute or absent; metapterygoid opposed to quadrate, not meeting ectopterygoid; preopercular not meeting symplectic (except in *Trypauchen*); anterior oculoscapular canal rarely extending across snout, and preopercular canal with three pores, when present."

Hoese (1984) recognized five sub-families within Gobiidae, including Sicydiinae, characterized by presenting "tongue fused to floor of mouth or free only at tip, highly modified jaw suspension; thickened and highly branched pelvic rays and fleshy pads at tips of pelvic spines". The author did not recognize Gobionellinae (*sensu* MILLER, 1973) as valid.

It was only later that the genus *Awaous* was treated as a member of the subfamily Sicydiinae, placed in the *Sicydium* group (BIRDSONG *et al.*, 1988) (**Figure 54**). *Awaous* was included in Sicydiinae by presenting the first pterygiophore of the first dorsal fin associated with the third vertebra and the others associated with the other vertebrae following the formula (12210) (**Figure 55**); 10 thoracic and 16 abdominal vertebrae; one epural and the first two pterygiophores of the anal fin located anteriorly to the first hemal spine. However, there is a disagreement between the authors. Pezold in BIRSONG et al. (1988), argued that *Awaous* should be included in *Gobionellus* group of the subfamily Gobiinae due to characteristics associated with superficial neuromast lines (BIRDSONG *et al.*, 1988).

Awaous was then postulated as the sister group of Sicydiinae and Gobionellinae (HARRISON, 1989), being excluded from the Sicydiinae due to the presence of a non-dorsally

expanded premaxilla. In addition, the palatine in *Awaous*, although long, has a smaller ethmoidprocess, ectopterygoid and quadrate with a more generalized morphology and a preopercle that does not expand anteriorly in the same way as in the Sicydiinae (HARRISON, 1989). Since *Awaous* share several characteristics related to the external morphology and life-style with Sicydiinae, it was proposed as sister group of the sub-family.

-	DF	(N)	v	(N)	EPU	(N)	AP	(N)
Awaous	3-12210	(18)	10+16=26	(18)	1	(18)	2	(18)
Evorthodus	3-12210	(15)	10+16=26 10+17=27	(15)	1	(16)	2	(16)
Lentipes	3-12210	(4)	10+16=26	(4)	1	(4)	2	(4)
Sicydium	3-12210	(12)	10+16=26	(12)	1	(12)	2	(12)
Sicyopterus	3-12210	(14)	10+16=26	(14)	I	(14)	2	(14)
Sicyopus*	3-12210		10+16=26					
Stiphodon	3-12210	(20)	10+16=26	(20)	1 2	(19) (1)	3 2	(14) (4)

Figure 54 – Table indicating members of the Sicydium group (*sensu* BIRDSONG *et al.*, 1988). DF: first dorsal fin pterygophores insertion formula; V: total vertebrae, including thoracic + abdominal; EPU: number of epurals; AP: number of anal fin pterygophores located anteriorly to the first hemal spine.



Figure 55 - Distribution pattern of the first dorsal fin pterygiophores (adapted from BIRDSONG et al., 1988).

Within Gobionellinae *Stenogobius* was proposed as the sister group of all remaining genera, and the sub-family was divided into two groups, the *Ctenogobius* lineage with *Evorthodus*, *Gobioides* and *Gobionellus*, among others and the *Oxyurichthys* lineage, including *Oxyurichthys* and members of Amblyopinae and Oxudercinae (*sensu* PEZOLD, 1993).

Subsequently, Parenti and Maciolek (1993) defined Sicydiinae based on six synapomorphies: (1) rounded pelvic disc with posteriorly rounded pelvic bones and thickened, highly branched pelvic-fin rays, and thickened pelvic-fin spine; (2) fleshy pads at posterior tips of pelvic-fin spines; (3) pelvic-fin spine and first ray close together at their proximal ends, and separated from remaining four pelvic-fin rays (**Figure 53**); (4) palatine bone with long dorsal

process that articulates with lateral ethmoid; (5) dorsal expansion of premaxilla, no differentiation between ascending and articular processes, and reduction in rostral cartilage e (6) adnate tongue. Since *Awaous* lacks all of these characteristics it was not included in Sicydiinae.



Figure 56 – Main differences in pelvic fins between A: *Awaous sp.* and B: *Sicyopus fehlmann*i (extracted from PARENTI; MACIOLEK, 1993). Pb: pelvic bone; ps: pelvic spine and pr: branched pelvic rays. The arrow indicates the separation between the first and second branched rays of the pelvic fin.

In 1993, Pezold defined the subfamily Gobiinae from inferred synapomorphies of cephalic sensory canal characteristics. The subfamily Gobionellinae, however, consisted only of a small assemblage of convenience, with no supporting synapomorphies.

Parenti and Thomas (1998) listed more synapomorphies for Sicydiinae including: (1) pelvic fin spine articulating directly with bone and in slightly perpendicular position and (2) basiyial in subretangular. *Awaous* was considered closely related to *Gnatholepis* and *Stenogobius* and Sicydiinae was considered sister group to a clade formed by *Rhinogobius* and *Tukugobius* (**Figure 57**).

Larson (2001) proposed Awaous within Gobionellinae in a clade called "Stenogobius group" (Figure 58) containing Awaous; Stenogobius Bleeker, 1874; Evorthodus Gill, 1859; Ctenogobius Gill, 1858; Gnatholepis Bleeker, 1874; Oligolepis Bleeker, 1874; Oxyurichthys Bleeker, 1857; Gobionellus Girard, 1858; Gobioides Lacepède, 1800 and Rhinogobius Gill, 1859. The group differs from the Mugilogobius group, another group within Gobionellinae, by the following characters: (A) anterior nasal opening present; (B) absence of villi in the head; (C) absence of infraorbital pores and (D) a modal pattern of transverse cephalic superficial 116 neuromast lines. The *Stenogobius* group was reaffirmed by Pezold (2004). Larson (2001) and Pezold (2004) did not included representatives of Sicydiinae in their analyses.



Figure 57 – Phylogenetic relations between Gobionellinae and Sicydiinae, (extracted from PARENTI; THOMAS, 1998).



Figure 58 – **Figure 58** – Phylogenetic relationships between some of the members of the *Stenogobius* group (*sensu* LARSON, 2001) (adapted from Larson, 2001).

Wang *et al.* (2001) using molecular data, considered *Stenogobius* a clade closely related to Sicydiinae and distantly related to other Gobionellinae taxa. They also considered a clade formed by *Stenogobius* plus Sicydiinae as sister group to *Oligolepis*, *Rhinogobius* and representatives of Oxudercinae and Amblyopinae. This big clade was called Gobionellinae. According to Gill and Mooi (2012) this decision was unwarranted since it predates Oxudercidae, Amblyopina and Trypauchenina.

Thacker (2003), also using molecular data, suggested the clade *Awaous* plus *Stenogobius* as sister to other Sicydiinae. It was also suggested that *Awaous* is more closely related to the subfamily Sicydiinae and that *Stenogobius* lies at the base of this clade, sister group to other Gobionellinae (*sensu* PEZOLD, 1993) (THACKER, 2009; 2013; 2015). This clade was then called "*Stenogobius* lineage" (Figure 59).



Figure 59 – Stenogobius lineage (sensu THACKER, 2013) (extracted from Thacker, 2013).

Keith *et al.* (2011), once again using molecular data, performed a phylogenetic analysis of the members of Sicydiinae. In this analysis, *Awaous* was considered the sister group of Sicydiinae (sensu THACKER, 2009). Such analysis placed *Cotylopus* Guichenot, 1863 at the base of the whole subfamily, named "Clade C". *Sicydium* Valenciennes, 1837, and *Sicyopterus* Gill, 1860 formed a later derivative clade called "Clade D". *Lentipes* Günther, 1861, *Akihito* Watson, Keith & Marquet, 2007 and one of the species of *Sicyopus* Gill, 1863 genera *Stiphodon* Weber, 1895, "Clade F" and some *Sicyopus* species "clade G" (KEITH *et al.*, 2011) (**Figure 60**).Caires (2012) performed a phylogenetic reconstruction of *Microphilypnus* Myers, 1927, using Gobiidae as an external group. His phylogeny recovered *Awaous* closely related to *Gnatholepis* being this clade sister group to *Evorthodus*, *Gobionellus* and *Gobioides*. Unfortunately, *Stenogobius* and Sicydiinae were also not included in this analysis.



Figure 60 – Phylogenetic reconstruction of Sicydiinae (adapted from KEITH et al., 2011).

Subsequently Agorreta and Ruber (2012) again proposed *Awaous* as the sister group of *Stenogobius* forming a clade called "Gobionellinae *clade III*", which was sister to the Sicydiinae clade. Together, these two formed the sister group of some other genera of Gobionellinae (*sensu* PEZOLD, 1993), placed in "Gobionellinae clade III" (**Figure 61**).



Figure 61 – Cladogram showing a hypothesis of division of the Gobionellinae. *Awaous* and *Stenogobius* form a clade called "Gobionellinae *clade III*" (extracted from AGORRETA; RÜBER, 2012).

Posteriorly, Agorreta (2013), again using molecular data, placed Awaous in the Gobionellinae-like division (sensu AGORRETA et al., 2013) (Figure 62). Awaous (Chonophorus) banana (Valenciennes 1837) was then considered sister group to Stenogobius sp. and this clade the sister clade of Awaous (Euctenogobius) flavus (Valenciennes 1837) both figuring as sister group to Sicydiinae. The whole clade was considered sister to a clade formed by genera currently placed in Gobionellinae (sensu PEZOLD, 1993) the junction of both clades would form the Stenogobius lineage (sensu AGORRETA et al., 2013) (Figure 63). Tornabene (2013) in his concatenated dataset of nuclear genes recovered the same previous results (AGORRETA; RÜBER, 2012). However, the tree generated using rhodopsin dataset recovered Awaous at the basis of the clade including Stenogobius and other Sicydiinae (Figure 64).



Figure 62 – Proposed relationships within Gobiidae, *Awaous* figures within Gobionellinae-like in a lineage represented by *Oxyurichthys stigmalophius* Mead & Böhlke, 1958 (extracted from AGORRETA *et al.*, 2013).



Figure 63 – Positioning of Awaous within "Stenogobius lineage" (sensu AGORRETA et al., 2013) (extracted from AGORRETA et al., 2013).



Figure 64 – Cladogram containing the phylogenetic relationships within part of the Gobiidae family using rhodopsin dataset (extracted from TORNABENE, 2013).

2.2. OBJECTIVE

• Understand the phylogenetic relationships of the subgenus *Awaous* (*Chonophorus*) by comparison with other species allocated at the *Stenogobius* lineage (*sensu* AGORRETA *et al.*, 2013).

2.3. MATERIAL AND METHODS

2.3.1. Material examined

The original idea was to include the majority of representatives of *Awaous* and genera considered cloded related to this genus in the past. The intention was to include the type species of each genera, following the recommendation of Prendini (2001).

Rhyacichthys aspro (Valenciennes, 1837) was included in the analysys for being considered the type species of the Rhyacichthydae subfamily, considered the basal family within Gobioidei (MILLER, 1973). *Odontobutis obscurus* (Temminck & Schlegel, 1845) is considered the type species of Odontobutidae family, currently also considered a basal family within Gobioidei (GILL; MOOI, 2012). *Eleotris* is currently the type genus of the family Eleotridae considered a sister family to Gobiidae (MILLER, 1973), thus were also included in

the analisys. Unforntunately the type species of *Eleotris* was not available, thus *Eleotris perniger* (Cope, 1871), were choosed representing the genus.

All exemplars of Awaous (Chonophorus) were included, Awaous (Euctenogobius) flavus was included representing the monotypic subgenus Awaous (Euctenogobius), Awaous (Awaous) ocellaris was included representing Awaous (Awaous) ocellaris group (sensu WATSON, 1992) and Awous (Awaous) commersoni was picked since it is the type species of the Awaous (Awaous) nigripinnis group (sensu WATSON, 1992).

Gobioides, Gobionellus, Oxyurichthys and Stenegobius were included as representatives of Gobionellinae "clade II" (sensu AGORRETA; RÜBER, 2012). The type species of Stenogobius were not available, thus Stenogobius (Insularigobius) genivittatus (Valenciennes, 1837) were examined representing the subgenus Stenogobius (Insularigobius) and Stenogobius (Stenogobius) laterisquamatus (Weber, 1907) were analyzed representing the Stenogobius (Stenogobius) subgenus. The type species of Oxyurichthys was not available, thus Oxyurichthys cornutus McCulloch & Waite, 1918 were choosed representing the genus.

Cotylopus Guichenot, 1863, *Lentipes* Günther, 1861, *Sicydium* Valenciennes, 1837 and *Sicyopterus* Gill, 1860 were picked representing the Sicydiinae subfamily (*sensu* PARENTI; MACIOLEK, 1993). The type species of *Sicyopterus* were also not available, thus *Sicyopterus longifilis* de Beaufort, 1912, was choosed representing this genus.

The Gobiinae subfamily was choosed as an external clade to Gobionellinae and Sicydiinae. *Gobius* Linnaeus, 1758 and *Bathygobius* Bleeker, 1878 were choosed representing the subfamily. The type species of *Bathygobius* were not available, thus *Bathygobius soporator* (Ginsburg, 1947) were choosed as a representative of the genus.

Awaous (Awaous) commersonii (Schneider in Bloch & Schneider, 1801):

MNHN 0558: 1 of 4 musc. 82.7 mm SL. Reunion island. 1998.

Awaous (Awaous) ocellaris (Broussonet 1782):

NMNH 52381: 1 of 5 musc. 90.3 mm SL. Samoa, Apia. Year not informed.

Awaous (Chonophorus) banana:

UCR 1352-8: 1 of 10 musc. 87 mm SL. Costa Rica, Limón, Hone Creek, 6 km W of Puerto Viejo. 1981. UCR 1352-8: 1 of 10 C&S. 61.2 mm SL. Costa Rica, Limón, Hone Creek, 6 km W of Puerto Viejo. 1981.

UCR 1144-6: 1 of 4 C&S. 58.8 mm SL. Costa Rica, Limón, Río Cocolis, 3.5 km SE of Shiroles, on Bratsi-Shiroles road. 1977.

Awaous (Chonophorus) lateristriga:

NMNH 292655: 1 of 3 musc. 68.8 mm SL. Sierra Leone, Foya Village, Tabe River, 16 mi. Southeast of Bo. 1962. **CAS** 214661: 2 of 2 C&S. 58.8 – 49.3 mm SL. Sao Tome and Principe, Sao Tome, Praia das conchas, near mouth, tidal mudflat area. 2001.

Awaous (Chonophorus) tajasica:

NMNH 272626: 4 of 16 musc. 182 – 152 mm SL. Brazil, Ceara, Reservoir at Pentecoste, Ceara. 1966. LIRP 1074: 2 of 21 musc. 90.4 – 88.6 mm SL. São Paulo, Ubatuba, rio Indaiá. 1984. LIRP 5745: 1 of 3 C&S. 74 mm SL. São Paulo, São Sebastiao, rio Paúba. 2004. LIRP 549: 1 C&S. 83.6 mm SL. Rio de Janeiro, Parati, rio Pedra Branca, faz. Muricana, Perequê-Açu. 1995.

Awaous (Chonophorus) transandeanus:

UCR 121-3: 1 of 8 musc. 76.6 mm SL. Costa Rica, Puntarenas, rio Agujas, 3 Km from the coast on Tárcoles-Jacó road. 1967. UCR 121-3: 1 of 8 C&S. 72.6 mm SL. Costa Rica, Puntarenas, rio Agujas, 3 Km from the coast on Tárcoles-Jacó road. 1967. UCR 101-14: 1 of 5 C&S. 64.1 mm SL. Costa Rica, Puntarenas, rio Nuevo, 12 km E of the río Claro village at Interamerican Highway. 1967.

Awaous (Euctenogobius) flavus:

CAS 78681: 2 of 2 C&S 34.5 – 33.6 mm SL. Colombia, puerto del rio cienega (marsh) on central rio Magdalena. Year not informed. **NMNH** 404258: 1 of 3 musc. 39.1 mm SL. French Guyana, Cayuni river. 2011.

Bathygobius soporator (Ginsburg, 1947):

LIRP 1414: 1 of 107 musc. 53.4 mm SL. Brasil, São Paulo, São Sebastião, entre a praia do Zimbro e a Praia Grande. 1996. **LIRP** 1414: 1 of 107 C&S. 60.6 mm SL. Brasil, São Paulo, São Sebastião, entre a praia do Zimbro e a Praia Grande. 1996.

Cotylopus acutipinnis Guichenot, 1863:

MNHN 1984-0809: 1 of 20 alc. 50.2 mm SL. Reunion. 1982. **MNHN** 1984-0809: 1 of 20 musc. 52.5 mm SL. Reunion. 1982.

Eleotris perniger (Cope, 1871):

NMNH 314440: 1 of 56 musc. 81.1 mm SL. Santo Domingo, Provincia San Pedro de Macoris, 5.5 km North Los Montones, headwater of creek feeding into rio Almirante. 1989. **NMNH** 314440: 1 of 56 C&S. 60.7 mm SL. Santo Domingo, Provincia San Pedro de Macoris, 5.5 km North Los Montones, headwater of creek feeding into rio Almirante. 1989.

Evorthodus lyricus (Girard, 1858):

MNHN 2016- 0618: 1 alc. 41.7 mm SL. French Guiana, Sinnamary, river mouth. 1982. **MZUSP** 66355: 1 de 2 musc. 54.6 mm SL. Brasil, Rio de Janeiro, Atafona, Ilha da convivência. 1964. **NMNH** 106630: 2 de 5 alc. 49 – 40.9 mm SL. Caribbean Sea, Virgin Island, St. Croix, Caledonia Stream. 1937. **NMNH** 147625: 2 alc. 60 – 50.2 mm SL. Puerto Rico, Guayanilla, Ojo de Agua, spring near central San Francisco. 1948. **NMNH** 192106: 1 of 2 C&S. 33.7 mm SL. Cuba, Havana, Province, rio de Almandarez, Marianao, 0.5 mile up rio from 23rd st. Bridge. 1953.

Gobioides broussonnetii Lacepède, 1800:

MZUSP 81124: 1 musc. 196 mm SL. Brasil, São Paulo, Iguape, exemplares coletados em Manguezal próximo à Itacapara. 2003.

Gobionellus oceanicus (Pallas, 1770):

MZUSP 66005: 1 alc. 132.5 mm CP. Brasil, São Paulo, Cananéia. 1985. NMNH 352117: 1 of 9 musc. 93.4 mm SL. Atlantic, Caribbean Sea, Jamaica, Kingston Harbor. 1934. NMNH 352117: 2 of 9 C&S. 72.4 4 – 69.3 mm SL. Atlantic, Caribbean Sea, Jamaica, Kingston Harbor. 1934.

Gobius niger Linnaeus, 1758:

NMNH 298489: 1 of 30 musc. 71.9 mm SL. Atlantic, Mediterranean Sea, St. George Bay, St. George Bay, R. of Lebanon. 1964.

Lentipes concolor (Gill, 1860):

NMNH 316119: 2 of 9 C&S. 46,1 – 48.6 mm SL. Hawai, Maui, Honolewa stream below wailua falls. 1991. NMNH 316119: 1 of 9 musc. 67.9 mm SL. Hawai, Maui, Honolewa stream below wailua falls. 1991.

Odontobutis obscurus (Temminck & Schlegel, 1845):

MZUSP 122849: 1 alc. 72.9 mm SL. Japan, Ehime-ken, Kamiekena Gun. 1979. MZUSP 122849: 1 musc. 77.6 mm SL. Japan, Ehime-ken, Kamiekena Gun. 1979

Oxyurichthys cornutus McCulloch & Waite, 1918:

NMNH 372811: 2 of 37 C&S. 62.3 – 59.5 mm SL. Republic of Philippines, Siquijor island., Tidal inlet at Sabanj. 1979. **NMNH** 372811: 4 of 37 musc. 79.2 mm SL. Filipinas, entrada de Maré em Sabanj, ilha de Siquijor. Maio de 1979.

Rhyacichthys aspro (Valenciennes, 1837):

NMNS 97135: 1 alc. 71.6 mm SL. Japan, Ryukyu island, Yaeyama group, Okynawa, Taketomi, Yutsun-gawa river. NMNH 371845: 1 musc. 59.9 mm SL. Taiwan. Date not informed.

Sicydium plumieri (Bloch, 1786):

MNHN 1998-0587: 1 alc. 91.3 mm SL. 1997. **ANSP** 144696: 1 of 2 musc. 63 mm SL. Puerto rico. Year not informed. **NMNH** 144033: 1 of 28. 73 mm SL. Caribbean Sea, Mameyes river, at the Y.M.C.A. Boys Camp, Palmer, Puerto Rico. **NMNH** 313724: 1 of 2 C&S. 73.3 mm SL. Atlantic, Caribbean Sea, Dominica, B.W.I., foot of Tra-Falgar falls and portion of trois pitons river behind hydro-electric station. 1964.

Sicyopterus longifilis de Beaufort, 1912:

MZB 24873: 1 of 5 alc. 79,5 mm CP. Island of Sulawesi, Province of Sulawesi Tengah, Kabupaten Tojo Una-una, Kecamatan Tojo, Tojo River. 2017.

Sicyopterus calliochromus Keith, Allen & Lord, 2012:

NMNH 313859: 1 of 6 musc. Indonesia, New Guinea, Irian Jaya, Northwest tip Waigeo Island between Tg. Manganeki and Tg. Boropen. 1979.

Stenogobius (Insularigobius) genivittatus (Valenciennes, 1837):

NMNH 278704: 1 of 18 alc. 63.9 mm SL. Pacific, Moorea Island, Society Islands, French Polynesia. 1986. NMNH 278704: 1 of 18 musc. 69.1 mm SL. Pacific, Moorea Island, Society Islands, French Polynesia. 1986. NMNH 278704: 2 of 18 C&S. 53.8 – 50,1 mm SL. Pacific, Moorea Island, Society Islands, French Polynesia. 1986.

Stenogobius (Stenogobius) laterisquamatus (Weber, 1907):

NMNH 298697: 1 of 10 alc. 72.8 mm SL. Papua New Guinea, Ramu river, approximately 4 km South of Bunapas Mission, Channel Between River Island + Eastern Bank. 1987. **NMNH** 298697: 1 of 10 alc. 83.9 mm SL. Papua New Guinea, Ramu river, approximately 4 km South of Bunapas Mission, Channel Between River Island + Eastern Bank. 1987. **NMNH** 298697: 2

of 10 alc. 58.1 – 58 mm SL. Papua New Guinea, Ramu river, approximately 4 km South of Bunapas Mission, Channel Between River Island + Eastern Bank. 1987.

2.3.2. Osteology

Specimens were cleared and stained following the protocol of TAYLOR AND VAN DYKE, 1985. Osteological nomenclature followed primarily Johnson and Patterson (1993) and Birdsong (1975).

Individuals of Awaous (Chonophorus) banana, Awaous (Chonophorus) lateristriga, Awaous (Chonophorus) tajasica, Awaous (Chonophorus) transandeanus), Awaous (Euctenogobius) flavus, Bathygobius soporator (Valenciennes 1837), Eleotris perniger (Cope, 1871), Gobionellus oceanicus, Oxyurichthys cornutus, Lentipes concolor, Sicyopterus longifilis, Stenogobius (Insularigobius) genivittatus and Stenogobius (Stenogobius) laterisquamatus were cleared and stained. The internship in the NMNH allowed examination of previously cleared and stained individuals of Evorthodus lyricus, Sicydium plumieri and Gobius niger.

Some exemplars obtained on loan are rare in collection and, therefore, permission for clear and stain was not granted. Thus, 3D reconstructions were performed through microtomography which allow the analysis of bone elements without damaging the material. 3D reconstruction of computed micro/nano- tomography was performed by the V/tomex P equipment, part of the FFCLRP / USP Documentation Center for Biodiversity, Biology Department. The machine analyzes the density of various layers of animal tissue allowing the differentiation between them.

3D reconstruction was performed in individuals of *Awaous* (*Awaous*) ocellaris, *Awaous* (*Awaous*) commersonii, Evorthodus lyricus, Sicydium plumieri, Cotylopus acutipinnis and *Rhyacichthys aspro*.

2.3.3. Myology

The specimens were stained following the protocol proposed by Datovo & Vari (2013), dissected and photographed.

Photographs were taken using Canon EOS 5D camera with Canon EF 100 mm macro and Canon MP-E 65 mm super macro lens and Zeiss Stereo Discovery.V12 stereomicroscope with attached Zeiss Axio-Cam HRc digital camera. Photographs were then edited in Adobe Photoshop CC and Adobe Illustrator CC. Illustrations were prepared using Wacom One digital pen tablet and Adobe Illustrator CC.

Nomenclature followed Datovo & Vari (2013) and Datovo & Rizzato (2018).

2.3.4. Phylogenetic Reconstruction

The morphological matrix of characters was made using Microsoft Excel 365 and notepad ++. Characters were ordinated from 0 to 75, respecting TNT default. Characters 0 to 5 were rescaled in a range from zero to one to avoid differences in the weighing. Characters: 19, 25, 41, 42, 62, 64 and 67 were ordinated to respect the parsimony in transformation series. Trees were generated using TNT software (GOLOBOFF *et al.*, 2008). The most parsimonious trees were obtained using exhaustive search and indexes were obtained using the script *statsall* (designed by Peterson L. Lopes).

Root was set in *Rhyacichthys aspro*, a basal representative of Gobioidei (MILLER, 1973; GILL; MOOI, 2012).

2.4. RESULTS

2.4.1. Morphometric characters

Character 0. Snout, length, proportion in relation to head length (adapted from Valenciennes (1837)).

Character states: from 0 to 1 (Table 57).

Valenciennes (1837) reported that "a small group of gobies could be divided under the name of *Awaous* due to their longer faces and distant eye position". Thus, the snout length, as a proportion of the head length, was compared throughout the lineages to verify if it is in fact a synapomorphy for *Awaous*.

Character 1. Upper lip, thickness, proportion in relation to head length (adapted from Larson (2001), character: 25).

Character states: from 0 to 1 (Table 57).

Larson (2001) discriminated thick and thin lips. Herein, lip thickness is presented as a proportion of head length. The measure of lip thickness was taken from the tip of the lip to the anterior margin of the mesethmoid.

Character 2. First dorsal fin, length, proportion in relation to standard length.

Character states: from 0 to 1 (**Table 57**).

The length of the fins in the examined taxa was highly variable, thus the length of dorsal fins was analyzed. The length of first dorsal fin was considered as a proportion of the standard length, was included in the list of characters in order to help in the phylogenetic reconstruction.

Character 3. Second dorsal fin, length, proportion in relation to standard length. Character states: from 0 to 1 (**Table 57**).

Second dorsal fin, as a proportion of the standard length, was also included.

Tomainal	Character							
Terminai	0	1	2	3				
Rhyacichthys aspro	0.51	0.11	0.16	0.16				
Odontobutis obscurus	0.22	0.04	0.12	0.15				
Eleotris perniger	0.19	0.05	0.13	0.16				
Bathygobius soporator	0.25	0.10	0.12	0.23				
Gobius niger	0.23	0.10	0.14	0.31				
Evorthodus lyricus	0.29	0.07	0.14	0.34				
Gobioides broussonnetii	0.23	0.05	0.15	0.49				
Gobionellus oceanicus	0.28	0.05	0.16	0.42				
Oxyurichthys cornutus	0.29	0.07	0.14	0.38				
Stenogobius (Insularigobius) genivittatus	0.32	0.05	0.14	0.31				
Stenogobius (Stenogobius) laterisquamatus	0.28	0.03	0.15	0.29				
Cotylopus acutipinnis	0.40	0.13	0.16	0.26				
Lentipes concolor	0.42	0.10	0.13	0.26				
Sicydium plumieri	0.37	0.18	0.15	0.26				
Sicyopterus longifilis	0.43	0.12	0.17	0.28				
Awaous (Awaous) commersonii	0.39	0.09	0.13	0.24				
Awaous (Awaous) ocellaris	0.39	0.13	0.15	0.27				
Awaous (Chonophorus) banana	0.36	0.18	0.12	0.26				
Awaous (Chonophorus) lateristriga	0.34	0.17	0.10	0.25				
Awaous (Chonophorus) tajasica	0.36	0.15	0.11	0.27				
Awaous (Chonophorus) transandeanus	0.39	0.13	0.14	0.29				
Awaous (Euctenogobius) flavus	0.38	0.16	0.05	0.13				

Table 56 – Morphometric characters in examined taxa, characters 0 and 1 are presented as a ratio of the head length and characters 2 and 3 as a ratio of the standard length.

Terminal	Character							
Terminar	0	1	2	3				
Rhyacichthys aspro	1.00	0.53	0.93	0.08				
Odontobutis obscurus	0.09	0.05	0.56	0.06				
Eleotris perniger	0.00	0.14	0.65	0.07				
Bathygobius soporator	0.17	0.44	0.58	0.28				
Gobius niger	0.12	0.46	0.78	0.48				
Evorthodus lyricus	0.32	0.26	0.76	0.57				
Gobioides broussonnetii	0.12	0.13	0.80	1.00				
Gobionellus oceanicus	0.29	0.13	0.92	0.80				
Oxyurichthys cornutus	0.30	0.25	0.79	0.70				
Stenogobius (Insularigobius) genivittatus	0.39	0.11	0.71	0.51				
Stenogobius (Stenogobius) laterisquamatus	0.29	0.00	0.80	0.45				
Cotylopus acutipinnis	0.67	0.65	0.93	0.34				
Lentipes concolor	0.72	0.46	0.69	0.36				
Sicydium plumieri	0.57	1.00	0.86	0.36				
Sicyopterus longifilis	0.75	0.56	1.00	0.41				
Awaous (Awaous) commersonii	0.63	0.40	0.68	0.29				
Awaous (Awaous) ocellaris	0.62	0.64	0.82	0.38				
Awaous (Chonophorus) banana	0.55	0.99	0.61	0.34				
Awaous (Chonophorus) lateristriga	0.48	0.89	0.43	0.31				
Awaous (Chonophorus) tajasica	0.52	0.75	0.46	0.37				
Awaous (Chonophorus) transandeanus	0.64	0.66	0.71	0.42				
Awaous (Euctenogobius) flavus	0.59	0.85	0.00	0.00				

Table 57 – Normalized data for morphometric characters in examined taxa.

2.4.2. Meristic characters

Character 4. Second dorsal fin, number of rays (adapted from Larson (2001), character: 10).

Character states: from 0 to 1 (Table 58).

Larson (2001) correlated the fin ray counts for second dorsal fin and anal fin, treating them as a single character. Herein fin ray counts were analyzed separately to better represent the homology of the rays. The number of rays in the second dorsal fin varied from seven in *Rhyacichthys* and *Odontobutis* to 17 in *Gobioides*.

Character 5. Anal fin, number of rays: 6 – 16 (adapted from Larson (2001), character: 10).

Character states: from 0 to 1 (Table 58).

The number off rays was also examined, varying from 6 in *Rhyacichthys* to 16 in *Gobioides*.

Character 6. Branchiostegal ray, number (AKIHITO, 1969; SPRINGER, 1983; GILL; MOOI, 2012).

Character states: (0) 6 rays, (1) 5 rays.

Gill and Mooi (2012) suggested that the presence of five branchiostegal rays would be a synapomorphy for Gobiidae. In fact, only *Rhyacichthys*, *Odontobutis* and *Eleotris* presented six branchiostegal rays, while other taxa had only five.

Character 7. Spines in first dorsal fin, number (BÖHLKE; ROBINS, 1968).

Character states: (0) 7 spines, (1) 6 spines.

This characteristic was mentioned by Böhlke and Robins (1968) to refer to Atlantic gobies. *Rhyacichthys*, *Odontobutis* and *Eleotris* have seven spines in the first dorsal fin while other genera have six.

Terminal		Character								
1 et fillitat	4	4n	5	5n	6	7				
Rhyacichthys aspro	7	0.00	6	0.00	0	0				
Odontobutis obscurus	7	0.00	7	0.10	0	0				
Eleotris perniger	9	0.20	9	0.30	0	0				
Bathygobius soporator	10	0.30	9	0.30	1	1				
Gobius niger	12	0.50	12	0.60	1	1				
Evorthodus lyricus	11	0.40	12	0.60	1	1				
Gobioides broussonnetii	17	1.00	16	1.00	1	1				
Gobionellus oceanicus	14	0.70	15	0.90	1	1				
Oxyurichthys cornutus	13	0.60	14	0.80	1	1				
Stenogobius (Insularigobius) genivittatus	12	0.50	12	0.60	1	1				
Stenogobius (Stenogobius) laterisquamatus	11	0.40	11	0.50	1	1				
Cotylopus acutipinnis	11	0.40	11	0.50	1	1				
Lentipes concolor	11	0.40	11	0.50	1	1				
Sicydium plumieri	11	0.40	11	0.50	1	1				
Sicyopterus longifilis	11	0.40	11	0.50	1	1				
Awaous (Awaous) commersonii	11	0.40	11	0.50	1	1				
Awaous (Awaous) ocellaris	11	0.40	11	0.50	1	1				
Awaous (Chonophorus) banana	11	0.40	11	0.50	1	1				
Awaous (Chonophorus) lateristriga	11	0.40	11	0.50	1	1				
Awaous (Chonophorus) tajasica	11	0.40	11	0.50	1	1				

Table 58 – State of meristic characters in examined taxa. 4n: normalized data for character 4; 5n: normalized datafor character 5.

2.4.3. Oral papillae

Character 8. Post-dental membrane, oral papillae, presence.

Character states: (0) present, (1) absent.

All examined taxa except *Gobionellus*, *Cotylopus*, *Sicydium* and *Sicyopterus* have papillae in this region.

Character 9. Vomerine region, oral papillae, presence.

Character states: (0) present, (1) absent

Papillae in this region are present in the majority of analyzed taxa, except in *Cotylopus*, *Lentipes*, *Sicydium*, *Gobionellus* and *Stenogobius* (*Stenogobius*) laterisquamatus.

Character 10. Vomerine region, oral papillae, form.

Character states: (0) digitiform, (1) conical.

All species of *Awaous* except *A*. (*Euctenogobius*) *flavus* have conical papillae in the vomerine region. Other examined taxa have digitiform papillae in this region.

Inapplicability: This character does not apply to taxa lacking oral papillae in the vomerine region.

Character 11. Parasphenoid region, oral papillae, presence.

Character states: (0) present, (1) absent.

Among examined taxa only *Gobioides*, *Oxyurichthys*, *Evorthodus*, *Bathygobius*, *Gobius* and *Eleotris* lack papillae in the parasphenoid region.

Character 12. Parasphenoid region, oral papillae, form.

Character states: (0) digitiform, (1) conical.

Papillae in the parasphenoid region are conical in all species of *Awaous*, except *A*. (*Euctenogobius*) *flavus*. *Sicyopterus* also have conical papillae in this region, whereas they are digitiform in all other examined taxa.

Inapplicability: This character does not apply to taxa lacking oral papillae in the parasphenoid region.

Character 13. Posterior region of the palate, oral papillae, presence.

Character states: (0) present, (1) absent.

Oral papillae are absent in the posterior region of the palate only in *Evorthodus*, *Gobionellus*, *Stenogobius* (*Stenogobius*) *laterisquamatus* and *Sicydium*.

Character 14. Posterior region of the palate, oral papillae, form.

Character states: (0) digitiform, (1) conical.

Papillae at the posterior region of the palate are digitiform in *Rhyacichthys*, *Eleotris*, *Bathygobius*, *Gobioides*, *Stenogobius* (*Insularigobius*) genivittatus, *Cotylopus*, *Lentipes* and *Sicyopterus*, being conical in *Awaous* except for *A*. (*Euctenogobius*) flavus.

Inapplicability: this character does not apply to taxa lacking papillae in the posterior region of the palate.

Character 15. Posterior region of the palate, conical oral papillae, form.

Character states: (0) single, (1) branched.

Conical papillae in the posterior region of the palate are single in *Awaous (Awaous)* commersonii and A. (Chonophorus) lateristriga, being branched in other representatives of *Awaous*. It was not possible to infer the States of this character in *Sicyopterus longifilis*, since the papillae were poorly preserved in the examined exemplar.

Inapplicability: this character does not apply to taxa lacking conical papillae in the posterior region of the palate.

Tamainal	Character									
Terminal Rhyacichthys aspro Odontobutis obscurus Eleotris perniger Bathygobius soporator Gobius niger Evorthodus lyricus Gobioides broussonnetii	8	9	10	11	12	13	14	15		
Rhyacichthys aspro	0	0	0	0	0	0	0	-		
Odontobutis obscurus	0	0	0	0	0	0	-	?		
Eleotris perniger	0	0	0	1	-	0	0	-		
Bathygobius soporator	0	0	0	1	-	0	0	-		
Gobius niger	0	0	0	0	0	0	0	-		
Evorthodus lyricus	0	0	0	1	-	1	-	-		
Gobioides broussonnetii	0	0	0	1	-	0	0	-		
Gobionellus oceanicus	1	1	-	0	0	1	-	-		

 Table 59 – State of oral papillae characters in examined taxa. Traces represent inapplicable characters (-). Question marks (?) represent missing data.

Torminal		Character									
1 erminal	8	9	10	11	12	13	14	15			
Oxyurichthys cornutus	0	0	0	1	-	1	-	-			
Stenogobius (Insularigobius) genivittatus	0	0	0	0	0	0	0	-			
Stenogobius (Stenogobius) laterisquamatus	0	1	-	0	0	1	-	-			
Cotylopus acutipinnis	1	1	-	0	0	0	0	-			
Lentipes concolor	0	1	-	0	0	0	0	-			
Sicydium plumieri	1	1	-	0	0	1	-	-			
Sicyopterus longifilis	1	0	0	0	1	0	0	?			
Awaous (Awaous) commersonii	0	0	1	0	1	0	1	0			
Awaous (Awaous) ocellaris	0	0	1	0	1	0	1	1			
Awaous (Chonophorus) banana	0	0	1	0	1	0	1	1			
Awaous (Chonophorus) lateristriga	0	0	1	0	1	0	1	0			
Awaous (Chonophorus) tajasica	0	0	1	0	1	0	1	1			
Awaous (Chonophorus) transandeanus	0	0	1	0	1	0	1	1			
Awaous (Euctenogobius) flavus	0	0	0	0	0	0	0	-			

2.4.4. Scale patterns

Character 16. Chest region, scales, presence (adapted from Caires (2012), character: 144).

Character states: (0) absent, (1) present.

Caires (2012) mentioned the importance of presence of scales in the ventral region. Herein only scales in the chest region were analyzed. *Rhyacichthys, Awaous (Chonophorus) tajasica, Awaous (Chonophorus) lateristriga, Awaous (Euctenogobius) flavus, Gobioides, Lentipes, Cotylopus, Sicydium* and *Sicyopterus* lack scales in the chest region. In other examined taxa this region is fully scaled.

Character 17. Region posterior to the first dorsal-fin spine, presence of cycloid scales (adapted from Caires (2012), character: 142).

Character states: (0) present, (1) absent.

The pre-dorsal region is usually covered with cycloid scales in examined taxa, gradually replaced by ctenoid scales posteriorly. In the most examined taxa cycloid scales are absent posterior to a vertical from the first dorsal-fin. However, in *Eleotris*, *Gobioides*, *Evorthodus*, *Gobionellus*, *Oxyurichthys*, *Cotylopus*, *Sicydium* and *Sicyopterus* cycloid scales are present posteriorly to this region.

Inapplicability: this character does not apply to *Lentipes*, it lacks scales. nor to *Rhyacichthys*, because it lacks cycloid scales in the dorsal region.

Character 18. Opercular and preopercular region, scales, presence.

Character states: (0) present, (1) absent.

Rhyacichthys, Awaous (Awaous) ocellaris, Stenogobius (Stenogobius) laterisquamatus and *Evorthodus lyricus* have scales on the opercle and preopercle. All other examined taxa lack then there.

Character 19. Base of pectoral fin, scales, presence.

Character states: (0) present, (1) absent.

Scales are present in the base of the pectoral fin in *Rhyacichthys*, *Awaous* (*Awaous*), *Stenogobius*, *Evorthodus*, *Bathygobius* and *Eleotris*. Other taxa lack scales in this region.

Tamain al	Character							
Terminal	16	17	18	19				
Rhyacichthys aspro	0	-	0	0				
Odontobutis obscurus	0	1	0	1				
Eleotris perniger	1	0	1	0				
Bathygobius soporator	1	1	1	0				
Gobius niger	1	1	1	1				
Evorthodus lyricus	1	0	0	0				
Gobioides broussonnetii	0	0	1	1				
Gobionellus oceanicus	1	0	1	1				
Oxyurichthys cornutus	1	0	1	1				
Stenogobius (Insularigobius) genivittatus	0	1	1	0				
Stenogobius (Stenogobius) laterisquamatus	1	1	0	0				
Cotylopus acutipinnis	0	0	1	1				
Lentipes concolor	0	-	1	1				
Sicydium plumieri	0	0	1	1				
Sicyopterus longifilis	0	0	1	1				
Awaous (Awaous) commersonii	1	1	1	0				
Awaous (Awaous) ocellaris	1	1	0	0				
Awaous (Chonophorus) banana	1	1	1	1				
Awaous (Chonophorus) lateristriga	0	1	1	1				
Awaous (Chonophorus) tajasica	0	1	1	1				
Awaous (Chonophorus) transandeanus	1	1	1	1				
Awaous (Euctenogobius) flavus	0	1	1	1				

Table 60 – State of scale pattern characters in examined taxa. Traces represent inapplicable characters.

2.4.5. Miscellaneous

Character 20. Mouth, position (LARSON, 2001, character: 11).

Character states: (0) inferior, (1) terminal, (2) superior.

Larson (2001) discriminated the mouth position as in inferior or terminal. Herein three categories are recognized: inferior, in *Rhyacichthys, Awaous, Stenogobius (Stenogobius) laterisquamatus, Lentipes, Cotylopus, Sicydium* and *Sicyopterus*; terminal, in *Stenogobius (Insularigobius) genivittatus, Evorthodus* and *Bathygobius;* and superior in *Eleotris, Gobius, Gobionellus* and *Oxyurichthys.*

Character 21. Floor of the mouth, tongue, fusion (HOESE, 1984; PARENTI; MACIOLEK, 1993, character: 6).

Character states: (0) tong not fused, (1) tong fused.

Hoese (1984) and Parenti and Maciolek (1993), suggested that the tong being fused to the floor of the mouth would be a synapomorphy presented by members of Sicydiinae. In addition to?? the members currently included in Sicydiinae, *Gobius, Evorthodus, Gobionellus, Oxyurichthys, Stenogobius* and *Awaous* also present the tong fused to the floor of the mouth.

Character 22. Tongue, shape (PEZOLD, 2004).

Character states: (0) triangular, (1) truncated, (2) round.

Pezold (2004) noted that tongue shape could be phylogenetic informative. *Rhyacichthys* has a triangular tongue, *Sicydium* and *Oxyurichthys* a round tongue and all other taxa a square (truncated) tongue shape.

Character 23. Inner edge of the pectoral girdle, fleshy lobes, presence (WATSON, 1992; LARSON, 2001, character: 4; PEZOLD 2004, character: 5).

Character states: (0) absent, (1) present.

Watson (1991), Larson (2001) and Pezold (2004) established that the presence of fleshy lobes on the inner edge of the pectoral girdle defines a clade formed by *Awaous* and *Stenogobius*. This is corroborated herein since among the examined genera only these two have it.

Character 24. Gills, papillae, presence (WATSON, 1992).

Character states: (0) absent, (1) present.

According to Watson (1992) the presence of sensory papillae over much of the gill structure is a unique synapomorphy of *Awaous* (Figure 1) corroborated herein.

Character 25. Caudal fin, format (VALENCIENNES, 1837).

Character states: (0) truncated, (1) oval, (1) lanceolate.

The group of "Lancettes" was initially proposed by Valenciennes (1837) based on the shape of the caudal fin. *Rhyacichthys, Bathygobius, Gobius, Awaous, Cotylopus, Lentipes, Sicydium* and *Sicyopterus* present a truncated caudal fin. In *Odontobutis, Eleotris* and *Stenogobius* the caudal fin has an oval aspect, while in *Gobioides, Gobionellus, Oxyurichthys* and *Evorthodus* this fin is lanceolate.

Character 26. Suction cup formed by the joint of the pelvic fins, format (PARENTI; MACIOLEK, 1993, character: 1).

Character states: (0) oval, (1) round.

The rounded shape of the suction cup formed by the joint of the pelvic fins was considered by Parenti and Maciolek (1993) a diagnostic character for Sicydiinae. In fact, among all analyzed taxa, it is round only *Cotylopus*, *Lentipes*, *Sicydium* and *Sicyopterus* being oval in all other examined taxa.

Inapplicability: this character does not apply to *Rhyacichthys*, *Odontobutis* and *Eleotris* because in these genera the pelvic fins are not fused.

Character 27. Membrane associated with the posterior most spine of the first dorsal fin, posterior attachment.

Character states: (0) not reaching the spine of the second dorsal fin, (1) reaching the spine of the second dorsal fin.

Posterior attachment of the membrane associated with the posterior most spine of the first dorsal fin never reaches the spine of the second dorsal fin in *Rhyacichthys*, *Odontobutis*, *Eleotris*, *Bathygobius*, *Awaous*, *Stenogobius* (*Stenogobius*) *laterisquamatus*, *Oxyurichthys*, *Cotylopus*, *Lentipes*, *Sicydium* and *Sicyopterus*. In *Gobius*, *Evorthodus*, *Gobioides*, *Gobionellus* and *Stenogobius* (*Insularigobius*) *genivittatus* this membrane attaches on the spine of the second dorsal fin.

Tampinal		Character								
Terminal	20	21	22	23	24	25	26	27		
Rhyacichthys aspro	0	0	0	0	0	0	-	0		
Odontobutis obscurus	1	0	1	0	0	0	-	0		
Eleotris perniger	2	0	1	0	0	1	-	0		
Bathygobius soporator	1	0	1	0	0	0	0	0		
Gobius niger	2	1	1	0	0	0	0	1		
Evorthodus lyricus	1	1	1	0	0	2	0	1		
Gobioides broussonnetii	2	1	1	0	0	2	0	1		
Gobionellus oceanicus	2	1	1	0	0	2	0	1		
Oxyurichthys cornutus	2	1	2	0	0	2	0	0		
Stenogobius (Insularigobius) genivittatus	1	1	1	1	0	1	0	1		
Stenogobius (Stenogobius) laterisquamatus	0	1	1	1	0	1	0	0		
Cotylopus acutipinnis	0	1	2	0	0	0	1	0		
Lentipes concolor	0	1	1	0	0	0	1	0		
Sicydium plumieri	0	1	2	0	0	0	1	0		
Sicyopterus longifilis	0	1	1	0	0	0	1	0		
Awaous (Awaous) commersonii	0	1	1	1	1	0	0	0		
Awaous (Awaous) ocellaris	0	1	1	1	1	0	0	0		
Awaous (Chonophorus) banana	0	1	1	1	1	0	0	0		
Awaous (Chonophorus) lateristriga	0	1	1	1	1	0	0	0		
Awaous (Chonophorus) tajasica	0	1	1	1	1	0	0	0		
Awaous (Chonophorus) transandeanus	0	1	1	1	1	0	0	0		
Awaous (Euctenogobius) flavus	0	1	1	1	1	0	0	0		

 Table 61 – State of external morphology characters in examined taxa. Traces represent inapplicable characters (-). Question marks (?) represent missing data.

2.4.6. Cephalic sensory system

Character 28. Oculoscapular canal, presence of discontinuity (adapted from Pezold (2004), character: 7 and Caires (2012), character: 118).

Character states: (0) absent, (1) present.

Some taxa had the oculoscapular canal interrupted between pores "H" and "K" (Figure 63). The discontinuous canal is found in *Awaous (Awaous), Awaous (Euctenogobius), Stenogobius, Gobionellus, Evorthodus, Lentipes, Bathygobius* and *Gobius*. In *Rhyacichthys, Gobioides, Cotylopus, Sicydium, Sicyopterus* and *Awaous (Chonophorus)* the canal is complete (Figure 65).

Inapplicability: *Oxyurichthys* lacks the oculoscapular canal posteriorly to the pore "G", thus this character is inapplicable. *Odontobutis* and *Eleotris* have no oculoscapular canal, so this character is also inapplicable to these taxa.

Character 29. Pore "A", presence (CAIRES, 2012).

Character states: (0) present, (1) absent.

According to Caires (2012) the presence of pore "A" would be a condition shared by Gobionellinae and Sicydiinae. *Rhyacichthys* and the analyzed taxa belonging to these subfamilies presented pore "A". In *Bathygobius* and *Gobius* this pore is absent (**Figure 66**). According to Akihito (1964) the presence of pore "A" was observed only in members of Sicydiinae, Gobionellinae and in some Butidae and Odontobutidae.

Inapplicability: *Odontobutis* and *Eleotris* have no oculoscapular canal, so this character is inapplicable to these taxa.



Figure 65 – *Gobioides broussonnetii* illustrating the pores and state of character of oculoscapular canal, along with the superficial cephalic neuromast lines. Pores are identified with capital letters, neuromast line colors and nomenclature follow the pattern presented in the methodology section of chapter 1. AN: anterior nasal opening, PN: posterior nasal opening (**MZUSP** 81124, 225.0 mm SL).



Figure 66 – *Gobius niger* illustrating the pores and state of character of oculoscapular canal, along with the superficial cephalic neuromast lines. Pores are identified with capital letters, neuromast line colors and nomenclature follow the pattern presented in the methodology section of chapter 1. AN: anterior nasal opening, PN: posterior nasal opening (**NMNH** 298489, 71.9 mm SL).

Character 30. Pore "A", position relative to the nares (adapted from Pezold (2004), character: 6).

Character states: (0) closer to the anterior nasal opening, (1) closer to the posterior nasal opening.

In *Stenogobius (Insularigobius) genivittatus* (**Figure 67**) and *Evorthodus* the pore "A" is located closer to the posterior nasal opening, while in other taxa this pore is located closer to the anterior nasal opening.

Inapplicability: *Bathygobius* and *Gobius* have no pore "A" and *Odontobutis* and *Eleotris* have no oculoscapular canal, therefore, this character is inapplicable to these taxa.



Figure 67 – *Stenogobius genivittatus* illustrating the pores and state of character of oculoscapular canal, along with the superficial cephalic neuromast lines. Pores are identified with capital letters, neuromast line colors and nomenclature follow the pattern presented in the methodology section of chapter 1. AN: anterior nasal opening, PN: posterior nasal opening (**NMNH** 278704, 63.9 mm SL).

Character 31. Pore "B", position relative to posterior nasal opening.

Character states: (0) anterior, (1) dorsal, (2) posterior.

In *Rhyacichthys*, *Sicydium* e *Sicyopterus* pore "B" is located anteriorly to the posterior nasal opening, in *Awaous* (*Chonophorus*), *Awaous* (*Awaous*), *Stenogobius*, *Cotylopus* and *Lentipes* this pore is placed dorsally to the posterior nasal opening, while in *Gobius*, *Evorthodus*, *Gobioides*, *Gobionellus*, *Oxyurichthys* and *Awaous* (*Euctenogobius*) *flavus* this pore was observed posteriorly to the posterior nasal opening.

Inapplicability: *Odontobutis* and *Eleotris* have no oculoscapular canal, thus this character is inapplicable to these taxa.

Character 32. Pore "E", presence (BIRDSONG *et al.*, 1988, LARSON, 2001, character: 41).

Character states: (0) present, (1) absent.

The absence of the pore "E" is considered characteristic of members of Sicydiinae and Gobionellinae by Birdsong *et. al* (1988) and Larson (2001). In fact, among the taxa analyzed only *Rhyacichthys*, *Gobius* and *Bathygobius* presented the pore "E" (Figure 66). In other taxa this pore is absent.

Inapplicability: *Odontobutis* and *Eleotris* have no oculoscapular canal, thus this character is inapplicable to these taxa.

Character 33. Pore "F", state of duplication (WATSON, 1996).

Character states: (0) single, (1) duplicated.

The F pore is duplicated only in *Awaous (Chonophorus) banana* (Figure 68) and *Awaous (Chonophorus) transandeanus*. In all other taxa there is a single pore "F".

Inapplicability: *Odontobutis* and *Eleotris* have no oculoscapular canal, thus this character is inapplicable to these taxa.



Figure 68 – *Awaous (Chonophorus) banana* illustrating the pores and state of character of oculoscapular canal, along with the superficial cephalic neuromast lines. Pores are identified with capital letters, neuromast line colors and nomenclature follow the pattern presented in the methodology section of chapter 1. AN: anterior nasal opening, PN: posterior nasal opening (**AMNH** 264747, 51.3 mm CP, 63,9 mm SL).
Character 34. Pore "G", presence

Character states: (0) present, (1) absent.

Pore "G" of the oculoscapular canal is absent in *Evorthodus*, *Gobionellus*, *Stenogobius* (**Figure 67**), *Lentipes* (**Figure 69**), *Cotylopus*, *Sicydium* and *Sicyopterus*. Other taxa have the pore "G" (**Figures 65**, **66** and **68**).

Inapplicability: *Odontobutis* and *Eleotris* have no oculoscapular canal, thus this character is inapplicable to these taxa.

Character 35. Pore "N", presence (adapted from Miller (1973), Larson (2001), character: 28, Pezold (2004), character: 8 and Caires (2012), character: 119).

Character states: (0) present, (1) absent.

Usually authors prefer to use the conformation of the canal as a whole in the character states (MILLER, 1973; LARSON, 2001; PEZOLD, 2004; CAIRES, 2012). The states adopted herein are the presence and absence of each pore of the opercular canal, in order to better reflect distinct homologies. Since the pore "M" is present in every taxon, the starting point was the presence of the pore "N". This pore is present in all of the examined genera, except in *Lentipes* (**Figure 69**) and *Cotylopus*.

Inapplicability: *Odontobutis*, *Eleotris* and *Oxyurichthys* have no opercular canal, thus this character is inapplicable to these taxa.

Character 36. Pore "P", presence (adapted from Miller (1973), Larson (2001), character: 28; Pezold (2004), character: 8; Caires (2012), character: 119).

Character states: (0) present, (1) absent.

Following the anterior description, in this character the presence and absence of pore "P" was observed. Only *Rhyacichthys* presented this pore, in all other taxa this pore is absent.

Inapplicability: *Odontobutis*, *Eleotris* and *Oxyurichthys* have no opercular canal, thus this character is inapplicable to these taxa.

Character 37. Pore "Q", presence (adapted from Miller (1973), Larson (2001), Character: 28; Pezold (2004), Character: 8; Caires (2012), Character: 119)

Character states: (0) present, (1) absent.

Finally, the presence and absence of pore "Q" was analyzed. This pore is also only present in *Rhyacichthys*.

Inapplicability: *Odontobutis*, *Eleotris* and *Oxyurichthys* have no opercular canal, thus this character is inapplicable to these taxa.



Figure 69 – *Lentipes concolor* illustrating the pores and state of character of opercular canal, along with the superficial cephalic neuromast lines. Pores are identified with capital letters, neuromast line colors and nomenclature follow the pattern presented in the methodology section of chapter 1. AN: anterior nasal opening, PN: posterior nasal opening (**NMNH** 316119, 63.9 mm SL).

Terminal	Character										
Terminar	28	29	30	31	32	33	34	35	36	37	
Rhyacichthys aspro	0	0	0	0	0	0	0	0	0	0	
Odontobutis obscurus	-	-	-	-	-	-	-	-	-	-	
Eleotris perniger	-	-	-	-	-	-	-	-	-	-	
Bathygobius soporator	1	1	-	1	0	0	0	0	1	1	
Gobius niger	1	1	-	2	0	0	0	0	1	1	
Evorthodus lyricus	1	0	1	2	1	0	1	0	1	1	
Gobioides broussonnetii	0	0	0	2	1	0	0	0	1	1	
Gobionellus oceanicus	1	0	0	2	1	0	1	0	1	1	
Oxyurichthys cornutus	-	0	0	2	1	0	0	-	-	-	
Stenogobius (Insularigobius) genivittatus		0	1	1	1	0	1	0	1	1	
Stenogobius (Stenogobius) laterisquamatus		0	0	1	1	0	1	0	1	1	
Cotylopus acutipinnis		0	0	1	1	0	1	1	1	1	
Lentipes concolor		0	0	1	1	0	1	1	1	1	
Sicydium plumieri	0	0	0	0	1	0	1	0	1	1	
Sicyopterus longifilis	0	0	0	0	1	0	1	0	1	1	
Awaous (Awaous) commersonii	1	0	0	1	1	0	0	0	1	1	
Awaous (Awaous) ocellaris	1	0	0	1	1	0	0	0	1	1	
Awaous (Chonophorus) banana	0	0	0	1	1	1	0	0	1	1	
Awaous (Chonophorus) lateristriga	0	0	0	1	1	0	0	0	1	1	
Awaous (Chonophorus) tajasica	0	0	0	1	1	0	0	0	1	1	
Awaous (Chonophorus) transandeanus	0	0	0	1	1	1	0	0	1	1	
Awaous (Euctenogobius) flavus	1	0	0	2	1	0	0	0	1	1	

Table 62 – State of cephalic sensory system characters in examined taxa. Traces represent inapplicable characters.

2.4.7. Superficial neuromast lines

Character 38. Superficial neuromast lines, suborbital portion, orientation (BIRDSONG *et al.*, 1988, LARSON, 2001, character 8; PEZOLD, 2004, character 9).

Character states: (0) longitudinal, (1) transversal

The orientation of the superficial neuromast lines has been vastly used in the determination of lineages within Gobiidae (BIRDSONG *et al.*, 1988; LARSON, 2001; PEZOLD, 2004). Pezold *in* Birdsong *et al.* (1988) claimed that *Awaous* would be more closely related to Gobionellinae by presenting superficial neuromast lines in a transverse orientation, disagreeing with the other authors who allocated the genus within the *Sicydium* group. An analysis of the available material revealed that *Eleotris*, *Gobius* (Figure 66), *Evorthodus*, *Gobionellus* (Figure 11), *Gobioides* (Figure 65), *Oxyurichthys*, *Stenogobius* (Figure 67), *Awaous* (Figure 68), *Lentipes* (Figure 69), *Cotylopus*, *Sicydium* and *Sicyopterus* present transverse-oriented superficial neuromast lines. Longitudinal oriented superficial neuromast

lines were only observed in *Rhyacichthys*, *Odontobutis* and *Bathygobius* (Figure 10). Since members of Sicydiinae and Gobionellinae had the suborbital neuromast lines oriented in a transversal way it is not possible to say that *Awaous* would be closely related to Gobionellinae based on this characteristic.

Character 39. Lines derived from the line *a* (*sensu* SANZO, 1911), anterior portion, number when transversally oriented.

Character states: (0) one line, (1) two lines.

Awaous (Awaous), Awaous (Chonophorus) (Figure 68), Gobioides (Figure 65), Lentipes (Figure 69), Sicydium and Sicyopterus present two lines derived from the line a anteriorly, while other taxa presented only one line derived from the line a in this region.

Inapplicability: this character does not apply to *Rhyacichthys* since it lacks the line *a* and *Odontobutis* and *Bathygobius* since in these genera lines derived from the line *a* are longitudinally oriented (**Figure 10**).

Character 40. Transverse lines derived from line *a* (*sensu* SANZO, 1911), posterior portion, number when transversally oriented.

Character states: (0) two lines, (1) one line.

Awaous (Euctenogobius) flavus, Gobioides, Gobionellus, Evorthodus and *Eleotris* have one line derived from the line *a* in the posterior region Other examined genera have two.

Inapplicability: this character does not apply to *Rhyacichthys* since it lacks the line *a*. Also, it does not apply to *Odontobutis* and *Bathygobius* since in these genera lines derived from the line *a* are longitudinally oriented.



Figure 70 – *Evorthodus lyricus* illustrating the pores and state of character of opercular canal, along with the superficial cephalic neuromast lines. Pores are identified with capital letters, neuromast line colors and nomenclature follow the pattern presented in the methodology section of chapter 1. AN: anterior nasal opening, PN: posterior nasal opening (**MZUSP** 66355, 54.6 mm SL).

Character 41. Superficial neuromast line b, posterior extension in relation to line c_4 (adapted from Pezold (2004), character: 10).

Character states: (0) not reaching line c_4 anteriorly, (1) reaching line c_4 anteriorly, (2) exceeding line c_4 anteriorly.

Pezold (2004) comments in his character 10 that the anterior extension of line *b* could be phylogenetically informative. The state (0) was found in *Awaous* (*Chonophorus*), *Awaous* (*Awaous*) ocellaris, Evorthodus, Lentipes and Sicyopterus (Figures 68 and 69). State (2) was found in *Awaous* (*Awaous*) commersonii, *Awaous* (Euctenogobius), Gobioides, Gobionellus and Oxyurichthys (Figure 65). Other taxa present the state (1). We were unable to set character state in Sicydium because lines were poorly preserved in the examined specimen.

Inapplicability: this character does not apply to *Rhyacichthys* since it lacks line *c* and *Odontobutis* and *Bathygobius* since lines are longitudinally oriented in these genera.

Character 42. Superficial neuromast line b, anterior extension in relation to transverse line c_3 (adapted from Pezold (2004), character: 10).

Character states: (0) not reaching line c_3 anteriorly, (1) reaching line c_3 anteriorly.

The state (1) was found in *Gobioides*, *Gobionellus* and *Oxyurichthys*. In *Awaous* (*Awaous*) commersonii and *Awaous* (*Euctenogobius*) flavus the line b does not reach the line c3 anteriorly. We were unable to set character state in *Sicydium* because lines were poorly preserved in the examined specimen.

Inapplicability: this character does not apply to *Rhyacichthys* as it lacks line c and *Odontobutis* and *Bathygobius* since in these genera the lines are longitudinally oriented. In addition, it does not apply to genera presenting the state (0) or (1) of character 41.

Character 43. Superficial neuromast line d, posterior extension in relation to transverse line a_1 (HARRISON, 1989).

Character states: (0) reaching line a_1 posteriorly (1) exceeding line a_1 posteriorly.

Gobioides (Figure 65), Gobionellus and Oxyurichthys (Figure 71) have the state (1), while other genera have state (0).

Inapplicability: this character does not apply to *Rhyacichthys*, *Odontobutis* and *Bathygobius* since all lack line *a1*.

Character 44. Superficial neuromast lines of the opercular series, line *os*, orientation.

Character states: (0) transversally oriented (closer to 90° angle), (1) not transversally oriented (closer to 45° angle).

Opercular line *os* is not transversally oriented in *Gobius*, *Evorthodus* (Figure 70), *Oxyurichthys* (Figure 71), *Lentipes* (Figure 69), *Sicydium* and *Sicyopterus*. In other taxa this line is transversally oriented (Figure 68).



Figure 71 – Oxyurichthys cornutus illustrating the pores and state of character of opercular canal, along with the superficial cephalic neuromast lines. Pores are identified with capital letters, neuromast line colors and nomenclature follow the pattern presented in the methodology section of chapter 1. AN: anterior nasal opening, PN: posterior nasal opening (NMNH 372810, 77.9 mm SL).

Character 45. Superficial neuromast lines on the lateral surface of the body, presence (adapted from Watson (1996)).

Character states: (0) present, (1) absent.

Lines on the lateral surface of the body are absent in Awaous (Euctenogobius), Stenogobius (Stenogobius) laterisquamatus and Sicydium. In other taxa these lines are present.

Torrainal		Character									
Terminar	38	39	40	41	haracter 1 42 43 $ 0$ $ 0$ $ 0$ $ 0$ $ 0$ $ 0$ $ 0$ $ 0$ 2 1 1 2 1 1 2 1 1 2 1 1 2 1 1 2 1 1 2 1 1 1 2 1 1 2 1 1 1 2 1 1 2 1 1 2 1 1 1 2 1 <td>43</td> <td>44</td> <td>45</td>	43	44	45			
Rhyacichthys aspro	0	-	-	-	-	-	-	0			
Odontobutis obscurus	0	0	-	-	-	-	1	0			
Eleotris perniger	1	-	1	0	-	0	0	0			
Bathygobius soporator	0	-	-	-	-	-	0	0			
Gobius niger	1	0	0	0	-	0	1	0			
Evorthodus lyricus	1	0	1	1	-	0	1	0			
Gobioides broussonnetii	1	1	1	2	1	1	0	0			
Gobionellus oceanicus	1	0	1	2	1	1	0	0			
Oxyurichthys cornutus		0	0	2	1	1	1	0			
Stenogobius (Insularigobius) genivittatus		0	0	0	-	0	0	0			
Stenogobius (Stenogobius) laterisquamatus		0	0	0	-	0	0	1			
Cotylopus acutipinnis		0	0	0	-	0	0	0			
Lentipes concolor		1	0	1	-	0	1	0			
Sicydium plumieri		1	0	?	?	0	1	1			
Sicyopterus longifilis	1	1	0	0	-	0	1	0			
Awaous (Awaous) commersonii	1	1	0	2	0	0	0	0			
Awaous (Awaous) ocellaris	1	1	0	1	-	0	0	0			
Awaous (Chonophorus) banana	1	1	0	1	-	0	0	0			
Awaous (Chonophorus) lateristriga	1	1	0	1	-	0	0	0			
Awaous (Chonophorus) tajasica	1	1	0	1	-	0	0	0			
Awaous (Chonophorus) transandeanus	1	1	0	1	-	0	0	0			
Awaous (Euctenogobius) flavus	1	0	1	2	0	0	0	1			

Table 63 – State of superficial neuromast lines characters in examined taxa. Traces represent inapplicable characters (-). Question marks (?) represent missing data.

2.4.8. Cranium

Character 46. Lateral ethmoid, dorsal margin, presence of crenulated surface (CAIRES, 2012, character: 9).

Character states: (0) absent, (1) present.

Caires (2012) affirmed that only *Awaous*, *Evorthodus* and *Ctenogobius* have the dorsal margin of the lateral ethmoid crenulated, indicating that this could be an informative feature for Gobionellinae. *Rhyacichthys*, *Odontobutis*, *Eleotris*, *Lentipes* and *Sicydium* lack a crenulated margin (0). Other genera have the dorsal surface of the lateral ethmoid crenulated in at least one region, demonstrating that this character may be present in more than one lineage of Gobiidae (Figure 72).



Figure 72 – Dorsal view of the head of *Evorthodus lyricus* (MZUSP 66355, 54.6 mm SL).

Character 47. Mesethmoid, anterolateral process, presence (adapted from Caires (2012), character: 12).

Character states: (0) absent, (1) present

Caires (2012) postulated three different states for the dorsal surface of the mesethmoid, being (0) dorsal surface without any dorsal process, (1) dorsal surface with two small triangular shaped dorsal projection and (2) dorsal surface with two large projections forming two dorsal *cornua*. We were unable to distinguish between the small and huge projections, thus herein only two states are considered, presence or absence of a dorsal process. In *Rhyacichthys*, *Odontobutis*, *Eleotris*, *Bathygobius* and *Gobius* the dorsal surface of the mesethmoid lacks any dorsal process, state (0). In all other taxa the dorsal process is present, state (1).

Character 48. Frontal, width in supraorbital region in relation to orbital diameter (adapted from Birdsong (1975); Caires (2012), character 1).

Character states: (0) width contained twice or less in orbital diameter, (1) width contained more than twice in orbital diameter.

Birdsong (1975) and Caires (2012), postulated that a large supraorbital portion of the is the a plesiomorphic state for gobioids. State (1) was found in *Rhyacichthys*, *Odontobutis* and *Eleotris*, the basal clades included in this phylogenetic analysis, but also in *Stenogobius* (*Stenogobius*) *laterisquamatus*, *Cotylopus*, *Lentipes*, *Sicydium* and *Sicyopterus*. *Gobius*, *Bathygobius*, *Awaous*, *Stenogobius* (*Insularigobius*) *genivittatus*, *Evorthodus*, *Gobionellus*, *Gobioides*, and *Oxyurichthys* have a narrow frontal in the suborbital region, state (1).

ı.

Terminal	Character						
Terminar	46	47	48				
Rhyacichthys aspro	0	0	0				
Odontobutis obscurus	0	0	0				
Eleotris perniger	0	0	0				
Bathygobius soporator	1	0	1				
Gobius niger	1	0	1				
Evorthodus lyricus	1	1	1				
Gobioides broussonnetii	1	1	1				
Gobionellus oceanicus	1	1	1				
Oxyurichthys cornutus	1	1	1				
Stenogobius (Insularigobius) genivittatus	1	1	1				
Stenogobius (Stenogobius) laterisquamatus	1	1	0				
Cotylopus acutipinnis	1	1	0				
Lentipes concolor	0	1	0				
Sicydium plumieri	0	1	0				
Sicyopterus longifilis	1	1	0				
Awaous (Awaous) commersonii	1	1	1				
Awaous (Awaous) ocellaris	1	1	1				
Awaous (Chonophorus) banana	1	1	1				
Awaous (Chonophorus) lateristriga	1	1	1				
Awaous (Chonophorus) tajasica	1	1	1				
Awaous (Chonophorus) transandeanus	1	1	1				
Awaous (Euctenogobius) flavus	1	1	1				

 Table 64 – State of cranial characters in examined taxa.

2.4.9. Jaws and Suspensorium

.

Character 49. Premaxilla, differentiation of ascending process in relation to articular process (PARENTI; MACIOLEK, 1993, character: 5)

Character states: (0) differentiated, (1) indistinct.

Parenti and Maciolek (1993) postulated that an indistinct ascending process of the premaxilla is a synapomorphy of Sicydiinae. In fact, in *Lentipes, Cotylopus, Sicydium* and *Sicyopterus* (Figure 74) the ascending process is indistinct. All other taxa have the articular process and the ascending process clearly separated (Figure 73).



Figure 73 – Medial view of palatine arch of *Stenogobius* (*Stenogobius*) *laterisquamatus* (NMNH 372810, 77.9 mm SL).



Figure 74 – Lateral view of palatine arch of Lentipes concolor (NMNH 316119, 67.1 mm SL).

Character 50. Premaxilla, indistinct ascending process, format (adapted from Parenti and Maciolek (1993), character: 5).

Character states: (0) triangular, (1) blunt

Parenti and Maciolek (1993) also commented that a blunt process could be indicative of a clade formed by *Sicydium* and *Sicyopterus*. *Lentipes* (Figure 74) and *Cotylopus* presents a process in a triangular shape, while in *Sicydium* and *Sicyopterus* (Figure 75) the blunt shape was observed.

Inapplicability: this character does not apply to taxa presenting different ascending and articular processes in the premaxilla.

Character 51. Pré-maxilla, sac of replacement teeth, presence (SAKAI; NAKAMURA, 1979; PARENTI; MACIOLEK, 1993).

Character states: (0) absent, (1) present.

Sakai and Nakamura (1979) and Parenti and Maciolek (1993) commented about the importance of a sac of replacement teeth in the premaxilla to diagnose the Sicydiinae. In the examined taxa only *Cotylopus*, *Sicydium* and *Sicyopterus* have structure (**Figure 75**), which is absent in *Lentipes* and all other examined genera.



Figure 75 – Lateral view of cheek region of Sicydium plumieri (NMNH 144033, 73 mm SL).

Character 52. Dentary, Coronoid process, format (adapted from Caires (2012), character 59).

Character states: (0) rectangular, (1) triangular

In *Gobionellus*, *Lentipes*, *Cotylopus*, *Sicydium* and *Sicyopterus* the dorsal face of the coronoid process of the dentary presents a triangular shape, while in other taxa this process is rectangular. We were unable to determine the state of this character in *Odontobutis*, because of an impossibility to observe the coronoid process in the exemplar stained for musculature.

Character 53. Dentary, number of rows of teeth (MILLER, 1973b; HARRISON, 1989).

Character states: (0) two or more, (1) only one.

Miller (1973b) and Harrison (1989) postulated that a single row of conic teeth in the dentary is a specialization of Sicydiinae. In *Rhyacichthys* and most examined taxa the dentary has several rows of teeth. A single row of teeth was only observed in *Lentipes* (Figure 74), *Cotylopus*, *Sicydium* and *Sicyopterus*.

Character 54. Dentary, teeth height in relation to the median portion of the dentary.

Character states: (0) height smaller than height of the median region of dentary, (1) at least one tooth with the height greater than height of the median region of dentary.

Usually the condition observed in examined taxa is the presence of several rows of small teeth. However, *Lentipes* (Figure 74), *Cotylopus*, *Sicydium*, *Sicyopterus* and *Bathygobius* presented at least one tooth with height greater than the height of the median region of the dentary.

Character 55. Dentary, presence of laterally oriented teeth (SAKAI; NAKAMURA, 1979; PARENTI; MACIOLEK, 1993).

Character states: (0) absent, (1) present

The presence of laterally oriented teeth in Sicydiinae is a noticeable feature. It is not clear in the literature if this is an exclusive characteristic for the whole subfamily or a characteristic defining a subgroup within Sicydiinae (see Parenti and Maciolek (1993) for further discussion). The purpose of this dissertation is not to understand the origins of laterally oriented teeth. However, this characteristic was only reported in *Lentipes*, *Cotylopus*, *Sicydium* (Figure 75) and *Sicyopterus*, taxa nowadays considered member of Sicydiinae.

Character 56. Ectopterygoid, format (HARRISON, 1989, PARENTI; MACIOLEK, (1993), character: 4; CAIRES, 2012, character: 58).

Character states: (0) triangular, (1) trapezoid.

The shape of the ectopterygoid is commonly considered an informative character in the classification of gobies (HARRISON, 1989; PARENTI; MACIOLEK, 1993; CAIRES, 2012). In *Rhyacichthys* and most examined taxa the ectopterygoid is triangular (**Figure 73**), but in *Cotylopus, Sicydium* and *Sicyopterus* it is trapezoidal in shape (**Figure 76**).



Figure 76 – Medial view of palatine arch of Sicyopterus longifilis (MZB 24873, 62.4 mm SL).

Character 57. Palatine, ethmoid process, length in relation to maxillary process (HARRISON, 1989; PARENTI; MACIOLEK, 1993, character: 4; CAIRES, 2012, character: 58).

Character states: (0) smaller than maxillary process, (1) as large as the maxillary process.

Several authors noted the importance of this character (HARRISON, 1989; PARENTI; MACIOLEK, 1993; CAIRES, 2012). In *Rhyacichthys*, *Odontobutis*, *Eleotris*, *Bathygobius* and *Gobius* the ethmoid process of the palatine is smaller than the maxillary process (**Figure 77**). However, in *Awaous*, *Stenogobius*, *Evorthodus*, *Gobioides*, *Gobionellus*, *Oxyurichthys*, *Cotylopus*, *Lentipes*, *Sicydium* and *Sicyopterus* (**Figure 71**) it is much more conspicuous being as large as the maxillary process.



Figure 77 – Medial view of palatine arch of *Eleotris perniger* (NMNH 314440, 60.7 mm SL).

Character 58. Preopercle, anterior expansion, presence (MILLER, 1973; HARRISON, 1989).

Character states: (0) present, (1) absent.

Harrison (1989) noted that the preopercle is not expanded toward the symplectic in the same way in *Awaous* and Sicydiinae. In *Rhyacichthys* and in most of the analyzed taxa, the preopercle is not anteriorly expanded, but in *Bathygobius*, *Gobius*, *Lentipes* (Figure 74), *Cotylopus*, *Sicydium* and *Sicyopterus* (Figure 76) a round dorsal expansion in the anterior region of preopercle is present.

Terminal		Character									
Terminar	49	50	50 51 52 53 54 55						57	58	
Rhyacichthys aspro	0	-	0	0	0	0	0	0	0	0	
Odontobutis obscurus	0	-	0	?	0	0	0	0	0	1	
Eleotris perniger	0	-	0	0	0	0	0	0	0	1	
Bathygobius soporator	1	0	0	0	0	1	0	0	0	1	
Gobius niger	1	0	0	0	0	0	0	0	0	1	
Evorthodus lyricus	0	-	0	0	0	0	0	0	1	0	
Gobioides broussonnetii	0	-	0	0	0	0	0	0	1	0	
Gobionellus oceanicus		-	0	1	0	0	0	0	1	0	
Oxyurichthys cornutus		-	0	0	0	0	0	0	1	0	
Stenogobius (Insularigobius) genivittatus		-	0	0	0	0	0	0	1	0	
Stenogobius (Stenogobius) laterisquamatus		-	0	0	0	0	0	0	1	0	
Cotylopus acutipinnis		1	1	1	1	1	1	1	1	1	
Lentipes concolor		1	0	1	1	1	1	0	1	1	
Sicydium plumieri		1	1	1	1	1	1	1	1	1	
Sicvopterus longifilis		1	1	1	1	1	1	1	1	1	
Awaous (Awaous) commersonii	0	-	0	0	0	0	0	0	1	0	
Awaous (Awaous) ocellaris	0	-	0	0	0	0	0	0	1	0	
Awaous (Chonophorus) banana	0	-	0	0	0	0	0	0	1	0	
Awaous (Chonophorus) lateristriga	0	-	0	0	0	0	0	0	1	0	
Awaous (Chonophorus) tajasica	0	-	0	0	0	0	0	0	1	0	
Awaous (Chonophorus) transandeanus	0	-	0	0	0	0	0	0	1	0	
Awaous (Euctenogobius) flavus	0	-	0	0	0	0	0	0	1	0	

 Table 65 – State of palatine arch characters in examined taxa. Traces represent inapplicable characters (-).

 Question marks (?) represent missing data.

2.4.10. Dorsal fins

Character 59. First dorsal-fin pterygiophores, interdigitation with neural spines (BIRDSONG *et al.*, 1988, HARRISON, 1989, CAIRES, 2012, character: 108).

Character states: (0) (3-2212), (1) (3-1221), (2) (3-2211), (3) (3-12201)

Birdsong *et al.* (1988) performed a detailed study of the vertebral column showing the importance of the pterygiophore formula in relation to vertebra among the lineages within Gobiidae. In *Rhyacichthys* the anterior most pterygiophore of the first dorsal fin is associated with the gap between the 3rd and 4th vertebrae, and the number of pterygiophores associated with other gaps follows the formula (3-2212). *Eleotris, Awaous, Stenogobius, Gobionellus, Oxyurichthys, Evorthodus, Lentipes, Cotylopus, Sicydium* and *Sicyopterus* have the formula (3-1221), state (1), *Bathygobius* and *Gobius* have state (2) and *Gobioides* presents a unique derived

formula, state (3). We were unable to determine the Character state in *Odontobutis*, since it was not possible to observe the relation of the vertebrae and pterygiophores in the exemplar stained for muscular analysis.

2.4.11. Pelvic fins

Character 60. Pelvic fin spine, position in relation to the first branched ray when the fin is fused to a suction cup (adapted from Hoese (1984) and Parenti and Maciolek (1993), character: 1).

Character states: (0) equidistanct between pelvic fin spines and rays, (1) pelvic-fin spine and first ray close together at their proximal ends, and separated from remaining four pelvicfin rays.

This character was used by Parenti and Maciolek (1993) to define the Sicydiinae family (**Figure 56**). In *Bathygobius*, *Gobius*, *Awaous*, *Evorthodus*, *Gobioides*, *Gobionellus*, *Oxyurichthys* and *Stenogobius* the spines and rays are equidistant with each other. However, in *Lentipes*, *Cotylopus*, *Sicydium* and *Sicyopterus* the spine and the first branched ray are closer to each other than to the others.

Inapplicability: this character does not apply to *Rhyacichthys*, *Odontobutis* and *Eleotris* since these genera do not have fused pelvic fins.

Character 61. Pelvic fin spine, position in relation to joint with bone (PARENTI; THOMAS, 1998, character: 1).

Character states: (0) spine inserted non-perpendicularly, (1) spine of pelvic fin inserted perpendicularly.

This character was enhanced by Parenti and Thomas (1998) as a complement to the characters defined in Parenti and Maciolek (1993) as a synapomorphy for Sicydiinae. Perpendicular insertion of pelvic-fin spine was only observed in *Lentipes*, *Cotylopus*, *Sicydium* and *Sicyopterus* (**Figure 56**) as opposed to the non-perpendicular insertion observed in other examined genera.

Inapplicability: this character does not apply to *Rhyacichthys*, *Odontobutis* and *Eleotris* since these genera do not have fused pelvic fins.

2.4.12. Caudal fin

Character 62. Epurals, number (MILLER, 1973, GOSLINE, 1955, SPRINGER, 1983, BIRDSONG *et al.*, 1988, LARSON (2001), character: 5; CAIRES (2012), character: 97).

Character states: (0) three epurals, (1) two epurals, (2) one epural

Birdsong *et al.* (1988) noted the presence of only a single epural in *Awaous* and Sicydiinae. Among the examined taxa a single epural characterizes *Bathygobius*, *Gobius*, *Awaous*, *Evorthodus*, *Lentipes*, *Cotylopus*, *Sicydium* and *Sicyopterus*. *Rhyacichthys* has three epurals, and *Eleotris*, *Stenogobius*, *Gobioides*, *Gobionellus* and *Oxyurichthys* have two We were unable to determine the character state in *Odontobutis*, since tese structures were not visible in the exemplar prepared for muscular analysis.

T I		Character							
Terminal	59	60	61	62					
Rhyacichthys aspro	0	-	-	0					
Odontobutis obscurus	?	-	-	?					
Eleotris perniger	1	-	-	1					
Bathygobius soporator	2	0	0	2					
Gobius niger	2	0	0	2					
Evorthodus lyricus	1	0	0	2					
Gobioides broussonnetii	3	0	0	1					
Gobionellus oceanicus	1	0	0	1					
Oxyurichthys cornutus	1	0	0	1					
Stenogobius (Insularigobius) genivittatus	1	0	0	1					
Stenogobius (Stenogobius) laterisquamatus	1	0	0	1					
Cotylopus acutipinnis	1	1	1	2					
Lentipes concolor	1	1	1	2					
Sicydium plumieri	1	1	1	2					
Sicyopterus longifilis	1	1	1	2					
Awaous (Awaous) commersonii	1	0	0	2					
Awaous (Awaous) ocellaris	1	0	0	2					
Awaous (Chonophorus) banana	1	0	0	2					
Awaous (Chonophorus) lateristriga	1	0	0	2					
Awaous (Chonophorus) tajasica	1	0	0	2					
Awaous (Chonophorus) transandeanus	1	0	0	2					
Awaous (Euctenogobius) flavus	1	0	0	2					

 Table 66 – State of fin characters in examined taxa. Traces represent inapplicable characters (-). Question marks

 (?) represent missing data.

2.4.13. Myological Characters

Dorsal view

Character 63. Epaxial musculature, medial portion, position relative to lateral portion.

Character states: (0) medial portion not covering lateral portion dorsally, (1) medial portion completely covering lateral portion dorsally.

In *Rhyacichthys* and *Odontobutis* the lateral portion of the epaxial musculature is lies lateral to the medial portion, not covering it (**Figure 77**). In the other genera exmined, the medial portion completely overlaps the lateral portion, leaving the lateral portion accessible only when the medial portion is dissected (**Figure 78**).



Figure 77 – Dorsal view of the head of Rhyacichthys aspro (NMNH 371845, 59.9 mm SL).



Figure 78 – Dorsal view of the head of *Bathygobius soporator* (LIRP 1414, 58.2 mm SL), green line indicates the anterior limit of insertion of the medial portion of the *epaxialis*, red line point to anterior limit of *supracarinalis*.

Character 64. Epaxial musculature, medial portion, insertion in relation to posterior limit of orbital region.

Character states: (0) insertion posterior to posterior margin of orbital region, (1) insertion into exact region of end of orbit, (2) insertion anterior to posterior margin of orbital region.

In *Rhyacichthys*, *Odontobutis Awaous*, *Stenogobius*, *Gobioides and Lentipes* the medial portion of the epaxial musculature is located posterior to the orbit limit as in *Gobionellus* (**Figure 79**), *Oxyurichthys* and *Cotylopus* this musculature inserts in the exact region of the end of the orbit. Lastly, in *Eleotris*, *Bathygobius*, *Gobius*, *Evorthodus*, *Sicydium* and *Sicyopterus* the medial portion of the epaxial musculature inserts anterior to the posterior limit of the orbit.

Character 65. Epaxial musculature, medial portion, insertion relative to orbital margins.

Character states: (0) insertion reaching the margin of the orbital region, (1) never inserting at the margin of the orbital region.

In *Bathygobius*, *Gobius*, *Gobionellus*, *Oxyurichthys* and *Evorthodus* the insertion never reaches the margin of the orbit, whereas in *Eleotris* (Figure 78), *Cotylopus*, *Sicydium* and *Sicyopterus* the insertion reaches the margin of the orbital region.

Inapplicability: this character does not apply to taxa which medial portion of epaxial musculature inserts posteriorly to the posterior limit of the orbital region.

Character 66. Epaxial musculature, medial portion, insertion in relation to orbital region, anterior limit of insertion at the orbital margin.

Character states: (0) anterior insertion limit reaching the final third of the orbital region, (1) anterior insertion limit not reaching the final third of the orbital region.

In *Cotylopus* the insertion limit of the epaxial musculature in the orbital region does not reach the final third of the orbit, while in *Eleotris*, *Sicydium* and *Sicyopterus* the insertion covers the final third of the orbit.

Inapplicability: this character does not apply to taxa presenting epaxial musculature that are inserted posteriorly to the posterior limit of the orbital region and does not apply to taxa which epaxial musculature does not reach the margins of the orbital region.

Character 67. Epaxial musculature, medial portion, anterior limit of insertion of lateral and medial portion.

Character states: (0) anterior limit of insertion of the medial portion of the epaxial musculature posterior in relation to the lateral region, (1) anterior limit of insertion of the lateral and medial portion aligned, (2) anterior limit of the medial region of the medial portion of the epaxial musculature anterior in relation to the lateral region.

In *Rhyacichthys*, *Odontobutis*, *Bathygobius*, *Gobius*, *Gobioides*, *Gobionellus*, *Oxyurichthys*, *Evorthodus*, *Sicydium* and *Sicyopterus* the anterior limit of insertion of the medial region of the medial portion of the epaxial musculature inserts posteriorly to the lateral region, state (0). In *Awaous* (*Awaous*) *ocellaris* and *Stenogobius* the anterior limit of insertion of medial and lateral portion of the medial portion of the epaxial musculature coincides, state (1). Finally, in *Eleotris*, *Awaous* (*Chonophorus*), *Awaous* (*Euctenogobius*), *Awaous* (*Awaous*) *Commersonii*, *Cotylopus* and *Lentipes* the anterior limit of insertion of the medial region of the medial portion of the epaxial musculature is located anteriorly in relation to the lateral portion, state (2).



Figure 79 – Dorsal view of the head of *Gobionellus oceanicus* (**NMNH** 352117, 93.4 mm SL), green line indicates the anterior limit of insertion of the medial portion of the *epaxialis*, red line point to anterior limit of insertion of *supracarinalis*.



Figure 80 – Dorsal view of the head of *Lentipes concolor* (**NMNH** 316119, 56.3 mm SL), green line indicates the anterior limit of insertion of the medial portion of the *epaxialis*, red line point to anterior limit of insertion of *supracarinalis*.



Figure 81 – Dorsal view of the head of *Stenogobius genivittatus* (NMNH 278704, 69.1 mm SL), green line indicates the anterior limit of insertion of the medial portion of the *epaxialis*, red line point to anterior limit of insertion of *supracarinalis*.

Character 68. *Supracarinalis*, insertion in relation to the medial portion of the epaxial musculature.

Character states: (0) insertion posterior to the anterior limit of insertion of the medial portion of the epaxial musculature, (1) insertion at the anterior limit of insertion of the epaxial musculature.

In Awaous (Awaous) ocellaris and Stenogobius (Stenogobius) laterisquamatus the anterior limit of insertion of the supracarinalis remains in the same region of the anterior limit of the medial portion of epaxial musculature. In all other taxa the supracarinalis insets posteriorly to the anterior limit of insertion of the medial portion of the epaxial musculature.

Character 69. *Supracarinalis*, insertion in relation to anterior limit of opercular region.

Character states: (0) insertion posteriorly to the vertical traced at the anterior margin of the opercle, (1) insertion anteriorly to the vertical traced in the anterior margin of the opercle

In Rhyacichthys, Odontobutis, Eleotris, Bathygobius, Gobius, Gobioides, Gobionellus, Oxyurichthys and Evorthodus the supracarinalis inserts posteriorly to vertical traced in the anterior margin of the opercle. Supracarinalis inserts anteriorly to the vertical traced in the anterior margin of the opercle in Awaous, Stenogobius (Figure 81), Cotylopus, Lentipes, Sicydium and Sicyopterus.

Character 70. Supracarinalis, insertion in relation to supraoccipital.

Character states: (0) not completely covering the anterior region of the supraoccipital, (1) completely covering the anterior region of the supraoccipital.

In *Rhyacichthys* (Figure 77), *Odontobutis*, *Awaous* (*Chonophorus*) *lateristriga*, *Gobioides*, *Cotylopus*, *Lentipes* and *Sicyopterus* the *supracarinalis* does not cover completely the anterior region of the supraccipital (Figure 82), while in other taxa this bone is completely covered by the *supracarinalis* in dorsal view.



Figure 82 – Dorsal view of the head of Gobius niger (NMNH 298489, 76.2 mm SL).

Ventral view

Character 71. Interhyoideus, posterior portion, medial fibers, medial expansion, presence.

Character states: (0) absent, (1) present.

In *Eleotris* and *Gobius* a medial expansion of the fibers of the posterior portion of *Interhyoideus (sensu* DATOVO; RIZZATO, 2018) (Figure 83) is present, this expansion is absent in all other taxa (Figure 84, 85 and 86).



Figure 83 - Dorsal view of the head of Gobius niger (NMNH 298489, 76.2 mm SL).

Character 72. Hyohyoides inferioris posterioris, presence.

Character states: (0) absent, (1) present.

In Rhyacichthys, Odontobutis, Eleotris, Bathygobius, Gobius (Figure 83), Evorthodus, Gobioides, Gobionellus and Oxyurichthys the posterior portion of the Hyohyoides inferioris is absent. However, this portion is present in Awaous (Figures 84 and 85), Stenogobius (Figure 86), Cotylopus, Lentipes and Sicydium. Unfortunately, this character cannot be observed in Sicyopterus longifilis, however, this structure was identified in a specimen of Sicyopterus calliochromus indicating that this muscle may be characteristic of this genus.



Figure 84 - Ventral view of Awaous (Chonophorus) tajasica. (MZUSP 26842, 90,3 mm SL).



Figure 85 – Illustration of the ventral view of Awaous (Chonophorus) tajasica. (MZUSP 26842, 90.3 mm SL).



Figure 86 – Ventral view of the head of *Stenogobius* (*Stenogobius*) *laterisquamatus* (NMNH 298697, 83.9 mm SL).

Lateral view

Character 73. Adductor mandibulae, segmentum facialis pars retromalaris, insertion.

Character states: (0) inserting on the coronoid process of the dentary, (1) inserting on the maxilla.

In *Rhyacichthys*, *Odontobutis*, *Eleotris*, *Awaous*, *Stenogobius*, *Gobionellus*, *Oxyurichthys* and *Gobius* the *segmentum facialis pars retromalaris* inserts on the coronoid process. Meantime in *Lentipes*, *Cotylopus* (**Figure 87**), *Sicydium* and *Sicyopterus* this muscle inserts on the maxilla.



Figure 87 – Lateral view of the check of Cotylopus acutipinnis (MNHN 1984-0809, 52.5 mm SL.).

Character 74. Adductor mandibulae, segmentum facialis pars stegalis, position in in relation to pars malaris and pars rictalis.

Character states: (0) placed medially to the *Adductor mandibulae*, *pars retromalaris* and *Adductor mandibulae*, *pars rictalis*, not visible in lateral view, (1), placed between the *Adductor mandibulae*, *pars retromalaris* and *Adductor mandibulae*, *pars rictalis*, visible in lateral view.

In Odontobutis, Eleotris (Figure 88), Awaous and Stenogobius (Figure 89) the pars stegalis of the segmentum facialis is placed between the pars retromalaris and pars rictalis. In other taxa the pars stegalis is placed medially.

Character 75. *Adductor mandibulae*, *segmentum facialis*, *pars stegalis*, position in relation to *pars malaris* and *pars rictalis*, when placed medially.

Character states: (0) placed medially, not visible in lateral view, (1) placed ventrally, visible in lateral view, (2) placed medially, visible in lateral view.

In *Bathygobius*, *Gobius*, *Gobioides*, *Gobionellus*, *Oxyurichthys* and *Lentipes* the *Adductor mandibulae*, *pars stegalis* is placed medially to *Adductor mandibulae*, *pars malaris* and *rictalis*, fully concealed in lateral view, state (0). In *Cotylopus* (Figure 87), *Sicydium* (Figure 74) and *Sicyopterus* the *Adductor mandibulae*, *pars stegalis* is placed medially and

ventrally to the *Adductor mandibulae*, *pars malaris* and *rictalis*, visible in lateral view, state (1). Lastly, in *Evorthodus* the *Adductor mandibulae*, *pars stegalis* is placed medially to *Adductor mandibulae*, *pars malaris* and *rictalis* but in this genus the posterior portion of this muscle is visible in lateral view, state (2).

Inapplicability: this character does not apply to *Eleotris*, *Awaous* and *Stenogobius* since in these genera the *Adductor mandibulae*, *pars stegalis* is placed in between the *Adductor mandibulae*, *pars malaris* and *pars rictalis*.



Figure 88 - Lateral view of the check of *Eleotris perniger* (NMNH 314440, 88.1 mm SL).



Figure 89 – Lateral view of the check of Stenogobius laterisquamatus (NMNH 298697, 83.9 mm SL).

Terminal		Character											
Terminai	63	64	65	66	67	68	69	70	71	72	73	74	75
Rhyacichthys aspro	0	0	-	-	0	0	0	0	0	0	0	0	0
Odontobutis obscurus	0	0	-	-	2	0	0	0	0	0	0	1	-
Eleotris perniger	1	2	0	0	2	0	0	1	1	0	0	1	-
Bathygobius soporator	1	2	1	-	0	0	0	1	0	0	0	0	0
Gobius niger	1	2	1	-	0	0	0	1	1	0	0	0	0
Evorthodus lyricus	1	2	1	-	0	0	0	1	0	0	0	0	2
Gobioides broussonnetii	1	0	-	-	0	0	0	0	0	0	0	0	0
Gobionellus oceanicus	1	1	1	-	0	0	0	1	0	0	0	0	0
Oxyurichthys cornutus	1	1	1	-	0	0	0	1	0	0	0	0	0
Stenogobius (Insularigobius) genivittatus		0	-	-	1	0	1	1	0	1	0	1	-
Stenogobius (Stenogobius) Iaterisquamatus	1	0	-	-	1	1	1	1	0	1	0	1	-
Cotylopus acutipinnis	1	1	0	1	0	0	1	0	0	1	1	0	1
Lentipes concolor	1	0	-	-	0	0	1	0	0	1	1	0	0
Sicydium plumieri	1	2	0	0	0	0	1	1	0	1	1	0	1
Sicyopterus longifilis	1	2	0	0	0	0	1	0	0	?	1	0	1
Awaous (Awaous) commersonii	1	0	-	-	2	0	1	1	0	1	0	1	-
Awaous (Awaous) ocellaris	1	0	-	-	1	1	1	1	0	1	0	1	-
Awaous (Chonophorus) banana	1	0	-	-	2	0	1	1	0	1	0	1	-
Awaous (Chonophorus) lateristriga	1	0	-	-	2	0	1	0	0	1	0	1	-
Awaous (Chonophorus) tajasica	1	0	-	-	2	0	1	1	0	1	0	1	-
Awaous (Chonophorus) transandeanus	1	0	-	-	2	0	1	1	0	1	0	1	-
Awaous (Euctenogobius) flavus	1	0	-	-	2	0	1	1	0	1	0	1	-

 Table 67 – State of myological characters in examined taxa. Traces represent inapplicable characters (-). Question marks (?) represent missing data.

2.4.14. Phylogenetic reconstruction

The analysis by implicit enumeration revealed two most parsimonious trees (Figures 90 and 91), with score of 190.760. The generated strict consensus tree presented the same topology as Tree 0 (Figure 92).



Figure 90 – Tree 0. Generated using implicit enumeration in TNT.



Figure 91 – Tree 1. Generated using implicit enumeration in TNT.



Figure 92 – Strict consensus tree. Generated using implicit enumeration in TNT.

2.4.15. List of synapomorphies

The nodes obtained in Trees 0 and 1 are almost identical, thus the nodes of Tree 1 presented below are the ones diverging from Tree 0.

Tree 0:

Rhyacichthys aspro:

No autapomorphies.

Odontobutis obscurus: Char. 1: 0.140-0.440 -> 0.050, Char. 2: 0.650 -> 0.560, Char. 3: 0.070-0.080 -> 0.060, Char. 19: 0 -> 1.

Eleotris perniger: Char. 0: 0.090-0.170 -> 0.000, Char. 17: 1 -> 0, Char. 25: 0 -> 1, Char. 71: 0 -> 1.

Bathygobius soporator: Char. 2: 0.650 -> 0.580, Char. 54: 0 -> 1.

Gobius niger: Char. 2: 0.710-0.760 -> 0.780, Char. 4: 0.400 -> 0.500, Char. 71: 0 ->

1.

Evorthodus lyricus: Char. 18: 1 -> 0, Char. 19: 1 -> 0, Char. 30: 0 -> 1, Char. 75: 0 ->

2.

Gobioides broussonnetii: Char. 0: 0.290 -> 0.120, Char. 3: 0.800 -> 1.000, Char. 4: 0.700 -> 1.000, Char. 5: 0.900 -> 1.000, Char. 13: 1 -> 0, Char. 16: 1 -> 0, Char. 28: 1 -> 0, Char. 39: 0 -> 1, Char. 59: 1 -> 3, Char. 64: 1 -> 0, Char. 70: 1 -> 0.

Gobionellus oceanicus: Char. 2: 0.800 -> 0.920, Char. 8: 0 -> 1, Char. 9: 0 -> 1, Char. 11: 1 -> 0, Char. 52: 0 -> 1.

Oxyurichthys cornutus: Char. 22: $1 \rightarrow 2$.

Stenogobius genivittatus: Char. 3: 0.450 -> 0.510, Char. 4: 0.400 -> 0.500, Char. 5: 0.500 -> 0.600, Char. 20: 0 -> 1, Char. 27: 0 -> 1, Char. 30: 0 -> 1.

Stenogobius laterisquamatus: Char. 0: 0.390 -> 0.290, Char. 1: 0.110 -> 0.000, Char. 2: 0.710-0.760 -> 0.800, Char. 9: 0 -> 1, Char. 13: 0 -> 1, Char. 16: 0 -> 1, Char. 18: 1 -> 0,

Char. 45: 0 -> 1, Char. 48: 1 -> 0, Char. 68: 0 -> 1.

Cotylopus acutipinnis: Char. 3: 0.360 -> 0.340, Char. 44: 1 -> 0, Char. 66: 0 -> 1.

Lentipes concolor: Char. 0: 0.670 -> 0.720, Char. 2: 0.710-0.760 -> 0.690, Char. 46: 1 -> 0.

Sicydium plumieri: Char. 0: 0.670 -> 0.570, Char. 1: 0.560-0.650 -> 1.000, Char. 13: 0 -> 1, Char. 45: 0 -> 1, Char. 46: 1 -> 0, Char. 70: 0 -> 1.

Sicyopterus longifilis: Char. 0: 0.670 -> 0.750, Char. 2: 0.860-0.930 -> 1.000, Char. 3: 0.360 -> 0.410, Char. 9: 1 -> 0, Char. 12: 0 -> 1.

Awaous (Awaous) commersonii: Char. 0: 0.620 -> 0.630, Char. 1: 0.640 -> 0.400, Char.

3: 0.340-0.370 -> 0.290, Char. 15: 1 -> 0, Char. 41: 1 -> 2.

Awaous (Awaous) ocellaris: Char. 2: 0.680 -> 0.820, Char. 3: 0.340-0.370 -> 0.380,

```
Char. 18: 1 -> 0, Char. 67: 2 -> 1, Char. 68: 0 -> 1.
```

Awaous (*Chonophorus*) *banana*: Char. 1: 0.660-0.750 -> 0.990.

Awaous (Chonophorus) lateristriga: Char. 0: 0.520 -> 0.480, Char. 1: 0.750 -> 0.890,

Char. 2: 0.460 -> 0.430, Char. 3: 0.340-0.370 -> 0.310, Char. 15: 1 -> 0, Char. 70: 1 -> 0. Awaous (Chonophorus) tajasica:

No autapomorphies.

Awaous (Chonophorus) transandeanus: Char. 0: 0.550-0.620 -> 0.640, Char. 2: 0.610-0.680 -> 0.710, Char. 3: 0.340-0.370 -> 0.420.

Awaous (Euctenogobius) flavus: Char. 0: 0.520 -> 0.590, Char. 1: 0.750 -> 0.850, Char. 2: 0.460 -> 0.000, Char. 3: 0.340-0.370 -> 0.000, Char. 31: 1 -> 2, Char. 40: 0 -> 1, Char. 41: 1 -> 2, Char. 45: 0 -> 1.

Node 23:

No synapomorphies.

Node 24: Char. 4: 0.000 -> 0.200, Char. 5: 0.100 -> 0.300, Char. 16: 0 -> 1, Char. 18: 0 -> 1, Char. 63: 0 -> 1, Char. 64: 0 -> 2, Char. 70: 0 -> 1.

Node 25: Char. 3: 0.070-0.080 → 0.280, Char. 4: 0.200 → 0.300, Char. 6: 0 → 1, Char. 7: 0 → 1, Char. 46: 0 → 1, Char. 48: 0 → 1, Char. 62: 1 → 2.

Node 26: Char. 2: 0.650 → 0.710-0.760, Char. 3: 0.280 → 0.360-0.480, Char. 4: 0.300 → 0.400, Char. 5: 0.300 → 0.500-0.600, Char. 19: 0 → 1, Char. 21: 0 → 1.

Node 27: Char. 1: 0.440-0.460 -> 0.260, Char. 3: 0.360-0.480 -> 0.570, Char. 13: 0 -> 1, Char. 25: 0 -> 2.

Node 28: Char. 0: 0.120-0.170 -> 0.300-0.320, Char. 32: 0 -> 1, Char. 47: 0 -> 1, Char. 57: 0 -> 1.

Node 29: Char. 0: 0.300 -> 0.290, Char. 1: 0.250 -> 0.130, Char. 2: 0.790 -> 0.800, Char. 3: 0.700 -> 0.800, Char. 4: 0.600 -> 0.700, Char. 5: 0.800 -> 0.900, Char. 44: 1 -> 0.

Node 30: Char. 1: 0.260 -> 0.250, Char. 2: 0.760 -> 0.790, Char. 3: 0.570 -> 0.700, Char. 4: 0.400 -> 0.600, Char. 5: 0.600 -> 0.800, Char. 41: 1 -> 2, Char. 43: 0 -> 1, Char. 62: 2 -> 1.

Node 31: Char. 1: 0.440-0.460 -> 0.110, Char. 19: 1 -> 0, Char. 25: 0 -> 1, Char. 62: 2 -> 1.

Node 32: Char. 23: 0 -> 1, Char. 44: 1 -> 0, Char. 67: 0 -> 1, Char. 74: 0 -> 1.

Node 33: Char. 0: 0.300-0.320 -> 0.390-0.520, Char. 16: 1 -> 0, Char. 20: 12 -> 0, Char. 69: 0 -> 1, Char. 72: 0 -> 1.

Node 34: Char. 1: 0.460 -> 0.560-0.650, Char. 2: 0.710-0.760 -> 0.860-0.930, Char. 8: 0 -> 1, Char. 28: 1 -> 0, Char. 51: 0 -> 1, Char. 56: 0 -> 1, Char. 75: 0 -> 1.

Node 35: Char. 0: 0.390-0.520 -> 0.670, Char. 9: 0 -> 1, Char. 26: 0 -> 1, Char. 48: 1 -> 0, Char. 49: 0 -> 1, Char. 52: 0 -> 1, Char. 53: 0 -> 1, Char. 54: 0 -> 1, Char. 55: 0 -> 1, Char. 60: 0 -> 1, Char. 61: 0 -> 1, Char. 70: 1 -> 0, Char. 73: 0 -> 1.

Node 36: Char. 31: 1 -> 0, Char. 50: 0 -> 1, Char. 64: 1 -> 2.

1.

Node 37: Char. 1: 0.660-0.750 -> 0.640, Char. 19: 1 -> 0, Char. 28: 0 -> 1.

Node 38: Char. 0: 0.520 -> 0.550-0.620, Char. 2: 0.460 -> 0.610-0.680, Char. 16: 0 ->

Node 39: Char. 10: 0 -> 1, Char. 12: 0 -> 1, Char. 14: 0 -> 1, Char. 28: 1 -> 0, Char. 39: 0 -> 1.

Node 40: Char. 1: 0.440-0.460 -> 0.750, Char. 2: 0.710-0.760 -> 0.460, Char. 24: 0 -> 1, Char. 67: 1 -> 2.

Node 41: Char. 33: 0 → 1. Tree 1: Node 37: Char. 0: 0.550-0.590 → 0.620, Char. 19: 1 → 0. Node 38: Char. 10: 0 → 1, Char. 12: 0 → 1, Char. 14: 0 → 1, Char. 39: 0 → 1. Node 39: Char. 1: 0.440-0.460 → 0.640-0.750, Char. 2: 0.710-0.760 → 0.610-0.680, Char. 24: 0 → 1, Char. 67: 1 → 2. Node 40: Char. 33: 0 → 1. Node 41: Char. 28: 1 → 0.

Node 42: Char. 0: 0.550-0.590 -> 0.520, Char. 2: 0.610-0.680 -> 0.460.

2.4.16. Character indexes

Index of consistence and rescaled consistence are presented in Table 68.

Character indexes											
Character		Tr	ee: 0			Tre	Tree: 1				
0	CI:	0.385	RC:	0.218	CI:	0.385	RC:	0.218			
1	CI:	0.292	RC:	0.138	CI:	0.292	RC:	0.138			
2	CI:	0.408	RC:	0.152	CI:	0.408	RC:	0.152			
3	CI:	0.532	RC:	0.352	CI:	0.532	RC:	0.352			
4	CI:	0.833	RC:	0.714	CI:	0.833	RC:	0.714			
5	CI:	0.833	RC:	0.741	CI:	0.833	RC:	0.741			
6	CI:	1.000	RC:	1.000	CI:	1.000	RC:	1.000			
7	CI:	1.000	RC:	1.000	CI:	1.000	RC:	1.000			
8	CI:	0.500	RC:	0.333	CI:	0.500	RC:	0.333			
9	CI:	0.250	RC:	0.063	CI:	0.250	RC:	0.063			
10	CI:	1.000	RC:	1.000	CI:	1.000	RC:	1.000			
11	CI:	0.250	RC:	0.063	CI:	0.250	RC:	0.063			
12	CI:	0.500	RC:	0.417	CI:	0.500	RC:	0.417			
13	CI:	0.250	RC:	0.063	CI:	0.250	RC:	0.063			
14	CI:	1.000	RC:	1.000	CI:	1.000	RC:	1.000			
15	CI:	0.500	RC:	0.000	CI:	0.500	RC:	0.000			
16	CI:	0.200	RC:	0.120	CI:	0.167	RC:	0.083			
17	CI:	0.333	RC:	0.238	CI:	0.333	RC:	0.238			
18	CI:	0.250	RC:	0.063	CI:	0.250	RC:	0.063			
19	CI:	0.200	RC:	0.086	CI:	0.200	RC:	0.086			
20	CI:	0.333	RC:	0.143	CI:	0.333	RC:	0.143			
21	CI:	1.000	RC:	1.000	CI:	1.000	RC:	1.000			
22	CI:	0.500	RC:	0.000	CI:	0.500	RC:	0.000			
23	CI:	1.000	RC:	1.000	CI:	1.000	RC:	1.000			

Table 68 – Index of consistence and rescaled consistence for each character. Indexes in bold diverge in each tree.
Character indexes											
Character	Tree: 0					Tree: 1					
24	CI:	1.000	RC:	1.000	CI:	1.000	RC:	1.000			
25	CI:	0.500	RC:	0.389	CI:	0.500	RC:	0.389			
26	CI:	1.000	RC:	1.000	CI:	1.000	RC:	1.000			
27	CI:	0.250	RC:	0.063	CI:	0.250	RC:	0.063			
28	CI:	0.200	RC:	0.100	CI:	0.250	RC:	0.156			
29	CI:	0.500	RC:	0.000	CI:	0.500	RC:	0.000			
30	CI:	0.500	RC:	0.000	CI:	0.500	RC:	0.000			
31	CI:	0.400	RC:	0.229	CI:	0.400	RC:	0.229			
32	CI:	1.000	RC:	1.000	CI:	1.000	RC:	1.000			
33	CI:	1.000	RC:	1.000	CI:	1.000	RC:	1.000			
34	CI:	0.250	RC:	0.143	CI:	0.250	RC:	0.143			
35	CI:	0.500	RC:	0.000	CI:	0.500	RC:	0.000			
36	CI:	1.000	RC:	1.000	CI:	1.000	RC:	1.000			
37	CI:	1.000	RC:	1.000	CI:	1.000	RC:	1.000			
38	CI:	0.500	RC:	0.250	CI:	0.500	RC:	0.250			
39	CI:	0.250	RC:	0.156	CI:	0.250	RC:	0.156			
40	CI:	0.250	RC:	0.063	CI:	0.250	RC:	0.063			
41	CI:	0.333	RC:	0.185	CI:	0.333	RC:	0.185			
42	CI:	1.000	RC:	1.000	CI:	1.000	RC:	1.000			
43	CI:	1.000	RC:	1.000	CI:	1.000	RC:	1.000			
44	CI:	0.200	RC:	0.067	CI:	0.200	RC:	0.067			
45	CI:	0.333	RC:	0.000	CI:	0.333	RC:	0.000			
46	CI:	0.333	RC:	0.167	CI:	0.333	RC:	0.167			
47	CI:	1.000	RC:	1.000	CI:	1.000	RC:	1.000			
48	CI:	0.333	RC:	0.238	CI:	0.333	RC:	0.238			
49	CI:	1.000	RC:	1.000	CI:	1.000	RC:	1.000			
50	CI:	1.000	RC:	1.000	CI:	1.000	RC:	1.000			
51	CI:	1.000	RC:	1.000	CI:	1.000	RC:	1.000			
52	CI:	0.500	RC:	0.375	CI:	0.500	RC:	0.375			
53	CI:	1.000	RC:	1.000	CI:	1.000	RC:	1.000			
54	CI:	0.500	RC:	0.375	CI:	0.500	RC:	0.375			
55	CI:	1.000	RC:	1.000	CI:	1.000	RC:	1.000			
56	CI:	1.000	RC:	1.000	CI:	1.000	RC:	1.000			
57	CI:	1.000	RC:	1.000	CI:	1.000	RC:	1.000			
58	CI:	0.333	RC:	0.238	CI:	0.333	RC:	0.238			
59	CI:	0.750	RC:	0.000	CI:	0.750	RC:	0.000			
60	CI:	1.000	RC:	1.000	CI:	1.000	RC:	1.000			
61	CI:	1.000	RC:	1.000	CI:	1.000	RC:	1.000			
62	CI:	0.500	RC:	0.333	CI:	0.500	RC:	0.333			
63	CI:	1.000	RC:	1.000	CI:	1.000	RC:	1.000			
64	CI:	0.250	RC:	0.135	CI:	0.250	RC:	0.135			
65	CI:	0.500	RC:	0.333	CI:	0.500	RC:	0.333			
66	CI:	1.000	RC:	1.000	CI:	1.000	RC:	1.000			

Character indexes												
Character	Tree: 0				Tree: 1							
67	CI:	0.286	RC:	0.202	CI:	0.286	RC:	0.202				
68	CI:	0.500	RC:	0.000	CI:	0.500	RC:	0.000				
69	CI:	1.000	RC:	1.000	CI:	1.000	RC:	1.000				
70	CI:	0.200	RC:	0.067	CI:	0.200	RC:	0.067				
71	CI:	0.500	RC:	0.000	CI:	0.500	RC:	0.000				
72	CI:	1.000	RC:	1.000	CI:	1.000	RC:	1.000				
73	CI:	1.000	RC:	1.000	CI:	1.000	RC:	1.000				
74	CI:	0.333	RC:	0.267	CI:	0.333	RC:	0.267				
75	CI:	1.000	RC:	1.000	CI:	1.000	RC:	1.000				

2.5. DISCUSSION

As expected *Odontobutis* is placed at the base of the trees. The families Rhyacichthyidae and Odontobutidae are considered a basal stock of the order Gobioidei (MILLER, 1973, GILL; MOOI, 2012).

Node 24, Eleotridae and Gobiidae: Eleotris, Bathygobius, Gobius, Awaous, Stenogobius, Cotylopus, Lentipes, Sicydium, Sicyopterus, Evorthodus, Gobioides, Gobionellus, Oxyurichthys.

Synapomorphies: Char. 4: 0.000 -> 0.200, Char. 5: 0.100 -> 0.300, Char. 16: 0 -> 1, Char. 18: 0 -> 1, Char. 63: 0 -> 1, Char. 64: 0 -> 2, Char. 70: 0 -> 1.

This clade is supported by an increase in in number of the second dorsal-fin rays (Char. 4: $0.000 \rightarrow 0.200$), increase in anal fin ray number (Char. 5: $0.100 \rightarrow 0.300$), presence of scales in the chest region (Char. 16: $0 \rightarrow 1$) and absence of cycloid scales posterior to the vertical from the anterior spine of the first dorsal fin (Char. 18: $0 \rightarrow 1$), the medial portion of the epaxial musculature overlapping the lateral portion (Char. 63: $0 \rightarrow 1$), the *epaxial* musculature inserting much more anteriorly (Char. 64: $0 \rightarrow 2$) and the *supracarinalis* completely covering the supraoccipital bone in dorsal view (Char. 70: $0 \rightarrow 1$). The epaxial musculature was never analyzed in a phylogenetic context for the examined taxa. Future analysis may confirm if the position of the epaxial and supracarinal musculature is different between Rhyacichthydae, Odontobutidae and the clade formed by Eleotridae and Gobiidae.

Node 25, Gobiidae (sensu GILL; MOOI, 2012): Bathygobius, Gobius, Awaous, Stenogobius, Cotylopus, Lentipes, Sicydium, Sicyopterus, Evorthodus, Gobioides, Gobionellus, Oxyurichthys.

Synapomorphies: Char. 3: 0.070-0.080 -> 0.280, Char. 4: 0.200 -> 0.300, Char. 6: 0 -> 1, Char. 7: 0 -> 1, Char. 46: 0 -> 1, Char. 48: 0 -> 1, Char. 62: 1 -> 2.

This clade was supported by an increase in length of the dorsal fin (Char. 3: 0.070-0.080 \rightarrow 0.280), increase in number of the second dorsal-fin rays (Char. 4: 0.200 \rightarrow 0.300), presence of five branchiostegal rays (Char. 6: 0 \rightarrow 1), presence of six spines in the first dorsal fin (Char. 7: 0 \rightarrow 1), dorsal margin of the lateral ethmoid crenulate (Char. 46: 0 \rightarrow 1), reduction of the width of the frontal (Char. 48: 0 \rightarrow 1) and presence of one epural (Char. 62: 1 \rightarrow 2).

The presence of five branchiostegal rays as a synapomorphy for this clade, as proposed by Gill and Mooi (2012), was herein corroborated. The presence of six spines in the first dorsal fin is a controversial synapomorphy for the family since some members of Gobiinae present seven spines (*e.g. Gobiosoma*). The presence of a crenulate margin in the lateral ethmoid was also recovered as a synapomorphy for Gobiidae. Caires (2012) commented that this characteristic would be important for the classification of Gobionellinae, but results obtained in this analysis suggests that this feature is a synapomorphy for a much more inclusive group.

Node 28, Stenogobius lineage (sensu AGORRETA et al., 2013): Awaous, Stenogobius, Cotylopus, Lentipes, Sicydium, Sicyopterus, Evorthodus, Gobioides, Gobionellus, Oxyurichthys.

Synapomorphies: Char. 0: 0.120-0.170 -> 0.300-0.320, Char. 32: 0 -> 1, Char. 47: 0 -> 1, Char. 57: 0 -> 1.

Synapomorphies for this clade include the absence of the pore E (Char. 32: $0 \rightarrow 1$), considered a characteristic for the members of Sicydiinae plus Gobionellinae by Birdsong et. *al* (1988), the presence of a dorsal expansion on the dorsal face of the mesethmoid (Char. 47: $0 \rightarrow 1$) and the presence of a long ethmoidal process in the palatine (57: $0 \rightarrow 1$).

This was the first time that a morphological analysis recovered, at the same time, *Awaous* and *Stenogobius* as sister genera (Clade 32), being this group closely related to Sicydiinae (Clade 34), while this clade was hypothesized to be the sister group of Gobionellinae (*sensu* PEZOLD, 1993). The phylogenetic placement of Sicydiinae in Pezold (1993) and Larson (2001) is undetermined since these authors did not included members of this subfamily. In addition, the results are not comparable with Parenti and Thomas (1998) since *Tukugobius* and

Rhinogobius were not included herein. The results disagree with Thacker (2009; 2015) and the rhodopsin-based tree of Tornabene (2013), since *Awaous* was considered closer to Sicydiinae than to *Stenogobius*. The consensus tree herein obtained also diverges from Thacker (2013) who suggested that the clades currently assigned to Gobionellinae would be basal lineages, successively closer to *Awaous*, *Stenogobius* and Sicydiinae, and, again, considering *Awaous* closer to Sicydiinae than to *Stenogobius*. Lastly, the results are not the same obtained by Agorreta (2013) who considered *Awaous* (*Chonophorus*) *banana* closely related to *Stenogobius*.

In conclusion the final phylogenetic tree agreed with Thacker (2002), Agorreta & Rüber (2012) and the consensus tree of Tornabene (2013), placing *Awaous* + *Stenogobius* as sister to Sicydiinae, being this clade sister to other Gobionellinae.

Node 27, Gobionellinae Clade II (sensu AGORRETA; RUBER, 2012): Evorthodus, Gobioides, Gobionellus, Oxyurichthys.

Synapomorphies: Char. 1: 0.440-0.460 -> 0.260, Char. 3: 0.360-0.480 -> 0.570, Char. 13: 0 -> 1, Char. 25: 0 -> 2.

The synapomorphies for this clade include the slightly increase in the upper lip thickness (Char. 1: 0.440-0.460 \rightarrow 0.260), the increase in the length of the second dorsal fin (Char. 3: 0.360-0.480 \rightarrow 0.570), absence of papillae in the posterior region of the palate (Char. 13: 0 \rightarrow 1) and the presence of a lanceolate caudal fin (Char. 25: 0 \rightarrow 2). The lanceolate caudal fin was recovered as a synapomorphy but it is controversial, since other members of the *Stenogobius* group (*sensu* LARSON, 2001), not included in this analysis, present a truncated caudal fin (*e.g. Rhinogobius* and *Schismatogobius* de Beaufort, 1912).

Node 30, unammed, Gobionellus, Gobioides and Oxyurichthys

Synapomorphies: Char. 1: 0.260 -> 0.250, Char. 2: 0.760 -> 0.790, Char. 3: 0.570 -> 0.700, Char. 4: 0.400 -> 0.600, Char. 5: 0.600 -> 0.800, Char. 41: 1 -> 2, Char. 43: 0 -> 1, Char. 62: 2 -> 1.

This clade is supported by some morphometric (Char. 1: $0.260 \rightarrow 0.250$, Char. 2: 0.760 $\rightarrow 0.790$, Char. 3: $0.570 \rightarrow 0.700$) and meristic characteristics (Char. 41: $1 \rightarrow 2$, Char. 43: $0 \rightarrow 1$, Char. 62: $2 \rightarrow 1$), in addition with line *b* exceeding line c_4 anteriorly (Char. 41: $1 \rightarrow 2$), line *d* exceeding line a_1 posteriorly (Char. 43: $0 \rightarrow 1$) and presence of two epurals (Char. 62: $2 \rightarrow 1$).

Harrison (1989) considered *Oxyurichthys* as distantly related to *Evorthodus*, *Gobioides* and *Gobionellus* forming a different lineage called '*Oxyurichthys* group'. In the present work this relation was not observed. *Evorthodus* was considered basal, since it has only one epural and shorter lines *b* and *d*.

Node 29, unnamed: Gobioides and Gobionellus.

Synapomorphies: Char. 0: 0.300 -> 0.290, Char. 1: 0.250 -> 0.130, Char. 2: 0.790 -> 0.800, Char. 3: 0.700 -> 0.800, Char. 4: 0.600 -> 0.700, Char. 5: 0.800 -> 0.900, Char. 44: 1 -> 0.

This clade is supported by decreasing in the snout length and upper lip thickness (Char. 0: $0.300 \rightarrow 0.290$; Char. 1: $0.250 \rightarrow 0.130$), and increase in the second dorsal and anal fin length (Char. 2: $0.790 \rightarrow 0.800$; Char. 3: $0.700 \rightarrow 0.800$). In addition, with an increase in second dorsal fin and anal fin rays (Char. 4: $0.600 \rightarrow 0.700$; Char. 5: $0.800 \rightarrow 0.900$), and by presenting the line *os* of the opercular series not transversally orientated, despite been transversal in *Gobionellus*. This relation was also proposed by Harrison (1989), Pezold (2004) and Caires (2012).

Node 33, unnamed: Awaous, Stenogobius, Cotylopus, Lentipes, Sicydium and Sicyopterus.

Synapomorphies: Char. 0: 0.300-0.320 -> 0.390-0.520, Char. 16: 1 -> 0, Char. 20: 2 -> 0, Char. 69: 0 -> 1, Char. 72: 0 -> 1.

This clade is supported by an increase in the snout length (Char. 0: $0.300-0.320 \rightarrow 0.390-0.520$), absence of scales in the chest region (Char. 16: $1 \rightarrow 0$), subterminal mouth (Char. 20: $2 \rightarrow 0$), *Supracarinalis* inserting anteriorly to the vertical traced in the anterior margin of the opercle (Char. 69: $0 \rightarrow 1$) and by the presence of *Hyohyoides inferioris posterioris* (Char. 72: $0 \rightarrow 1$).

The synapomorphies obtained herein, including two new myological, offer strong support for this clade. Based on these synapomorphies and in the fact that subfamilies must be comparable to groups in the same category it would be better to refer at this clade as the Sicydiinae subfamily.

Node 35, Sicydiinae (sensu PARENTI; MACIOLEK, 1993): Lentipes, Cotylopus, Sicydium and Sicyopterus.

Synapomorphies: Char. 0: 0.390-0.520 → 0.670, Char. 9: 0 → 1, Char. 26: 0 → 1, Char. 48: 1 → 0, Char. 49: 0 → 1, Char. 52: 0 → 1, Char. 53: 0 → 1, Char. 54: 0 → 1, Char. 55: 0 → 1, Char. 60: 0 → 1, Char. 61: 0 → 1, Char. 70: 1 → 0, Char. 73: 0 → 1.

This clade is supported by increase in snout length (Char. 0: 0.390-0.520 \rightarrow 0.670), absence of papillae in the vomerine region (Char. 9: 0 \rightarrow 1), round suction cup formed by fusion of the pelvic fins (Char. 26: 0 \rightarrow 1), increased width of supraorbital region (Char. 48: 1 \rightarrow 0), no differentiation of ascending process in relation to articular process (Char. 49: 0 \rightarrow 1), triangular shape of the coronoid process (Char. 52: 0 \rightarrow 1), one row of teeth in the dentary (Char. 53: 0 \rightarrow 1), at least one tooth higher than the median region of the dentary (Char. 54: 0 \rightarrow 1), presence of laterally oriented teeth (Char. 55: 0 \rightarrow 1), pelvic-fin spine and first ray close together at their proximal ends and separated from remaining four pelvic-fin rays (Char. 60: 0 \rightarrow 1), pelvic-fin spine inserted perpendicularly (Char. 61: 0 \rightarrow 1), *supracarinalis* not completely covering the anterior region of the supraoccipital (Char. 70: 1 \rightarrow 0) and *Adductor mandibulae, segmentum facialis pars retromalaris* inserting on the maxilla.

This clade unequivocally monophyletic and was recovered in a number of previous phylogenetic reconstructions (PARENTI; MACIOLEK, 1993; PARENTI; THOMAS, 1998; WANG *ET AL.*, 2001; THACKER, 2003; KEITH *ET AL.*, 2011; AGORRETA; RÜBER, 2012; TORNABENE, 2013). Results herein revealed six new synapomorphies for this clade, including the absence of papillae in the vomer region, at least one tooth higher than the median region of the dentary and the *Adductor mandibulae*, *segmentum facialis pars retromalaris* inserting on the maxilla. This clade is frequently referred as Sicydiinae sub-family, but based on the topology obtained herein it is referred as the tribe Sicydiini of the Sicydiinae.

Node 34, unnamed: Cotylopus, Sicydium and Sicyopterus.

Synapomorphies: Char. 1: 0.460 -> 0.560-0.650, Char. 2: 0.710-0.760 -> 0.860-0.930, Char. 8: 0 -> 1, Char. 28: 1 -> 0, Char. 51: 0 -> 1, Char. 56: 0 -> 1, Char. 75: 0 -> 1.

Features supporting this clade include an increase in the upper lip thickness (Char. 1: $0.460 \rightarrow 0.560-0.650$), increase in the first dorsal fin length (Char. 2: $0.710-0.760 \rightarrow 0.860-0.930$), absence of papillae in the post-dental membrane (Char. 8: $0 \rightarrow 1$), oculoscapular canal interrupted between pores "H" and "K" (Char. 28: $1 \rightarrow 0$), presence of a sac of replacement teeth in pre-maxilla (Char. 51: $0 \rightarrow 1$), trapezoidal shape of the ectopterygoid (Char. 56: $0 \rightarrow 1$), Adductor mandibulae, segmentum facialis, pars stegalis placed medially, visible in lateral view (Char. 75: $0 \rightarrow 1$).

Parenti and Maciolek (1993) commented that *Lentipes* figures as a basal member of the Sicydiinae, and interpreted the presence of a sac of replacement teeth as a derived feature among this lineage. Moreover, Harrison (1989) and Parenti and Maciolek (1993) noted a change in the shape of the ectopterygoid.

Keith *et al.* (2011) suggested *Cotylopus* in the base of the Sicydiinae and *Sicydium* plus *Sicyopterus* forming a derivative clade. *Lentipes* would form an even more derivative clade. The final topology obtained herein reflects almost the opposite result.

This clade is congruent with others obtained previously (PARENTI; MACIOLEK, 1993; PARENTI; THOMAS, 1998). In addition, two new unique synapomorphies were proposed by this clade including absence of papillae in the post-dental membrane (Char. 8: 0 - 1) and *Adductor mandibulae*, *segmentum facialis*, *pars stegalis* placed medially, visible in lateral view (Char. 75: 0 - 1).

Node 36, unnamed: Sicydium and Sicyopterus

Synapomorphies: Char. 31: 1 -> 0, Char. 50: 0 -> 1, Char. 64: 1 -> 2.

Three synapomorphies support this clade, including B pore located anteriorly to the posterior nasal pore (Char. 31: 1 \rightarrow 0), blunt form of the indistinct ascending process (Char. 50: 0 \rightarrow 1) and medial portion of epaxial musculature inserting anterior to posterior margin of orbital region (Char. 64: 1 \rightarrow 2).

This result agrees with Parenti and Maciolek (1993) and Parenti and Thomas (1998). The anterior insertion of the epaxial musculature is reported as synapomorphic for this clade, and future research may confirm if it is present in other Sicydiini taxa.

Node 32, unnamed: Awaous and Stenogobius.

Synapomorphies: Char. 23: 0 -> 1, Char. 44: 1 -> 0, Char. 67: 0 -> 1, Char. 74: 0 ->

1.

Synapomorphies of this clade include the presence of fleshy lobes on the inner edge of the pectoral girdle (Char. 23: $0 \rightarrow 1$), line *os* of the opercular series transversally orientated (Char. 44: $1 \rightarrow 0$), the medial region of the medial portion of the epaxial musculature inserting anterior to the lateral portion (Char. 67: $0 \rightarrow 1$), and placement of the *pars stegalis* of the *segmentum facialis* between the *pars retromalaris* and *pars rictalis*. Usually only the presence

of fleshy lobes in the inner edge of the pectoral girdle is mentioned in the literature as synapomorphic for this clade, but herein three additional characters support it.

This clade is referred as *Stenogobini*, a tribe within the Sicydiinae subfamily, because the *Stenogobius* group (LARSON, 2001) and *Stenogobius* lineage (THACKER, 2013) were already proposed.

Tree zero, node 40, and tree 1 node 39, Awaous sensu stricto: Awaous (Awaous) ocellaris, Awaous (Awaous) commersonii, Awaous (Chonophorus) banana, Awaous (Chonophorus) lateristriga, Awaous (Chonophorus) tajasica, Awaous (Chonophorus) transandeanus and Awaous (Euctenogobius) flavus.

Synapomorphies: Char. 1: 0.440-0.460 -> 0.750, Char. 2: 0.710-0.760 -> 0.460, Char. 24: 0 -> 1, Char. 67: 1 -> 2.

Awaous was recovered as a monophyletic genus based on the following synapomorphies : an increase in upper lip thickness (Char. 1: 0.440-0.460), increase in first dorsal-fin length (Char. 2: 0.710-0.760), presence of sensory papillae over much of the gill structure (Char. 24: $0 \rightarrow 1$) and limit of insertion of the medial region of the medial portion of the epaxial musculature located anteriorly in relation to the lateral portion (Char. 67: $1 \rightarrow 2$).

Watson (1992) established monophyly of *Awaous* based on the exclusive presence of papillae in the gill structure, reaffirmed herein. The limit of insertion of the medial region of the medial portion of the epaxial musculature located anteriorly in relation to the lateral portion is considered a synapomorphy for the genus, despite absent in *Awaous (Awaous) ocellaris*. The same synapomorphies were obtained by both generated trees.

Tree zero, node 39 and tree 1, node 38, unnamed, new: Awaous (Awaous) ocellaris, Awaous (Awaous) commersonii, Awaous (Chonophorus) banana, Awaous (Chonophorus) lateristriga, Awaous (Chonophorus) tajasica and Awaous (Chonophorus) transandeanus.

Synapomorphies: Tree 0: Char. 10: 0 -> 1, Char. 12: 0 -> 1, Char. 14: 0 -> 1, **Char.** 28: 1 -> 0, Char. 39: 0 -> 1.

Tree 1: Char. 10: 0 -> 1, Char. 12: 0 -> 1, Char. 14: 0 -> 1, Char. 39: 0 -> 1.

Two different most parsimonious trees were generated during the phylogenetic analysis, differing in the relative placement of the subgenus within *Awaous*. Since *Awaous* is the main focus of this dissertation both trees will be discussed. Both trees recovered *Awaous* (*Euctenogobius*) *flavus* as the basal clade. Despite recovering *Stenogobius sp* as a member of

Awaous, Agorreta et al. (2013) also postulated a basal position of Awaous (Euctenogobius) flavus in the diversification of Awaous.

Awaous (Chonophorus) is considered paraphyletic in tree 0 and monophyletic in tree 1. Synapomorphies presented in both trees include: conic papillae in the vomer region (Char. 10: $0 \rightarrow 1$), conic papillae in the parasphenoid region (Char. 12: $0 \rightarrow 1$) and conic papillae in the posterior region of the palate (Char. 14: $0 \rightarrow 1$), (Char. 28: $1 \rightarrow 0$). In tree 0 presence of a continuous oculoscapular canal is also considered a synapomorphy for this clade (Char. 28: $1 \rightarrow 0$).

Since the support for the subgenus *Awaous* (*Chonophorus*) is weak, and *Awaous* (*Euctenogobius*) is monotypic, the subgeneric classification is not recommended. Thus, *Awaous flavus* is considered a basal species of *Awaous* and the monophyletic clades *Awaous banana* plus *Awaous transandeanus* and *Awaous ocellaris* plus *Awaous commersonii* derivative linages of the genus.

Node 37, Awaous (Awaous) (sensu WATSON, 1992): Awaous ocellaris and Awaous commersonii.

Synapomorphies: tree 0: Char. 1: 0.660-0.750 -> 0.640, Char. 19: 1 -> 0, Char. 28: 0 -> 1.

Tree 1: Char. 0: 0.550-0.590 -> 0.620, Char. 19: 1 -> 0.

The only synapomorphy recovered by both trees is the presence of scales in the base of the pectoral fin (Char. 19: $1 \rightarrow 0$). In Tree a thin upper lip (Char. 1: 0.660-0.750 $\rightarrow 0.640$) and a discontinuous oculoscapular canal (Char. 28: $0 \rightarrow 1$) are synapomorphic, while in tree 1 the increase in the snout length is considered synapomorphic (Char. 0: 0.550-0.590).

Tree one, node 41, Awaous (Chonophorus) (sensu WATSON, 1996): Awaous banana, Awaous lateristriga, Awaous tajasica and Awaous transandeanus.

Synapomorphies: Char. 28: $1 \rightarrow 0$.

Tree 1 one recovered only the presence of a complete oculoscapular canal as synapomorphic for *Awaous* (*Chonophorus*) (Char. 28: $1 \rightarrow 0$). This character presented a higher index of consistency and rescaled consistence in tree 1: CI: 0.250, RC: 0.156 (*vs.* CI: 0.200, RC:0.100 in tree zero). This was the only character which index varied in both trees.

Tree zero, node 41 and tree one, node 40, new, unnamed: Awaous banana and Awaous transandeanus.

Synapomorphies: tree zero: Char. 33: $0 \rightarrow 1$.

Tree one: Char. 33: $0 \rightarrow 1$.

The synapomorphy recovered in both trees for this clade is the presence of a duplicated pore "F" in the oculoscapular canal (Char. 33: $0 \rightarrow 1$). This is a characteristic not found in any other examined taxa.

Tree one, node 42, new, unnamed: Awaous lateristriga and Awaous tajasica.

Synapomorphies: Char. 0: 0.550-0.590 -> 0.520, Char. 2: 0.610-0.680 -> 0.460.

Only tree 1 recovered the clade formed by *Awaous lateristriga* and *Awaous tajasica*. Synapomorphies include an increase in snout length (Char. 0: $0.550-0.590 \rightarrow 0.520$) and decrease in the length of the first dorsal fin (Char. 2: $0.610-0.680 \rightarrow 0.460$). The taxonomic revision reveled that the measurements tend to be extremely conservative in the species formerly grouped in *Awaous (Chonophorus)*, thus to consider this clade based on two morphometric synapomorphies would be preposterous.

2.6. FINAL CONSIDERATIONS

The two most parsimonious trees revealed some interesting results. This was the first time that oral papillae and myological characters were include in a phylogenetic hypothesis of members of *Stenogobius* lineage.

Among the most interesting results remain the insertion of the *supracarinalis* and the position of medial portion of the *epaxialis* in all representatives of Eleotridae and Gobiidae, Diverging from members of Rhyacichthydae and Odontobutidae. Future analysis including more members of basal families within Gobioidei are needed to determine if the observed changes in the arrangement of *epaxialis* and *supracarinalis* are synapomorphic for the clade formed by Gobiidae and Eleotridae.

A new Sicydiinae subfamily is proposed, including *Awaous* and *Stenogobius*, based on five synapomorphies including two new myological ones. This subfamily comprises the tribe Stenogobini, with *Awaous* and *Stenogobius* and the tribe Sicydiini including the taxa currently considered Sicydiinae (*sensu* PARENTI; MACIOLEK, 1993).

The clade formed by *Cotylopus*, *Sicydium* and *Sicyopterus* have the medially placed *Adductor mandibulae*, *segmentum facialis*, *pars stegalis* visible in lateral view. This distinctive feature should be examined in more Sicydiini taxa to elucidate the phylogenetic significance of its overall distribution.

Node 39 of tree 0 and node 38 of tree 1 placed *Awaous flavus* as the basal species of *Awaous*, and recovered at least four exclusive synapomorphies for the clade containing *Awaous* (*Awaous*) and *Awaous* (*Chonophorus*). Despite tree 1 recovering *Awaous* (*Chonophorus*) as monophyletic this decision may present some problems. The only synapomorphy for this clade would be the presence of an oculoscapular canal, and if the subgenus *Awaous* (*Chonophorus*) is considered monophyletic, the clade formed by *Awaous lateristriga* and *Awaous tajasica* would be supported only by morphometric synapomorphies. Based on this result it might be better to consider *Awaous* (*Chonophorus*) a paraphyletic lineage within *Awaous*, pending additional research that includes all *Awaous* species.

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