Universidade Federal do Rio de Janeiro
Campus UFRJ-Macaé Professor Aloísio Teixeira
Programa de Pós-Graduação em Ciências Ambientais e Conservação

Revisão taxonômica de *Anchoviella cayennensis* (Puyo, 1945) (Clupeiformes: Engraulidae), uma espécie de manjuba pouco conhecida do Atlântico ocidental

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Dissertação de Mestrado apresentada ao Programa de Pós-Graduação em Ciências Ambientais e Conservação, Campus UFRJ-Macaé, Professor Aloísio Teixeira, da Universidade Federal do Rio de Janeiro, como parte dos requisitos necessários à obtenção do título de Mestre em Ciências Ambientais e Conservação.

Orientador: Dr. Fabio Di Dario

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RESUMO

Revisão taxonômica de *Anchoviella cayennensis* (Puyo, 1945) (Clupeiformes: Engraulidae), uma espécie de manjuba pouco conhecida do Atlântico ocidental

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Resumo da Dissertação de Mestrado submetida ao Programa de Pós-Graduação em Ciências Ambientais e Conservação, *Campus* UFRJ-Macaé Professor Aloísio Teixeira, da Universidade Federal do Rio de Janeiro, como parte dos requisitos necessários à obtenção do título de Mestre em Ciências Ambientais e Conservação.

Anchoviella é um gênero de Engraulidae composto por 15 espécies popularmente conhecidas como manjubas, com distribuição restrita ao Novo Mundo. *Anchoviella cayennensis* (Puyo, 1945) foi descrita com base em dois espécimes coletados no rio Cayenne, na Guiana Francesa. Registros da espécie na literatura são reportados para o Atlântico, entre a Suriname e o Espírito Santo, Brasil. *Anchoviella perfasciata* (Poey, 1860), que é morfologicamente similar à *A. cayennensis*, é reportada para o Atlântico Ocidental central e norte. Caracteres diagnósticos propostos para ambas espécies se sobrepõem parcialmente, havendo dúvidas na literatura sobre a validade de *A. cayennensis*. Recentemente, *Anchoviella sanfranciscana* Barbosa *et al*., 2017 foi descrita como uma espécie endêmica do estuário do rio São Francisco, nordeste do Brasil. Os caracteres diagnósticos propostos para esta espécie são semelhantes ou sobrepõem-se parcialmente aos de *A. cayennensis*, tornando este cenário taxonômico ainda mais complexo. O presente estudo teve por objetivo testar a validade de *A. cayennensis* e *A. sanfranciscana* utilizando caracteres morfológicos. Foram analisados um total de 24 caracteres morfométricos e 13 caracteres merísticos de 191 espécimes, depositados em Coleções Científicas nacionais e internacionais, incluindo o holótipo de *A. perfasciata* e a série tipo de *A. sanfranciscana*. Análises de Componentes Principais realizadas com dados morfológicos indicam a existência de dois grupos distintos, um correspondendo a *A. perfasciata* e outro incluindo os exemplares identificados como *A. cayennensis* e a série tipo de *A. sanfranciscana*. Caracteres relacionados à dentição dos arcos branquiais também corroboram a distinção entre *A. perfasciata* e *A. cayennensis*. Portanto, *A. perfasciata* e *A. cayennensis* são reconhecidas como espécies válidas, ao passo que *A. sanfranciscana* é considerada sinônimo júnior de *A. cayennensis*. Uma redescrição taxonômica de *A. cayennensis* é apresentada, com a proposição de um neótipo para a espécie. A correta identificação de exemplares em Coleções também indica que *A. cayennensis* distribui-se do Suriname, no norte da América do Sul, ao estado do Rio de Janeiro, sudeste do Brasil. Uma chave taxonômica para as espécies costeiras e estuarinas de *Anchoviella* do Atlântico também é apresentada.

Palavras-chave: Engraulinae, Taxonomia, Sistemática.

ABSTRACT

Taxonomic revision of *Anchoviella cayennensis* (Puyo, 1945) (Clupeiformes: Engraulidae), a poorly known species of anchovy from western Atlantic.

Lorena Soares Agostinho
Main advisor: Prof. Dr. Fabio Di Dario
Co-advisor: Dra. Marina Vianna Loeb

Abstract of the Master Dissertation submitted to the Graduate Program in Environmental Sciences and Conservation (PPG-CiAC), campus Macaé of the Federal University of Rio de Janeiro (UFRJ), as a requisite to obtaining the Master's degree in Environmental Sciences and Conservation.

Anchoviella is a genus of the Engraulidae composed of 15 species commonly known as anchovies, exclusively distributed in the New World. *Anchoviella cayennensis* (Puyo, 1945) was described based on two specimens collected in the Cayenne River, French Guiana. Records of the species in the literature are reported for the western Atlantic, between French Guiana and Espírito Santo, Brazil. *Anchoviella perfasciata* (Poey, 1860), which is morphologically similar to *A. cayennensis*, is reported for the western Central and North Atlantic. Diagnostic characters proposed for both species overlap partially, with doubts in the literature about the validity of *A. cayennensis*. Recently, *Anchoviella sanfranciscana* Barbosa *et al*., 2017 was described as a species endemic to the estuary of the São Francisco River, northeastern Brazil. Diagnostic characters proposed for this species are similar or overlap partially with those of *A. cayennensis*, turning this taxonomic scenario even more complex. The goal of this study is to test the validity of *A. cayennensis* and *A. sanfranciscana* using morphological characters. A total of 24 morphometric and 13 meristic characters from 191 specimens deposited in National and International Collections were analyzed, including the holotype of *A. perfasciata* and the type series of *A. sanfranciscana*. Principal Component Analyzes performed with morphological data indicate the existence of two distinct groups, one corresponding to *A. perfasciata* and the other including specimens identified as *A. cayennensis* and the type series of *A. sanfranciscana*. Characters related to gill arch dentition also corroborate the distinction between *A. perfasciata* and *A. cayennensis*. Therefore, *A. perfasciata* and *A. cayennensis* are recognized as valid species, whereas *A. sanfranciscana* is considered a junior synonym of *A. cayennensis*. A taxonomic redescription of *A. cayennensis* is presented, with the proposition of a neotype for the species. The correct identification of specimens in Collections also indicates that *A. cayennensis* is distributed from Surinam, in north South America, to the state of Rio de Janeiro, southeastern Brazil. A taxonomic key for the Atlantic coastal and estuarine species of *Anchoviella* is also presented.

Keywords: Anchovies, Engraulinae, Systematics, Taxonomy.

SUMÁRIO

1. Contextualização do estudo

Clupeomorpha é uma superordem de Teleostei que inclui os peixes popularmente conhecidos como sardinhas e manjubas, distribuídos em cerca de 92 gêneros e aproximadamente 410 espécies recentes, além de 150 espécies fósseis (Grande, 1985; Lavoué *et al*., 2014; Nelson *et al*., 2016; Malabarba e Di Dario, 2017). Parte expressiva das espécies de Clupeomorpha possui relevância pesqueira, seja na pesca industrial ou de pequena escala (Whitehead, 1985; Whitehead *et al*., 1988). A família Engraulidae, que inclui 17 gêneros e cerca de 146 espécies dos peixes popularmente conhecidos como manjubas (Loeb, 2012, 2014, 2016; Nelson *et al*., 2016, Barbosa *et al*., 2017), destaca-se no grupo justamente por sua importância econômica: o total pescado de apenas uma espécie de manjuba, *Engraulis ringens* Jenyns 1842, que ocorre do Peru ao Chile, chegou a corresponder a 5,7 milhões de toneladas no passado recente, sendo uma das espécies de peixes mais pescadas em 2013 em nível global (FAO, 2015). *Engraulis ringens* já havia sido o peixe mais explorado comercialmente na história até o ano de 1982, com cerca de 13 milhões de toneladas pescadas apenas no ano de 1970 (Whitehead, 1985). Engraulidae é também um grupo de grande relevância para os ecossistemas costeiros em diversas regiões do mundo: manjubas são tipicamente micrófagas e formadoras de grandes cardumes, e por esses motivos desempenham um papel trófico relevante nos ambientes onde ocorrem (James, 1988).

As relações filogenéticas entre os grupos de Clupeomorpha são controversas, mas considerando-se apenas as formas modernas, apenas uma ordem, Clupeiformes, com as subordens Clupeoidei e Denticipitoidei, são reconhecidas (e.g., Grande, 1985; Grande & Nelson, 1985; Di Dario, 2002, 2004, 2009; Di Dario & de Pinna, 2006; de Pinna & Di Dario, 2010; Lavoué *et al*., 2014; Malabarba e Di Dario, 2017; Egan *et al.,* 2018). Cinco famílias são tradicionalmente incluídas em Clupeoidei: Engraulidae, com 146 espécies, Pristigasteridae, com 36 espécies, Chirocentridae, com duas espécies, e Clupeidae, com aproximadamente 218 espécies (de Pinna & Di Dario, 2003; Di Dario, 2005, 2009, 2013; Nelson *et al*., 2016). Denticipitoidei, por sua vez, inclui apenas *Denticeps clupeoides*, uma sardinha de pequeno porte de água doce que ocorre em rios costeiros entre Benin e Camarões, na África Ocidental (Teugels, 2003; Di Dario & de Pinna, 2006).

No Brasil, são reportados nove gêneros de Engraulidae, com um total de 26 espécies reconhecidas como válidas (Whitehead *et al*., 1988; Loeb, 2009, 2012, 2014, 2016; Loeb & Figueiredo, 2014; Loeb *et al*., 2018). *Anchoviella* Fowler, 1911 é um

gênero de Engraulidae que inclui peixes de pequeno a médio porte (3 a 16 cm de comprimento padrão) distribuídos nas porções costeiras das Américas, tanto do Atlântico quanto do Pacífico. Também são conhecidas nove espécies de *Anchoviella* de água doce na América do Sul, e outra espécie continental do gênero ainda aguarda descrição formal (Loeb *et al.,* 2018). *Anchoviella* distingue-se entre os gêneros de Engraulidae pela seguinte combinação de caracteres (Whitehead *et al*., 1988; Loeb, 2009, 2016): corpo alongado, ligeiramente comprimido, com a maior altura do corpo situada na vertical que passa pela origem da nadadeira dorsal; cabeça mais longa que alta, boca inclinada em relação ao eixo longitudinal do corpo, subterminal; extremidade posterior da maxila superior arredondada, sua extremidade posterior estendendo-se desde a vertical sob a margem anterior da pupila, até além da margem posterior da órbita por 28,5% do Comprimento Padrão (CP); focinho longo e pontudo; dentes pontiagudos, pequenos, afilados, curvados posteriormente, arranjados em uma única fileira no pré-maxilar, maxilar e dentário; pseudobrânquia presente, menor que o diâmetro da órbita, não ultrapassando a distância entre a margem anterior do pré-opérculo e o opérculo; rastros branquiais diminutos presentes na face interna do terceiro arco branquial, 15 a 35 rastros branquiais longos e afilados presentes na face externa do ramo inferior do primeiro arco branquial; 37 a 42 vértebras; nadadeira dorsal com 7 a 14 raios ramificados; nadadeira anal com 11 a 32 raios ramificados, sua origem na vertical sob a base do primeiro raio da nadadeira dorsal, ou mais posteriormente, além da base do último raio da nadadeira dorsal por até 5,5% do CP; nadadeiras peitoral e pélvica possuem, respectivamente, de 8 a 15 raios, e 7 raios; nadadeira caudal furcada, os lobos superior e inferior com o mesmo tamanho em todas as espécies.

Embora *Anchoviella* seja considerado um dos gêneros mais numerosos de Engraulidae, o número exato de espécies reconhecidas varia ligeiramente entre autores recentes. Whitehead *et al.* (1988), que foram os últimos autores a lidarem com a taxonomia de Engraulidae em escala global, reconheceram 15 espécies válidas em *Anchoviella*. Loeb (2016), em sua Tese de Doutorado que avaliou a taxonomia de *Anchoviella*, também reconheceu 15 espécies válidas no gênero, mas em um arranjo distinto daquele proposto por Whitehead *et al*. (1988). Fricke *et al*. (2019), por sua vez, reconhecem 18 espécies válidas em *Anchoviella.*

Considerando-se apenas estudos já publicados e que portanto incluem espécies descritas cientificamente, são reportadas nove espécies de *Anchoviella* para o Brasil. Três delas, *Anchoviella lepidentostole* (Fowler, 1911), *A. brevirostris* (Günther, 1868) e

A. cayennensis (Puyo, 1946), são marinhas e ocorrem em regiões costeiras, podendo penetrar em estuários e nas porções baixas de rios que desembocam no mar (Hildebrand, 1943, 1964; Whitehead, 1978; Whitehead *et al*., 1988; Menezes & Figueiredo, 2003). Recentemente, Barbosa *et al.* (2017) descreveram *Anchoviella sanfranciscana* Barbosa, Gomes da Silva, da Rocha Araújo & Carvalho, 2017, como sendo endêmica do estuário do Rio São Francisco, no nordeste do Brasil. As outras 11 espécies atualmente válidas de *Anchoviella* ocorrem em água doce, sua maioria nas bacias Amazônica e do Orinoco (*A. guianensis*, *A. carrikeri*, *A. jamesi A. juruasanga*, *A. manamensis, A. vaillanti*, *A. hernanni*), no Pacífico, também na América do Sul (*A. balboae*, *A. analis*) ou no Atlântico Ocidental Central e do Norte (*A. elongata*, *A. perfasciata*) (Whitehead *et al*., 1988; Loeb *et al*., 2018).

Uma das espécies de manjubas marinhas da América do Sul menos conhecida é *Anchoviella cayennensis*. Sua distribuição reportada em literatura vai do sul da Guiana Francesa até Vitoria, Espírito Santo (Whitehead *et al*., 1988; Menezes & Figueiredo, 2003). A baixa disponibilidade de exemplares identificados como sendo da espécie em coleções científicas faz com que existam incertezas sobre sua ocorrência em um longo trecho do Atlântico Sul ocidental, entre aproximadamente a foz do rio Amazonas, no norte do Brasil, e a foz do Rio São Francisco, entre Alagoas e Sergipe (Whitehead *et al*., 1988). Além disso, exemplares identificados como *A. cayennensis* foram recentemente coletados no baixo Paraíba do Sul, Estado do Rio de Janeiro, aproximadamente na altura das cidades de São Fidélis e Campos dos Goytacazes (NPM 1883, 1884 e 3265). As incertezas em relação à distribuição geográfica da espécie podem ser sanadas apenas através de um estudo aprofundado, com a identificação correta de exemplares em coleções científicas.

Parte das incertezas sobre a distribuição geográfica de *A. cayennensis* deve-se também ao escasso conhecimento sobre a taxonomia das manjubas no Atlântico Sul ocidental como um todo. Na revisão mais recente disponível que tratou da espécie (Whitehead *et al*., 1988), o seguinte conjunto de características foi proposto como diagnóstico: corpo alongado (altura cabendo aproximadamente 5,5 vezes no comprimento padrão); focinho moderado (cerca de l/2 do diâmetro do olho); maxila superior curta (deixando de atingir o pré-opérculo por uma distância igual a ½ do diâmetro da pupila) e com extremidade posterior uniformemente arredondada; 29 a 35 rastros branquiais no ramo inferior do primeiro arco branquial; pseudobrânquia curta (comprimento equivalendo a aproximadamente ¾ do diâmetro do olho); canais

operculares do tipo "*panamensis*"; nadadeiras peitorais com um raio não ramificado (i) seguido de 14 a 15 raios ramificados; nadadeira anal curta, com três raios não ramificados (iii) e 12 a 14 raios ramificados; faixa longitudinal prateada ao longo do corpo, com altura de cerca de ¾ do diâmetro do olho, margeada de pigmento enegrecido em sua parte superior.

Uma característica particularmente marcante de *A. cayennensis* entre as manjubas marinhas do Atlântico Sul ocidental é a origem da nadadeira anal situada posteriormente à reta que passa pela base do último raio da nadadeira dorsal (Whitehead *et al*., 1988). Dentre as espécies de *Anchoviella* da América do Sul, essa característica é tipicamente encontrada apenas em algumas formas de águas continentais, como *A. carrikeri* (Fowler, 1941), *A. alleni* (Myers, 1940), *A. hernanni* Loeb *et al*., 2018 (as três da bacia Amazônica), *A. guianensis* (Eigenmann, 1912) (bacias dos rios Orinoco e Amazonas e rios costeiros do norte da América do Sul) e *A. vaillanti* (Steindachner, 1908) (bacia do rio São Francisco, Brasil).

Essa mesma característica ocorre em *Anchoviella perfasciata* (Poey, 1860), outra manjuba marinha costeira cuja distribuição geográfica reportada na literatura está restrita a certas partes do Atlântico ocidental Central e do Norte, como a Carolina do Norte e a Flórida nos EUA, o Panamá, na América Central, além das Antilhas, Cuba e Trinidad (Whitehead *et al*., 1988). Na verdade, *A. perfasciata* e *A. cayennensis* são dificilmente distinguíveis a partir de características morfológicas externas. Sobre *A. cayennensis*, Whitehead *et al*. (1988: 331), por exemplo, afirmou que "The very close resemblance to *A. perfasciata* and the apparently clear geographical separation of the two suggests that *A. cayennensis* may in the future be considered merely a subspecies of *A. perfasciata*". O conceito de subespécie era razoavelmente adequado ao paradigma taxonômico da época, embora já naquele momento ele fosse pouco utilizado na ictiologia. Entretanto, conforme essa questão é mais comumente entendida na ictiologia moderna, pode-se dizer que Whitehead *et al*. (1988) sugeriram que *A. cayennensis* poderia ser um sinônimo júnior de *A. perfasciata* e, portanto, *A. cayennensis* pode não ser uma espécie válida. Existem também dúvidas sobre o limite sul da distribuição geográfica de *A. perfasciata*, que poderia sobrepor-se ao limite norte atribuído à *A. cayennensis*, como pode ser inferido pelas informações oriundas dos mapas de distribuição de Whitehead *et al*. (1988). Essa possível simpatia das duas espécies atualmente reconhecidas como válidas pode ser um indício adicional de que as duas formas na verdade tratam-se da mesma entidade biológica.

Anchoviella sanfranciscana, descrita em dezembro de 2017, tornou o cenário taxonômico envolvendo *A. perfasciata* e *A. cayennensis* ainda mais complexo. De acordo com Barbosa *et al*. (2017), nessa espécie a origem da nadadeira anal também é posterior à base da nadadeira dorsal, sendo esta a única outra espécie do gênero a possuir esse atributo dentre as formas marinhas/estuarinas do Atlântico Sul ocidental. *Anchoviella cayennensis*, *A. perfasciata* e *A. sanfranciscana* também compartilham praticamente todos os caracteres propostos como diagnósticos na literatura para a primeira, com exceção de um número ligeiramente menor de rastros branquiais no ramo inferior do primeiro arco branquial em *A. perfasciata* (24 a 30; Whitehead *et al*., 1988). A similaridade morfológica entre *A. cayennensis* e *A. sanfranciscana*, baseada nas informações disponíveis na descrição desta última, são ainda mais notáveis: de acordo com Barbosa *et al*. (2017), *A. sanfranciscana* e *A. cayennensis* possuem o mesmo número de rastros branquiais, por exemplo. Outras supostas diferenças entre as duas espécies são indicadas em radiografias de baixa qualidade disponíveis no artigo de Barbosa *et al*. (2017:167), não sendo explicitamente mencionadas no texto.

As questões levantadas acima, sobre a validade de *A. cayennensis* e a distribuição geográfica da espécie, podem ser respondidas apenas com uma comparação minuciosa de exemplares atribuídos à *A. cayennensis*, *A. perfasciata* e *A. sanfranciscana*, que idealmente deve abranger uma área substancial das distribuições geográficas reportadas para estas espécies. Embora a indicação de um problema taxonômico claro envolvendo *A. perfasciata* e *A. cayennensis* tenha sido feita há quase 30 anos por Whitehead *et al*. (1988), essa questão ainda não foi abordada de maneira adequada. Apenas recentemente, Loeb (2016), em uma Tese de Doutorado não publicada, apresentou evidências adicionais sugerindo que *A. cayennensis* e *A. perfasciata*, pelo menos, podem tratar-se de táxons distintos: um número de raios ramificados da nadadeira anal levemente maior em *A. perfasciata* (14 a 16 *vs*. 11 a 14) e o comprimento da maxila superior ligeiramente maior em *A. perfasciata* (63,6% a 74,8% do comprimento da cabeça *vs*. 53,3% a 65,5%). Apesar de sugerirem uma separação entre essas duas espécies, esses caracteres também possuem sobreposição de valores. Além disso, a Tese Doutorado de Loeb (2016) é anterior à descrição de *A. sanfranciscana*, de modo que a validade dessa espécie naturalmente não foi verificada. Portanto, a confirmação desses atributos como distintivos entre as espécies depende da análise de material atribuído a estas três formas. Vale ressaltar que *A. perfasciata* é a

espécie tipo do gênero *Anchoviella*, o que torna a resolução dessa questão taxonômica ainda mais relevante.

2. Objetivo

O objetivo deste estudo é testar a validade de *Anchoviella cayennensis* e *A. sanfranciscana*, através de uma revisão taxonômica que envolve a análise de caracteres merísticos e morfométricos e de anatomia interna. Uma redescrição de *A. cayennensis* e/ou *A. sanfranciscana*, reportadas para o litoral brasileiro, será apresentada, caso estas espécies sejam válidas.

3. Estrutura da Dissertação

O conjunto central deste estudo é apresentado em um único capítulo, no formato de manuscrito redigido na língua inglesa. Ao final, também é apresentada uma breve conclusão geral do estudo, em língua Portuguesa, complementar à "Contextualização do Estudo".

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Taxonomic status of *Anchoviella perfasciata* (Poey, 1860), *A. cayennensis* (Puyo, 1945) and *A. sanfranciscana* Barbosa, Gomes da Silva, da Rocha Araújo & Carvalho 2017 from the western Atlantic, with a redescription of *A. cayennensis* (Clupeiformes: Engraulidae)

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ABSTRACT

Anchoviella cayennensis (Puyo, 1945) is a relatively small sized, coastal, and estuarine western Atlantic species of anchovy distributed from Surinam to southeastern Brazil. The species is morphologically similar to *A. perfasciata* (Poey, 1860) from the Central and western North Atlantic, and it has been suggested in the literature that both are actually synonyms. The recently described *Anchoviella sanfranciscana* Barbosa, Gomes da Silva, da Rocha Araújo & Carvalho 2017, in turn, was reported as endemic to the estuary of the São Francisco river, northeastern Brazil. Most characters proposed as diagnostic for that species are, however, similar to the ones reported for *A. cayennensis* and *A. perfasciata*. In order to clarify the complex taxonomic scenario involving the three species, 24 morphometric and 13 meristic characters of 171 specimens tentatively identified as *A. perfasciata* (including the holotype) and *A. cayennensis* from the Central and South Atlantic in addition to the holotype and 19 paratypes of *A. sanfranciscana* (total: 191 specimens) were analyzed. The Principal Component Analyses of morphometric characters indicates the existence of two groups, which are recognized as *A. perfasciata* and *A. cayennensis*, with *A. sanfranciscana* proposed as a junior synonym of the later. Further evidence from gill arch dentition also indicates that the two species are valid and distinct. A redescription of *A. cayennensis* based on the data uncovered in the study is presented, and a neotype is proposed for the species. Confirmation of the identity of specimens attributed to *A. cayennensis* indicates that its southern limit of distribution is in the Rio de Janeiro State, southeastern Brazil. A taxonomic key for the estuarine and coastal Atlantic species of *Anchoviella* is also presented.

Keywords: Anchovies, Engraulinae, Systematics, Taxonomy, Morphology.

RESUMO

Anchoviella cayennensis (Puyo, 1945) é uma espécie de manjuba do Atlântico ocidental de porte relativamente pequeno, costeira e estuarina, distribuída do Suriname ao sudeste do Brasil. A espécie é morfologicamente similar a *A. perfasciata* (Poey, 1860), do Atlântico Norte central e ocidental, e tem sido sugerido na literatura que ambas são na verdade sinônimas. A recentemente descrita *Anchoviella sanfranciscana* Barbosa, Gomes da Silva, da Rocha Araújo & Carvalho 2017, por sua vez, foi reportada como endêmica do estuário do rio São Francisco, nordeste do Brasil. A maioria dos caracteres propostos como diagnósticos para esta espécie é, entretanto, similar àqueles relatados para *A. cayennensis* e *A. perfasciata*. A fim de esclarecer o complexo cenário taxonômico envolvendo as três espécies, 24 caracteres morfométricos e 13 merísticos de 171 espécimes tentativamente identificados como *A. perfasciata* (incluindo o holótipo) e *A. cayennensis*, além do holótipo e 19 parátipos de *A. sanfranciscana* (total: 191 espécimes) foram analisados. Análises de Componentes Principais de caracteres morfométricos indicaram a existência de dois grupos, que são reconhecidos como *A. perfasciata* e *A. cayennensis*, com *A. sanfranciscana* proposto como sinônimo júnior desta última. Evidência adicional de dentição dos arcos branquiais também indica que as duas espécies são válidas e distintas. Uma redescrição de *A. cayennensis* com base nos dados descobertos no estudo é apresentada, e um neótipo é proposto para a espécie. A confirmação da identidade dos espécimes atribuídos a *A. cayennensis* indica que seu limite sul de distribuição é no Estado do Rio de Janeiro, sudeste do Brasil. Uma chave taxonômica para as espécies costeiras e estuarinas de *Anchoviella* do Atlântico também é apresentada.

Palavras-chave: Engraulinae, Taxonomia, Sistemática, Morfologia.

Introduction

The Engraulidae includes about 17 genera and 146 species of the typically small to medium-sized, coastal and schooling fishes commonly known as anchovies (Whitehead *et al*., 1988; Nelson *et al*., 2016; Loeb *et al*., 2018). The family is currently divided into two subfamilies, the Coiliinae (6 genera, Indo-Pacific region) and Engraulinae (11 genera, World-wide distribution; Whitehead *et al*., 1988; Grande & Nelson, 1985; Di Dario, 2009; Bloom & Lovejoy, 2012; Lavoué *et al*., 2014). Anchovies are relevant to artisanal and industrial fisheries in a global scale, with recent catches of just a single species, *Engraulis ringens* (Eastern Pacific of South America) reaching up to 5.7 million tons (FAO, 2015). They are also relevant to the maintenance of coastal ecosystems since anchovies typically form large schools and compose a substantial portion of primary consumers among coastal fishes (James, 1988).

The Engraulinae is particularly diverse in the New World, where nine genera and about 70 valid species are known to occur (Whitehead *et al*., 1988; Fricke *et al*., 2019). Phylogenetic relationships among members of the subfamily remain contentious, with most genera probably representing non-monophyletic assemblages (e.g., Bloom & Lovejoy, 2012). Giving the relevance of the group to both fisheries and coastal ecosystems, the level of "hidden diversity" reported for the clade is also surprisingly high; a few unnamed forms are already recognized in the literature, whereas some currently valid species represent taxonomic complexes (Bloom & Lovejoy, 2012; Loeb, 2013; Loeb *et al*., 2018).

The New World genus *Anchoviella* Fowler 1911 stands out in this context. A total of 15 species is currently recognized in the genus, yet other more await formal description, especially in the Amazon and Orinoco basins (Bloom & Lovejoy, 2012; Loeb, 2012, 2013; Barbosa *et al*., 2017; Van der Sleen & Bloom, 2018; Loeb *et al*., 2018). Diagnostic characters of *Anchoviella* within Engraulidae, based on Whitehead *et al*. (1988) and emended herein, are: body relatively slender, moderately compressed (depth about 4.75 to 5 times in SL), greatest height at dorsal fin origin ; snout moderate, a little over ½ eye diameter; maxilla moderate, posterior tip bluntly rounded and posterior to anterior margin of pupil, also failing to reach preoperculum by at least about ¼ of pupil diameter; teeth reduced, arranged in a single row in the premaxilla, maxilla

and dentary; 15-35 gill rakers on the lower branch of first branchial arch; pseudobranch shorter than orbit diameter; a few, short gill rakers on hind face of upper portion of third branchial arch; anal fin small to moderate, iii 11-32 rays; forked caudal fin, upper and lower lobes of similar sizes; a silver stripe along flank.

Six coastal marine species of *Anchoviella* are currently recognized as valid in the western Atlantic (Loeb *et al*., 2018). *Anchoviella cayennensis* (Puyo, 1945) was described based on two specimens collected in the lower portion of the Cayenne River, French Guiana. The two syntypes of the species were apparently not preserved and could not be found at the NMHN Fish Collection, where they might have been deposited (Whitehead, 1973; Fricke *et al*., 2019; pers. obs.). Diagnostic characters proposed in the original description of the species are succinct, with comparative material mostly restricted locally. Whitehead (1973) redescribed the species based on a single 56.2 mm SL specimen collected in the mouth of the Coppename river, Surinam, with the interesting remark that "Puyo's original description of *S. cayennensis* is poor but *seems* to refer to the species described here" (Whitehead, 1973:161; italics added). Validity of the species was subsequently recognized in Whitehead's *et al.* (1988) FAO Catalogue, which represents the most recent global review of the Engraulidae. Records of *A. cayennensis* in the literature are now reported exclusively from South America, between French Guiana and Espírito Santo, Brazil (e.g, Whitehead *et al*., 1988; Menezes & Figueiredo, 2003). However, identification of the species among congeners remains difficult given the problematic scenario upon which the species was described.

The morphologically similar *Anchoviella perfasciata* (Poey, 1860), also from the western Atlantic, was described based on specimens collected off Cuba. Its geographic distribution is reported as being restricted to certain parts of the western Central and North Atlantic, between North Carolina and Panama and possibly off Venezuela. Records in the Gulf of Mexico require verification (*e.g*., Hildebrand, 1963; Whitehead *et al*., 1988; McEachran & Fechhelm, 1998; Hoese & Moore, 1998). When comparing the two species, Whitehead *et al*. (1988) stated that "(…) *Anchoviella perfasciata* and (…) *A. cayennensis* differ from all other members of the genus in having the anal fin origin behind the dorsal fin basin. Possibly *cayennensis* is merely a southern subspecies [of the former]" (Whitehead *et al*., 1988:338). Actually, the origin of the anal fin is also distinctly placed posteriorly in relation to the base of the dorsal fin in some South American freshwater species of the genus, such as *A. carrikeri* Fowler, 1941 (Amazon

basin) and *A. guianensis* (Eigenmann, 1912) (Orinoco and Amazon basins, also coastal between Venezuela and Pará, northern Brazil), but the condition was indeed restricted to *A. cayennensis* and *A. perfasciata* among coastal/estuarine species of the genus until the recent description of *Anchoviella sanfranciscana* Barbosa, Gomes da Silva, da Rocha Araújo & Carvalho 2017.

Confirmed records of *A. sanfranciscana* are so far restricted to the 20 specimens that compose the type series collected in the estuary of the São Francisco river, northeastern Brazil, to which the species was regarded as endemic at its description. In addition to sharing the posterior origin of the anal fin in relation to the dorsal-fin base, *A. perfasciata. A. cayennensis*, and *A. sanfranciscana* share practically all characters proposed as diagnostic in the literature, with the exception of a slightly smaller number of gill rakers in the lower branch of the first branchial arch in *A. perfasciata* (24 to 30, *vs*. 29-35 in *A. cayennensis* and *A. sanfranciscana*; Whitehead *et al*., 1988; Barbosa *et al*., 2017). All other diagnostic characters proposed in the literature so far for those three species overlap, at least partially. The morphological similarities between *A. cayennensis* and *A. sanfranciscana*, according to the description presented by Barbosa *et al*. (2017), are even more remarkable, and some proposed diagnostic characters of the later are rather problematic in terms of description.

Aiming to clarify the taxonomic status of *Anchoviella perfasciata, A. cayennensis* and *A. sanfranciscana*, focusing on the validity and geographic distribution of the South American forms of the group, a thorough morphological analysis was performed. Results are presented herein, and a new taxonomic identification key of marine and estuarine species of *Anchoviella* of the Atlantic is provided based on the literature and newly examined specimens.

Material and methods

Specimens: a total of 191 specimens of *Anchoviella* were analyzed in this study. Specimens were tentatively identified based on current literature (Whitehead, 1985; Whitehead *et al*., 1988; Loeb, 2012, 2014; Loeb & Figueiredo, 2014; Barbosa *et al*., 2017; Loeb *et al*., 2018) and geographic distribution (Fig. 1), resulting in the pre-identification of 131 specimens as *Anchoviella cayennensis* (South America) and 40 as *Anchoviella perfasciata,* which includes the holotype (MCZ 17965) (Central and North

America). The type series of *A. sanfranciscana*, which includes the holotype and 19 paratypes, all collected in the estuary of the São Francisco river, Brazil (Barbosa *et al.*, 2017), was also examined. As mentioned in the introduction, the two syntypes of *A. cayennensis* have not been preserved. The specimen examined by Whitehead (1973; RMNH 26294) was not available for this study, but *A. cayennensis* MNHN-IC 2005-2320, which was more recently collected close to the type locality in the Cayenne River, French Guyana, was included in the analyses.

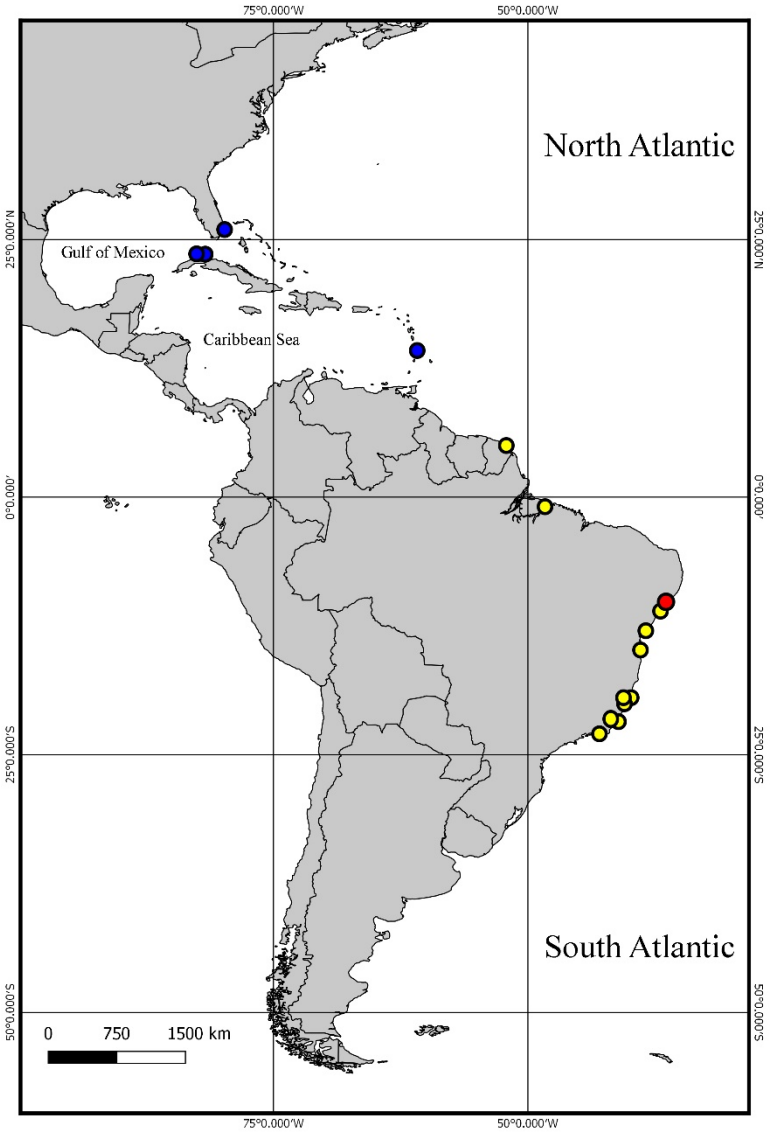

Figure 1. Collection localities of 191 specimens of *Anchoviella* examined in this study, tentatively identified as *Anchoviella perfasciata* (blue circles), *Anchoviella cayennensis* (yellow circles), and the type series of *A. sanfranciscana* (red circle).

Morphological data: counts and measurements were taken according to Hubbs & Lagler (1947) and recent literature focused on the taxonomy of the Engraulidae, mainly

Whitehead (1985), Whitehead *et al*. (1988), Loeb (2012, 2014) Loeb & Figueiredo (2014), and Loeb *et al*. (2018). Measurements of Standard Length (SL) and Head Length (HL) were expressed in millimeters (mm), all other measurements were expressed as a percentage of SL, except subunits of the head that are expressed as percentages of HL (Table 1). Meristic data are provided in Table 2 and in the redescription of *A. cayennensis*, with an asterisk indicating counts of *A. cayennensis* MNHN-IC 2005-2320; frequency of each count is given in parentheses in the redescription.

Five specimens identified as *Anchoviella cayennensis* (NPM1883, 2; NPM1884, 1; NPM3265, 2; 102.2-141.2 mm SL) and four identified as *Anchoviella perfasciata* (UF 220202; 65-78 mm SL) were cleared and stained for visualization of bones and cartilages (Dingerkus & Uhler, 1977; Taylor & Van Dyke, 1985; Song & Parenti, 1995). Osteological observations were complemented by x-ray images, obtained with a Digital Faxitron X-Ray Machine model LX-60, of 13 specimens identified as *Anchoviella cayennensis* and 10 as *Anchoviella perfasciata*, in addition to 10 specimens of the type series of *A. sanfranciscana*, including the holotype (INPA-ICT 053278).

Osteological and lateral line terminology follows Nelson (1967, 1970), Grande (1985), Grande & Nelson (1985) and Di Dario (2004).

Statistical analyses: Principal Component Analyses (PCA) were used to investigate morphometric patterns of the species studied. The main goal of the PCA is to reduce a large number of variables to few dimensions with minimum loss of information, allowing the detection of main patterns of similarity, association, and correlation between variables (Everitt & Hothorn, 2011).

Two PCAs were performed with the morphometric data. The first PCA included a non-standardized matrix of 191 specimens of *Anchoviella* directly examined in this study as rows, and all 22 morphometric data as columns (Table 1). The second PCA was performed with data from those same 191 specimens in addition to data from *A. cayennensis* RMNH 26294 examined by Whitehead (1973) in the redescription of the species. As this specimen was not examined in this study, only the following 10 morphometric data reported by Whitehead (1973) were included in the second PCA: body depth; anal-fin base length; pectoral-fin length; pelvic-fin length; pre-pelvic distance; pre-anal distance; HL; snout length; upper-jaw length; and orbit diameter. All

analyses were performed using the R Program (www.r-project.org) with assistance of the packages “Factominer”, “Factoextra” and “Ggplot2”.

Institutional abbreviations: Coleção Ictiológica da Universidade Federal do Espírito Santo, Vitória, ES (CIUFES); Coleção Ictiológica da Universidade Federal de Sergipe, Aracajú, SE (CIUFS); Instituto Nacional de Pesquisas da Amazônia, Manaus, AM (INPA); Museum of Comparative Zoology, Harvard University, USA (MCZ); Muséum national d’Histoire naturelle, Paris, France (MNHN); Museu Nacional, Rio de Janeiro, RJ (MNRJ); Museu Paraense Emilio Goeldi, Belém, PA (MPEG); Museu de Zoologia da Universidade de São Paulo, São Paulo, SP (MZUSP); Coleção de Peixes do Instituto de Biodiversidade e Sustentabilidade, Universidade Federal do Rio de Janeiro, Macaé, RJ (NPM); Naturalis Biodiversity Center, Leiden, Netherlands (RMNH); Florida Museum of Natural History, Gainesville, USA (UF); National Museum of Natural History, Smithsonian Institution, Washington, DC (USNM).

Results

Morphometric and meristic data of specimens identified as *Anchoviella perfasciata*, *A. cayennensis* and the type series of *A. sanfranciscana* are presented in Tables 1 and 2, respectively. The 13 meristic characters examined failed to provide evidence for the distinction of the three groups of specimens, since values of all characters overlap partially or totally (Table 2). Therefore, PCA analyses were performed only with the morphological data.

Results of the first PCA performed with all morphometric data are indicated in Fig. 2. The PCA concentrated 46% of the total variation in morphometric data, with 33.1% explained by the first axis and 12.9% explained by the second axis. The first axis indicate the existence of two largely distinct groups, one formed by specimens identified as *Anchoviella cayennensis*, including MNHN-IC 2005-2320, in addition to the type series of *A. sanfranciscana*, and the other formed by specimens identified as *Anchoviella perfasciata* (Fig. 2).

Table 1: Morphometric data of 191 specimens identified as *Anchoviella cayennensis* (n=131), *Anchoviella perfasciata* (n=40), including the holotype (MCZ17965), and the type series of *Anchoviella sanfranciscana* (n=20), including the holotype and 19 paratypes (SD: Standard Deviation).

	Anchoviella cayennensis					***Anchoviella perfasciata***					***Anchoviella sanfranciscana***				
	MNHN-IC 2005-2320	**Other specimens**				**Holotype**	**Other specimens**				**Holotype**	**Paratypes**			
		Range	**Mean**	**SD**	**Mode**		**Range**	**Mean**	**SD**	**Mode**		**Range**	**Mean**	**SD**	**Mode**
SL (mm)	98.55	54.00 – 145.5	112.44	-	-	79.39	42.80 – 81.00	63.10	-	-	105.00	97.00 – 114.70	106.80	-	-
HL (mm)	22.35	13.70 – 32.10	25.472	-	-	19.46	10.40 – 21.10	15.88	-	-	23.50	22.20 – 26.00	18.60	-	-
Percents of SL															
Body Depth	15.81	11.33 - 19.86	17.10	1.66	18.00	13.8	12.75-17.44	14.58	1.23	14.75	19.04	16.50 – 19.64	18.60	0.69	19.04
Caudal peduncle depth	7.59	6.52 - 10.10	7.87	0.48	7.69	8.00	6.52 - 8.64	7.60	0.46	7.88	7.90	6.97 – 9.72	8.56	0.66	8.75
Head Length	22.67	19.85 – 25.00	22.72	0.84	22.41	24.50	23.62 -26.37	25.18	0.64	25.32	22.38	20.92 – 24.32	22.74	0.75	22.88
Dorsal-fin base length	9.75	8.65 - 15.16	11.82	1.01	11.56	10.20	9.85 – 14.46	12.37	0.98	12.75	12.28	9.85 – 14.43	12.19	0.92	12.72
Anal-fin base length	11.23	9.36 - 14.35	11.53	0.99	10.52	13.10	12.50 – 18.00	14.64	1.27	14.46	12.90	10.40 – 12.90	11.34	0.80	11.49
Pectoral-fin length	15.43	12.76 - 19.76	14.97	0.99	14.53	11.20	12.30 – 15.4	13.46	0.81	13.4	14.85	13.51 – 16.49	15.15	0.72	15.65
Pelvic-fin length	8.64	7.40 - 12.44	9.39	1.23	10.00	6.60	6.72 – 10.98	8.11	0.87	8.13	10.00	8.72 – 11.51	9.80	0.63	9.92
Pre-dorsal length	49.81	45.66 - 56.33	52.55	1.94	52.23	51.60	47.00 – 56.19	52.08	1.99	48.00	50.19	45.3 – 55.06	52.39	2.09	52.05
Pre-pectoral length	23.12	21.49 - 30.32	23.81	1.12	23.60	23.70	24.21 – 28.27	26.40	0.85	26.55	24.19	19.18 – 25.52	24.03	1.43	24.2
Prepelvic length	43.12	40.66 – 53.00	43.17	3.23	44.31	46.10	40.32 – 47.55	44.60	1.85	43.60	44.28	39 – 45.11	43.74	2.20	43.96
Preanal length	65.40	58.71 - 75.68	67.73	2.44	67.95	64.00	61 – 67.01	64.35	1.72	62.50	67.90	59.45 – 70.27	67.73	2.38	68.00
Pectoral-fin axillary scale length	15.43	9.48 - 17.40	13.51	5.67	14.20	10.10	7.17 – 12.46	10.33	1.25	10.10	-	-	-	-	-
Pelvic-fin axillary scale length	8.94	7.78 - 11.14	9.30	0.94	9.62	-	-	-	-	-	-	-	-	-	-

Table 1 (cont.): Morphometric data of 191 specimens identified as *Anchoviella cayennensis* (n=131), *Anchoviella perfasciata* (n=40), including the holotype (MCZ17965) and the type series of *Anchoviella sanfranciscana* (n=20), including the holotype and 19 paratypes (SD: Standard Deviation):

	Anchoviella cayennensis					***Anchoviella perfasciata***					***Anchoviella sanfranciscana***				
	MNHN-IC 2005-2320	**Other specimens**				**Holotype**	**Other specimens**				**Holotype**	**Paratypes**			
		Range	**Mean**	**SD**	**Mode**		**Range**	**Mean**	**SD**	**Mode**		**Range**	**Mean**	**SD**	**Mode**
Percents of SL (cont.)															
Distance: tip of pectoral-fin, pelvic-fin insertion	4.76	2.88 – 10.02	6.48	1.77	6.66	10.10	4 – 13.89	7.54	2.01	8.10	8.09	5.76 – 10.10	7.56	1.19	8.20
Distance: tip of pelvic-fin, anal-fin	12.85	8.59 - 20.29	14.74	2.28	15.83	11.50	8.64 – 14.02	11.08	1.56	10.00	14.28	10.76 – 18.15	14.87	1.62	13.81
Percents of HL															
Snout length	14.67	13.00 – 25.00	18.69	2.60	20.00	14.40	15.71 – 24.17	18.67	2.17	20.30	17.87	17.46 – 21.25	18.96	1.07	18.55
Upper jaw length	56.55	56.12 – 69.42	65.14	1.98	65.38	69.90	69.23- 77.30	74.10	1.90	75.00	67.65	62.50 – 67.65	65.07	1.24	65.18
Upper jaw depth	4.92	3.85 - 8.75	5.21	0.69	5.00	4.30	6.15 – 8.33	7.34	0.84	8.00	5.53	4.61 – 6.30	5.60	0.36	5.83
Upper jaw length beyond posterior margin of orbit	19.14	13.21 - 25.46	17.04	1.98	17.85	19.40	17.6 – 27.02	23.58	2.18	24.7	19.57	15.31 – 21.96	18.41	1.85	16.66
Orbit diameter	29.48	28.00 - 37.50	32.43	1.97	33.33	31.70	30.67 – 37.82	33.67	2.38	34.26	29.78	27.77 – 34.58	31.73	1.52	32.30
Post-orbital distance	50.06	44.00 - 58.62	52.20	2.53	52.00	48.40	46.79 – 56.00	50.47	2.10	50.00	52.76	46.69 – 56.6	52.56	2.15	52.10
Interorbital width	25.36	19.80 - 31.98	24.21	1.66	25.75	23.50	16.53 – 25.13	21.51	1.46	20.27	25.53	22.91 – 26.25	24.87	0.96	25.30

Table 2: Meristic data of 191 specimens identified as *Anchoviella cayennensis* (maximum n=131), *Anchoviella perfasciata* (maximum n=40), including the holotype (MCZ17965), and the type series of *Anchoviella sanfranciscana* (maximum n=20), including the holotype and 19 paratypes. Frequency of each count is indicated in parentheses ("i" indicates number of unbranched fin-rays):

	Anchoviella* cf. *cayennensis		***Anchoviella* cf. *perfasciata***		***Anchoviella sanfranciscana***	
	MNHN-IC 2005-2320	**Other specimens**	**Holotype**	**Other specimens**	**Holotype**	**Paratypes**
Dorsal-fin rays	iii+12	ii(3), iii(130), 9(1), 10(3), 11(18), 12(61), 13(41), 14(4)	ii+11	ii(6), iii(33), 11(3), 12(30), 13(6)	iii+12	iii(19), 11(4), 12(14), 13(1)
Pectoral-fin rays	i+14	i(125), 10(1), 11(2), 12(23), 13(36), 14(57), 15(4)	i+14	i(36), ii(3), 12(2), 13(5), 14(31), 15(2)	i+13	i(19), 13(10), 14(9)
Pelvic-fin rays	i+6	i(126), ii(1), 5(3), 6(110), 7(14)	i+6	i(39), 5(1), 6(37), 7(1)	i+6	i(19), 6(19)
Anal-fin rays	iii+14	ii(2), iii(125), 11(9), 12 (51), 13(61), 14(6)	ii+14	ii(4), iii(35), 14(16), 15(5), 16(13)	iii+13	iii(19), 11(2), 12(8), 13(9)
Caudal-fin rays: upper portion	-	iiii(130), 9(61), 10(56), 11(13)	-	iiii(39), 9(18), 10(15), 11(6)	iii+10	iiii(19), 9(10), 10(8), 11(1)
Caudal-fin rays: lower portion	-	iiii(130), 9(55), 10(60), 11(15)	-	iiii(39) 9(16), 10(17), 11(6)	iii+10	iiii(19), 9(10), 10(6), 11(3)
Total gill rakers: first branchial arch	50	49(2), 50(5), 51(6), 52(9), 53(20), 54(20), 55(23), 56(14), 57(10), 58(12), 59(7), 60(1), 61(1).	49	45(2), 46(6), 47(9), 48(8), 49(7), 50(3), 52(3)	55	49(1), 50(1), 51(3), 52(4), 53(3), 54(2), 55(2), 56(2), 57(1)
Upper portion gill rakers: first branchial arch	20	19(1), 20(10), 21(17), 22(19), 23(24), 24(31), 25(18), 26(6), 27(2), 28(2)	21	19(2), 20(13), 21(13), 22(10), 23(1)	23	20(1), 21(4), 22(3), 23(5), 24(5), 25(1)
Lower portion gill rakers: first branchial arch	30	28(2), 29(3), 30(26), 31(36), 32(24), 33(30), 34(7), 35(2)	28	25(6), 26(12), 27(9), 28(8), 30(3)	32	29(5), 30(6), 31(2), 32(5), 33(1)
Total vertebrae	41	41(7), 42(2), 43(3)	42	42(6), 43(3)	42	41(7), 42(2)
Precaudal vertebrae	24	23(2), 24(10)	23	23(6), 24(3)	24	23(2), 24(7)
Caudal vertebrae	17	17(8), 18(2), 20(2)	19	18(1), 19(6), 20(2)	18	17(6), 18(2), 19(1)
Pre-dorsal bones	10	10(12)	10	10(9)	10	10(9)

In the first PCA, ten morphometric characters had a greater influence on the first axis in the separation of the two groups recovered: HL; anal-fin base length; upper jaw length; length of maxilla beyond posterior margin of orbit; distance between the tip of pelvic fin and anal-fin origin; body height; interorbital distance; pre-anal length; pelvic-fin length (Fig. 4). Basically, the group formed by *Anchoviella* cf. *cayennensis* and the type series of *A. sanfranciscana* on the left of PCA 1 is mostly characterized by specimens in which values of those parameters are proportionately smaller in relation to SL and HL when compared with specimens on the right, identified as *Anchoviella* cf. *perfasciata*.

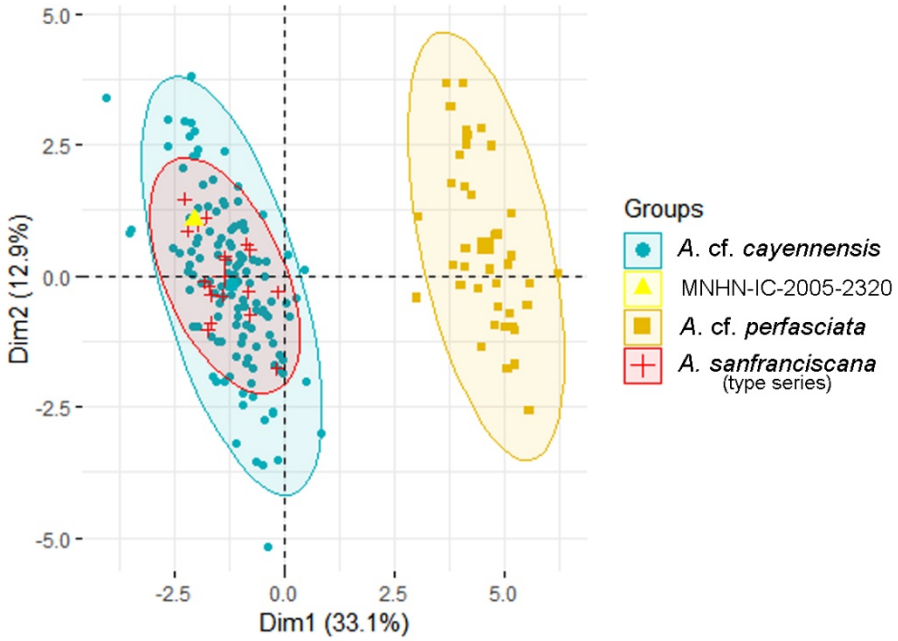

Figure 2. Principal Component Analysis (PCA) of 22 morphometric data with 191 specimens of *Anchoviella* examined.

The second PCA explains 54.7% of the total variation, with 37.9% on the first axis, and 16.8% on the second (Fig. 3). The PCA again indicates the existence of two morphologically distinct groups, one formed by specimens identified as *Anchoviella* cf. *cayennensis*, including RMNH 26294 [based on Whitehead (1973)], in addition to the type series of *A. sanfranciscana*, and the other formed by *Anchoviella* cf. *perfasciata*.

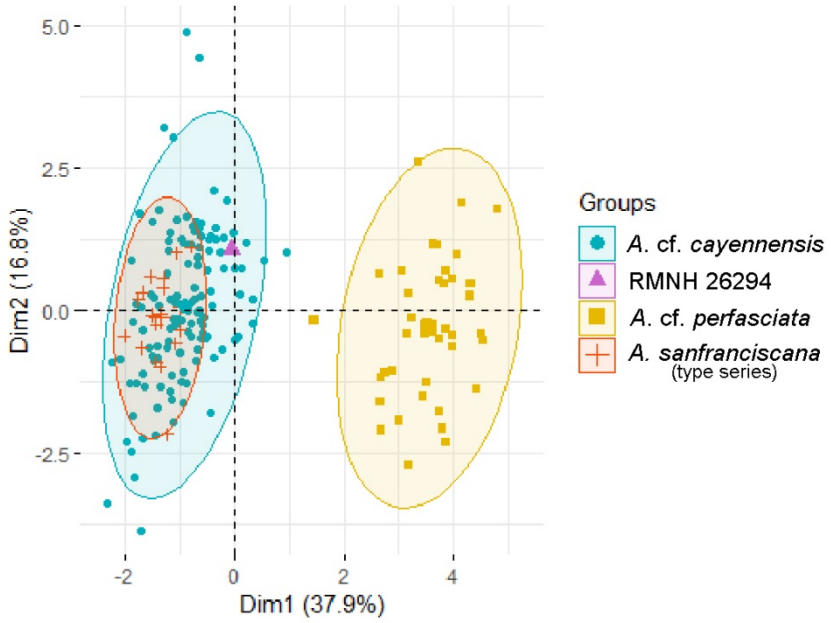

Figure 3. Principal Component Analysis (PCA) of 10 morphometric characters with 191 specimens of *Anchoviella* examined in this study and information from *A. cayennensis* RMNH 26294 obtained from Whitehead (1973).

In the second PCA, four morphometric characters were more relevant to the ordination of specimens on the first axis: anal-fin base length; upper jaw length; head length; body height. In general terms, and similar to the conclusions obtained on PCA 1, those results indicate that the group formed by *Anchoviella* cf. *cayennensis* and the type series of *A. sanfranciscana* is characterized by specimens in which values of those characters are proportionately smaller in relation to SL and HL, when compared with specimens of *Anchoviella* cf. *perfasciata*.

Discussion

Results of the analyses of morphometric data obtained in both PCAs indicate the existence of two morphologically distinct groups among specimens examined, one of them including specimens identified as *Anchoviella cayennensis* and the type series of *A. sanfranciscana*, and the other including specimens identified as *Anchoviella perfasciata* (Figs. 2 and 3). The 10 morphometric characters that are more relevant for the separation between those two groups are indicated in Fig. 4 and are further explored in the redescription of *A. cayennensis*, presented in the next section.

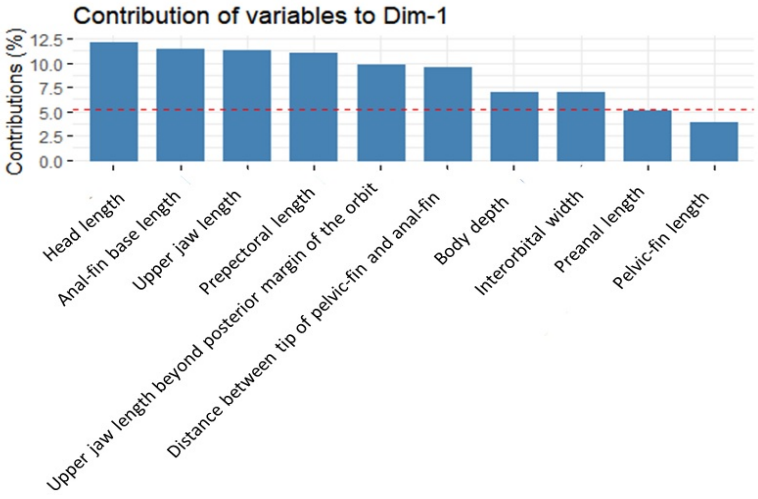

Figure 4. The 10 morphometric characters that most influenced the distribution of specimens along the first axis of the first PCA, which explained 33.1% of the variation between the two morphologically distinct groups herein recognized as *A. cayennensis* and *A. perfasciata*.

Anchoviella sanfranciscana was described based on a relatively small number of specimens (20) and without proper access to comparative material (Barbosa *et al*., 2017). The morphological similarity between *A. sanfranciscana* and *A. cayennensis* was recognized by the authors at the description of the species. Basically, three characters where indicated as diagnostic of *A. sanfranciscana* by Barbosa *et al*. (2017): the presence of a wide silvery lateral stripe, with a well-defined dark brown and yellow lateral band above it, its total width 1.5 to 2 times wider than the ocular (presumably eye) diameter; the distance from the tip of the pectoral fin [apparently wrongly referred to as dorsal fin in the Abstract and in page 164 of Barbosa *et al*. (2017)] and the pelvic-fin base [apparently wrongly referred to as the anal fin in the abstract and in page 164 of Barbosa *et al*. (2017)] similar in length to the pectoral-fin length; and the number of gill rakers in the lower branch of the first branchial arch "unique", 29-35.

Characters proposed by Barbosa *et al*. (2017) as diagnostic for *A. sanfranciscana* are rather problematic or not clearly defined, at least in part reflecting the absence of proper comparative material. The presence of a silvery lateral stripe, for instance, is shared by several species of anchovies, but the stripe tends to reduce significantly or totally disappear in most engraulids stored in scientific collections. In order to test if the width of the silvery lateral stripe in relation to eye diameter is a valid diagnostic feature of *A. sanfranciscana*, a linear regression was performed. In this analysis, values of the width of the silvery stripe measured at the origin of the dorsal fin (where the stripe is

typically larger) and values of the eye diameter of the 20 specimens that compose the type series of *A. sanfranciscana* where compared to the same features of 20 selected specimens of *A. cayennensis* where the stripe was significantly intact after preservation (Table 3).

Table 3: Values (mm) of eye diameter and width of the silvery lateral stripe at the dorsal-fin origin of 20 selected specimens of *A. cayennensis* and in the 20 specimens that compose the type series of *A. sanfranciscana* (SD: Standard Deviation).

	Anchoviella cayennensis			***Anchoviella sanfranciscana***			
	Selected 20 specimens			Holotype	Paratypes		
	Range	Mean	SD		Range	Mean	SD
Eye diameter	7.5 – 9.29	8.37	0.74	7.5	7.2 – 8.4	7.8	0.4
Width of silvery lateral stripe	7.2 – 12.2	10.11	1.16	8.6	8.5 – 10.4	9.18	0.6

Results of the linear regression based on values of eye diameter *vs*. width of the silvery lateral stripe fail to discriminate between the two sets of specimens, *i.e*., width of the silvery lateral stripe is not diagnostic of *A. sanfranciscana* according to the results obtained (Fig. 5).

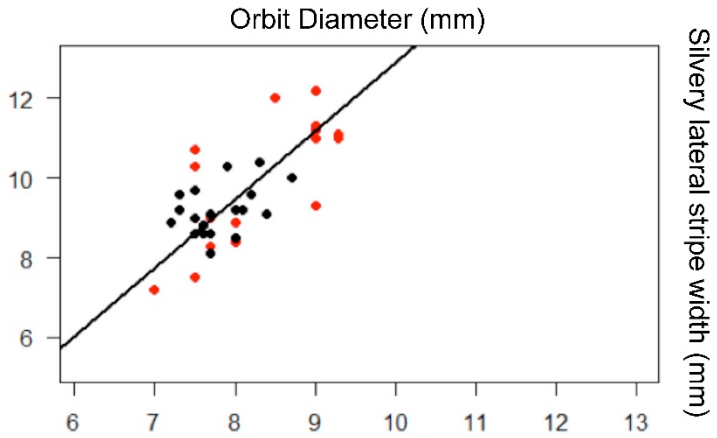

Figure 5. Linear regression of silvery lateral stripe width at dorsal-fin origin *vs.* eye diameter of the type series of *A. sanfranciscana* (black circles) and 20 selected specimens of *A. cayennensis* (red circles).

In addition to the width of the silvery lateral stripe in relation to eye diameter, another feature proposed as diagnostic of *A. sanfranciscana* by Barbosa *et al*. (2017) is the distance between the tip of pectoral-fin to pelvic-fin origin similar to pectoral-fin

length, *vs*. distance between the tip of pectoral-fin to pelvic-fin origin less than half pectoral-fin length in *A. cayennensis* (Barbosa *et al*., 2017:166). To test the validity of this character as diagnostic between the two species, another linear regression was performed with measurements of those parameters in the type series of *A. sanfranciscana* and in 131 specimens herein identified as *Anchoviella cayennensis* (Table 4).

Table 4: Values (mm) of pectoral-fin length and distance between pectoral-fin tip and pelvic-fin base in 131 specimens of *A. cayennensis*, including MNHN-IC 2005-2320, and in the type series of *A. sanfranciscana* (SD: Standard Deviation).

	Anchoviella cayennensis				***Anchoviella sanfranciscana***			
	MNHN-IC 2005-2320	Other specimens			Holotype	Paratypes		
		Range	Mean	SD		Range	Mean	SD
Pectoral-fin length	15.21	14.20 – 20.10	16.85	1.69	15.30	15.00 – 17.00	16.06	0.55
Distance pectoral-fin tip/ pelvic-fin base	4.70	2.40 – 14.00	7.65	2.62	8.30	6.30 – 11.20	8.55	1.27

Results of this linear regression also failed to discriminate between the two sets of specimens, *i.e*., distance from the pectoral-fin tip and pelvic-fin base is not distinctly different in *Anchoviella cayennensis* in comparison to the type series of *A. sanfranciscana* (Fig. 6) according to the data.

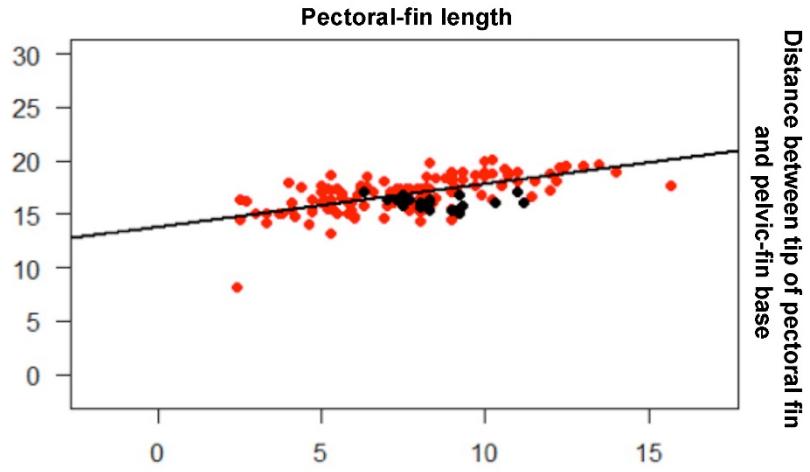

Figure 6. Linear regression of pectoral-fin length *vs.* distance between tip of pectoral-fin and base of pelvic fin of the type series of *A. sanfranciscana* (black circles) and 131 specimens of *Anchoviella cayennensis* (red circles).

Barbosa *et al*. (2017) also noted that in respect to the number of gill rakers, values in the type series of *A. sanfranciscana* are similar in *A. cayennensis* among congeners, a situation that is indeed confirmed by the meristic data presented herein (Table 2). The authors further added that, in spite of all anatomical similarities between *A. sanfranciscana* and *A. cayennensis*, *A. sanfranciscana* has "...a more robust body than *A. cayennensis* and is anatomically similar to […] *A. lepidentostole* [misspelled as "*lepisdostostole*" in the original text]…" (Barbosa *et al*., 2017:162). This supposedly more robust body shape of *A. sanfranciscana* compared with that of *A. cayennensis* was also suggested in x-ray pictures of specimens of the two species presented by the authors (Barbosa *et al*., 2017:fig. 5). However, in addition to this character not being clearly defined, morphometric data presented herein (Table 1) indicates that the apparently more robust shape of *A. sanfranciscana* indicated by Barbosa *et al*. (2017) is most likely an artifact, probably related to the lack of proper comparative material of *A. cayennensis* at the description of *A. sanfranciscana*.

Therefore, all characters proposed as diagnostic for *A. sanfranciscana* are actually shared with *Anchoviella cayennensis*. A boxplot with the scores of each of the groups (*Anchoviella cayennensis*, *Anchoviella perfasciata*, and the type series of *A. sanfranciscana*) in the first PCA, using the morphometric data presented in Table 1, further supports the conclusion that *Anchoviella cayennensis* and *A. sanfranciscana* are not significantly different from each other, but that both are distinct from *A. perfasciata* (Fig. 7).

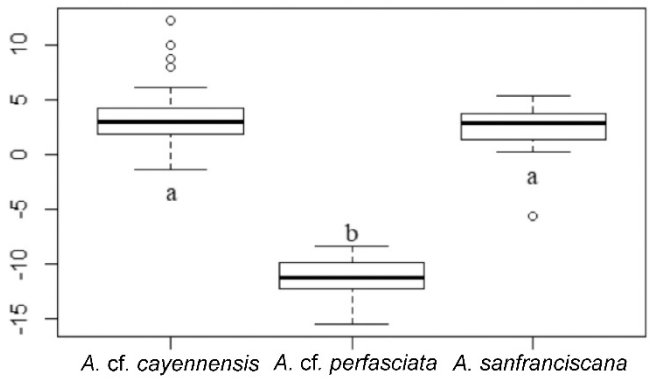

Figure 7. Boxplot with the scores of each group in the first PCA using the morphometric data presented in Table 1; *Anchoviella* cf. *cayennensis* (a; left) and the type series of *A. sanfranciscana* (a; right) are not significantly distinct, but both groups are significantly distinct from *Anchoviella* cf. *perfasciata* (b).

Results obtained herein therefore indicate that *A. cayennensis* and *A. perfasciata* are both valid species, with *A. sanfranciscana* being a junior synonym of the first. Further evidence from gill arch dentition indicating that the two species are distinct is also discussed in the next section, where a redescription of *Anchoviella cayennensis* is presented in light of these conclusions. In addition, all evidence indicates that the syntypes of *Stolephorus cayennensis* either have been lost for decades or have never been deposited in the MNHN Fish Collection (*e.g.*, Whitehead, 1973; pers. obs.). Given the complex taxonomic situation involving these three nominal species, in the following section the specimen deposited under MNHN-IC 2005-2320 is designated as the neotype of *A. cayennensis* in order to define the nominal taxon more objectively (ICZN, 1999).

Anchoviella cayennensis (Puyo, 1945)

Figs. 8, 9 -Tabs. 5 and 6.

Stolephorus cayennensis Puyo, 1945:101-103, fig.1 [type locality: "rivière Cayenne à hauteur de la pointe Macouria, à environ quatre kilomètres de son embouchure" (Cayenne river in Macouria, about four kilometers from its mouth), French Guiana; also reported from "rivière Mahury et le fleuve Kourou" (Mahury and Kourou rivers)]. -Puyo, 1949:157, fig.80 [list of fishes from French Guiana; description republished, no new observations]. -Hildebrand, 1963:212 [assignment to *Anchoviella*; redescription based on published accounts and figures by Puyo (no specimens examined); taxonomic key].

Anchoviella victoriae Hildebrand & Carvalho, 1948:292. [type locality: Vitória, State of Espírito Santo, Brazil]. -Carvalho, 1951:51, fig.1 [list of Brazilian species of *Anchoviella*]. -Santos, 1952:75 [list of marine fishes of Brazil]. -Whitehead, 1973:161 [subjective junior synonym of *Anchoviella cayennensis*]. -Menezes, 1974:216 [holotype information].

Anchoviella cayennensis. -Whitehead, 1973:161, figs.61,62 [redescription based on one specimen from Surinam]. -Whitehead & Bauchot, 1986:49 [information on the type-series specimens]. -Whitehead *et al.*, 1988:330 [diagnosis, biology, and distribution; possible subjective junior synonym of *A. perfasciata*]. -Camargo & Isaac, 2001:140 [list of estuarine fishes of northern Brazil]. -Kullander, & Ferraris Jr. 2003:40 [list of freshwater fishes of Central and South America]. -Nizinski &

Munroe, 2003:766 [list of fishes from Western Central Atlantic]. -Barbosa *et al.,* 2017:167 [list of comparative material].

Anchoviella cayenensis. -Menezes & Figueiredo, 2003:39 [list of marine fishes of Brazil)]. -Loeb, 2012:18 [list of comparative material; taxonomic key]. -Loeb & Figueiredo, 2014:35 [list of comparative material]. -Loeb *et al.*, 2018:2 [list of valid species of *Anchoviella*].

Anchoviella sanfranciscana Barbosa *et al*., 2017. [type locality: northeastern Brazil, São Francisco River estuary between the cities of Brejo Grande, State of Sergipe, and Piaçabuçu, State of Alagoas, Brazil].

Neotype. MNHN-IC-2005-2320, 98.5 mm SL, Atlantic Ocean, Caribbean Sea, Vieux port, Cayenne, French Guiana, 4°55'1.2" N, 52°7'58.8" W, 19 March 2002, M. Leopold (Ifremer).

Non-type specimens examined. Brazil, Pará: MPEG 6304 (1, 115 mm SL), Jubim beach, Marajó bay, Amazon River, 0°48'07.6"S, 48°31'56.5"W , 26 May 1982; MPEG 6306 (1, 115.7 mm SL), Jubim beach, Marajó bay, Amazon River, 0°48'07.6"S, 48°31'56.5"W, 26 June 1982. **Alagoas:** MZUSP 113730 (2, 115.2-117.0 mm SL), Penedo, São Francisco River, 20 January 2013. **Sergipe**: CIUFS 1132 (19, 92.3-122.0 mm SL), povoado Cabeço, São Francisco River, 10°30’2.6”S, 36°24’28”W, September 1975. CIUFS 1131 (1, 114.5 mm SL), continental shelf off Sergipe, 2000; CIUFS 1128 (2, 97.5-115.1 mm SL), continental shelf off Sergipe, 10°52’33”S, 36°56’32”W, August 1999; CIUFS 1129 (2, 96.2-115.9 mm SL), continental shelf off Sergipe, 10°50’53”S, 36°54’53”W, November 1988; CIUFS 1130 (3, 58.2-125.1 mm SL), continental shelf off Sergipe, 2000. CIUFES 3001 (3, 102.7-105.7 mm SL), Neópolis, São Francisco River, 10°18'56.4"S, 36°34'28.2"W, 14 September 2013; MZUSP 11579 (1, 86.3 mm SL), Aracaju, August 1961. **Bahia:** MNRJ 8204 (1, 116.0 mm SL), Caixa Prego, 12 December 12 1944; MZUSP 11583 (1, 113.8 mm SL), praia do Pontal, Ilhéus, 25 October 1971; MZUSP 11582 (8, 92.00-118.3 mm SL), praia do Malhadinho, Ilhéus, 25 October 1971; MZUSP 11580 (1, 107.00 mm SL), praia do Malhadinho, Ilhéus, 26 October 1971. UEFS 12712 (4, 117.0-118.8 mm SL), in front of “Ponta da Tulha”, Ilhéus; UEFS 9860 (2, 90.2-92.4 mm SL), Malhado beach, Ilhéus. **Espírito Santo:** MZUSP 108171 (3, 133.0- 135.0 mm SL), Vila Regência, Doce River. 15 September 2005. MZUSP 011581 (4, 84.4-89.6 mm SL), Vitoria. CIUFES 130808 (22, 93.6-121.0

mm SL), Itapina, Doce River, 19°31'58.9"S, 40°37'59.8"W, 9 May 1980; CIUFES uncatalogued (1, 127.5 mm SL), Regência, Doce River, 19°38'02.1"S, 39°49'10.8"W, July 2016; MZUSP 060368 (23, 104.0-145.5 mm SL), Colatina, Doce River, 1 May 1944. **Rio de Janeiro**: MNRJ 11126 (1, 54.0 mm SL), Itaipu beach, Niterói, 6 October 1978; MNRJ 37790 (2, 108.7-126.7 mm SL), Capixete island, Itaocara, Paraíba do Sul River, 29 October 2010; MNRJ 17869 (3, 123.5-145.0 mm SL) São Fidélis, Paraíba do Sul River, 1996; MNRJ 14774 (1, 135.3 mm SL), São Fidélis, Paraíba do Sul River, 21°40'S 41°45'W, November 1989; MZUSP 109205 (1, 126.9 mm SL), São Fidélis, Paraíba do Sul River, 21°38'00''S, 041°45'30''W, 29 March 2010; NPM 1883 (6, 91-141.6 mm SL), São Fidélis, Paraíba do Sul River, 21°37'60.0"S, 41°38'16.0"W, 29 April 2012; NPM 1884 (5, 101.1-113.1 mm SL), Campos dos Goytacazes, Paraíba do Sul River, 30 March 2012; NPM 3265 (7, 125.0-137.6 mm SL), São Fidélis, Paraíba do Sul River, 21°37'60.0"S, 41°38'16.0"W, 5 August 2013.

Type series of *Anchoviella sanfranciscana*, junior synonym of *A. cayennensis*: Holotype: INPA-ICT 053278 (106.0 mm SL) northeastern Brazil, São Francisco River estuary between cities of Brejo Grande, State of Sergipe, and Piaçabuçu, State of Alagoas, 10°24'44.1"S 36°27'28.4"W, A.G.S. Silva & A.R.R. Araújo, April 12, 2015. **Paratypes**: INPA-ICT 053279 (4, 105.5-114.7), São Francisco River estuary between the cities of Brejo Grande, State of Sergipe, and Piaçabuçu, State of Alagoas, 10°24'44.1"S 36°27'28.4"W, 12 April 2016. **Sergipe**: INPA-ICT 053280 (15, 103.6-128.0 mm SL), São Francisco River estuary near Saramen Village in the municipality of Brejo Grande, 10°28'22.2"S 36°25'02.6"W. A.G.S. Silva & A.R.R. Araújo, 19 November 2015.

Diagnosis. *Anchoviella cayennensis* is distinguished from congeners, except *A. juruasanga, A. guianensis, A. carrikeri, A. vaillanti* nd *A. perfasciata* by the anal-fin origin under or behind the vertical through the base of the last dorsal-fin ray (*vs.* origin of anal fin anterior to vertical through the base of last dorsal-fin ray). *Anchoviella cayennensis* can also be distinguished from *A. juruasanga*, *A. guianensis*, *A. carrikeri*, *A. vaillanti*, except *A. perfasciata*, by 28-35 gill rakers in the lower portion of first branchial arch (*vs.* 12-27). *Anchoviella cayennensis* is distinguished from *A. perfasciata* by a reduced basibranchial dentition, consisting of a narrow median tooth plate over

basibranchials 1-3, not expanded posteriorly over hypobranchials 2 (*vs.* a developed basibranchial dentition, tooth plate over basibranchials 1-3 wide and expanded posteriorly over hypobranchials 2). In addition, *A. cayennensis* can be distinguished from *A. perfasciata* by 11-14 branched rays in the anal fin (*vs.* 14-16), and the upper jaw slightly smaller, 56.12%-69.42% (usually 65.38%) of HL (*vs.* 69.23%-77.30% (usually 74,1%) of HL.

Figure 8. (A) *Anchoviella perfasciata* (Poey, 1890), Holotype; MCZ 17965, 79.4 mm SL (Credit: Museum of Comparative Zoology, Harvard University); (B) *Anchoviella cayennensis* (Puyo, 1945), Neotype, MNHN-IC-2005-2320, 98.5 mm SL; (C) *Anchoviella sanfranciscana*, Holotype, INPA-ICT 053278, 105 mm SL (after Barbosa *et al*., 2017).

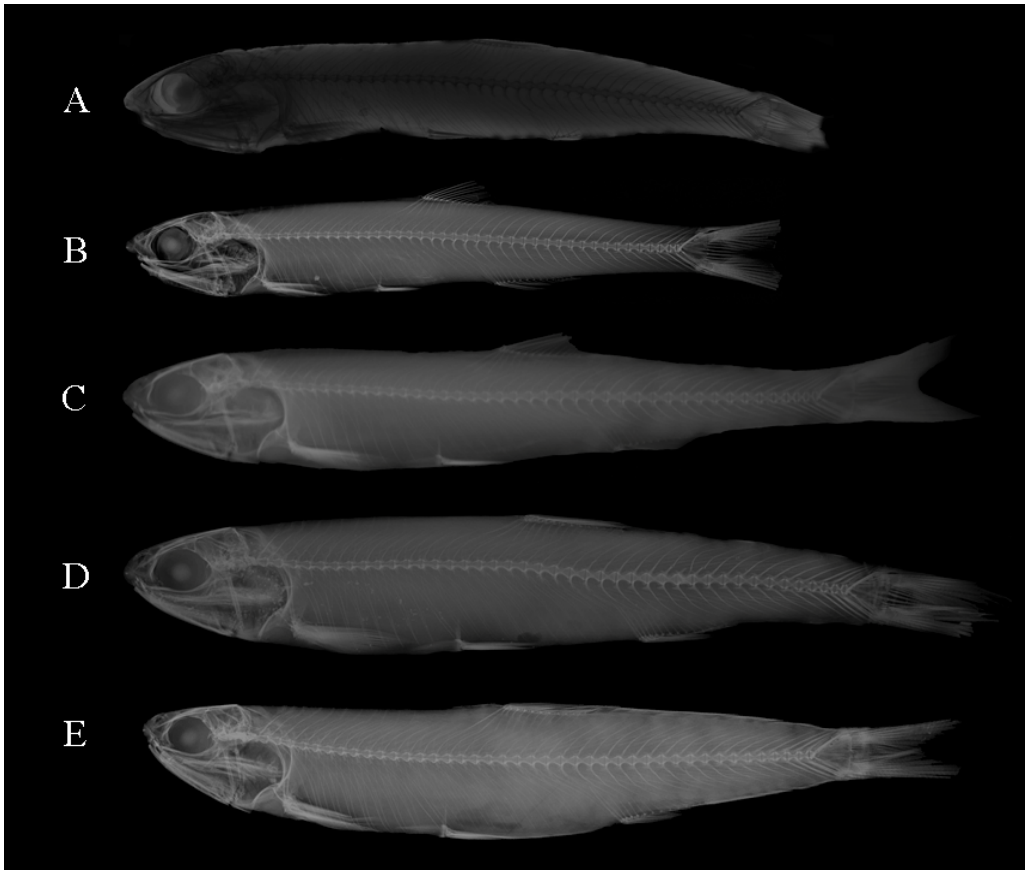

Figure 9. (A) *Anchoviella perfasciata*, holotype, MCZ17965, 79,39 mm SL; (B) *Anchoviella perfasciata*, UF208245, 64 mm SL; (C) *Anchoviella cayennensis* (Puyo, 1945), Neotype, MNHN-IC-2005-2320, 98,5 mm SL (Credit: MNHN - ICHTYOLOGIE - J. PFLIGER & Z. GABSI); (D) *Anchoviella cayennensis*, CIUFES1131, 110 mm SL; (E) *Anchoviella sanfranciscana*, Holotype INPA-ICT 053278, 105 mm SL.

Description. Morphometric and meristic data of holotype and specimens examined summarized in Tables 5 and 6, including the type series of *A. sanfranciscana*. Body elongated and slightly compressed laterally, maximum height at vertical through dorsal-fin origin, approximately 5 times in SL; a longitudinal silvery stripe along lateral of the body, from mid- to upper-third of branchial opening to middle of caudal-fin base, height of stripe at origin of dorsal fin 1-1.5 times eye diameter; upper and ventral margins of lateral stripe with black pigment, more evident at upper margin in preserved specimens; predorsal bones 10(23), total vertebrae including compound centrum (first preural+first ural centrum+uroneural) 41(15)*, 42(5) or 43(3); precaudal vertebrae 23(4) or 24(19)*, caudal vertebrae 17(15)*, 18(5) or 20(3); maximum body size 145,5 mm SL.

Head longer than high, tip gently pointed dorsally; snout short, about half orbit diameter, two slit-like parallel nostrils on top of snout at each side of head; mouth slightly inclined posteriorly, subterminal; upper jaw slightly curved, relatively short,

56.12%-69.42% (usually 65%) HL; posterior margin of upper jaw rounded, slightly projecting beyond tip of second supra-maxilla, failing to reach anterior margin of preopercle by half the pupil diameter; upper-jaw length beyond posterior margin of orbit 13.21-25.46% (usually 17%) of HL; a single row of delicate, sharp, tapered curved teeth in the premaxilla, maxilla and dentary; teeth in the maxilla slightly inclined backwards in the anterior third of the bone, slightly inclined forward in the remaining structure; a "gap" composed of a toothless area at the anterior portion of the dentary; posterior projections of vomer with one to three minute teeth; conical teeth present at the ventral border of the palatine, continuous to a similar row of teeth at the ventral border of the ectopterygoid; small, conical teeth also forming a medial row on the anterior half of the endopterygoid; first supramaxilla long, scale-like, about 2/3 of maxilla length and partially covered laterally by infraorbital series; second supramaxilla also developed but smaller, a little less than half maxilla length, posterior half scale-like, anterior portion in the form of a spike; eyes large, about 27.77–37.5% (usually 33.33%) of HL, dorsally located in relation to the longitudinal line passing through the dorsal point of insertion of pectoral fin, also visible in ventral and dorsal views; operculum length about twice in height, lower margin oriented at an angle of about 60 degrees; posterior and lower margins of preopercle forming an angle of about 90 degrees; exposed portion of subopercle long and narrow; posterior border of gill opening evenly rounded; pseudobranch present on inner side of operculum, smaller than orbit diameter, between 14.8-23.3% HL; lateral line channels of the *panamensis*-type on the operculum, *i.e.*, without a secondary preopercular branch projecting into the opercle (Fig. 10; Whitehead *et al.*, 1988).

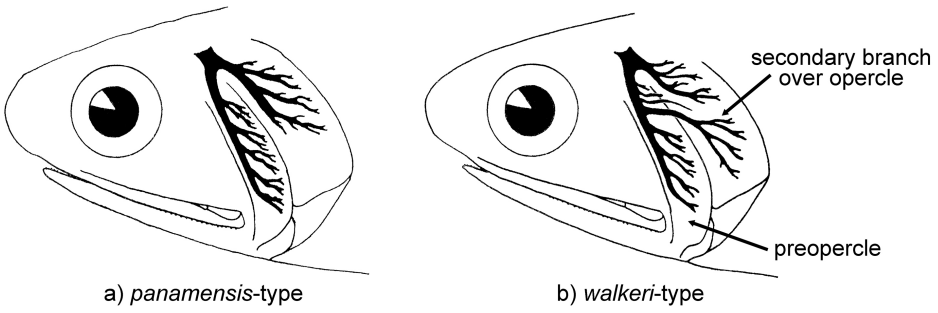

Figure 10. Variations of sensory canals on the gill cover of species of *Anchoviella* according to the absence (a) or presence (b) of a secondary preopercular branch over the opercle (after Whitehead *et al.*, 1988)

Recessus lateralis chamber developed, in the approximate shape of a bell, tapered dorsally to the supraorbital canal, mostly covered laterally by the lateral wing of the frontal; anterior opening of the *recessus* (connected to infraorbital canal) mostly downward directed, developed, lateral wall formed by the lateral wing of the frontal, located between the anterior (sphenotic) and posterior (pterotic) sockets for articulation of the hyomandibula head; middle opening of the *recessus* (connected to preopercular canal) located immediately posterior to anterior opening and about half its size, lateral wall formed by the lateral wing of the frontal but also partially encircled by the pterotic; middle opening of the *recessus* apparently continuous with a scythe-like posterior opening of the *recessus* at the posteroventral border of the lateral wing of the frontal (possibly an expanded accessory canal opening to the *recessus* chamber); posterior opening of the *recessus* (connected to the single branch shared anteriorly by the extrascapular and posttemporal canals at the extrascapular bone) developed, oblong-shaped, its height about four times its maximum length at the middle of the opening; posterior opening of the *recessus* laterally restricted to the pterotic, totally encircled by a flange of the bone; posterior portion of the opening at the pterotic wall forming an approximately triangular process with a posterodorsally directed tip.

Prootic and pterotic bulla inconspicuous but fairly developed, pterotic bulla laterally round, not bulging into pre-epiotic fossa, and at the level of the *recessus* chamber floor in lateral view; temporal foramen exposed, not covered laterally by the frontal, shaped in the form of an upside-down triangle; pre-epiotic fossa also developed, somewhat round in shape but bulged posteroventrally, mostly limited anterodorsally by the parietal, anteroventrally by the pterotic, and posteriorly by the epiotic; a conspicuous circular opening at the posteroventral region of the pre-epiotic fossa in the epiotic, leading to the back of the skull; extrascapular canals at parietal not totally encircled by bone, ossified segment of canals restricted to distal third of the dorsal portion of the parietals; extrascapular canals at parietals immediately posterior to posterior margin of frontals at the top of cranium.

Dorsal profile of postorbital region of head uniformly plain but gently bulged in cross section, crests absent at postorbital region, frontals developed and extended posteriorly; median dorsal-strut of supraoccipital almost totally obliterated dorsally by the frontals, which are in close proximity medially throughout their extent; a pair of slit-like small fontanels present laterally to the supraoccipital median strut, bordered

anteriorly by the posterior margin of the frontals and posteriorly by the lateral walls of the supraoccipital; a median ridge on top of head at orbital region separating the supraorbital canals laterally; two bony bridges on each frontal between the median crest and the lateral margin of the bone, shielding above the supraorbital canal; the anterior bony bridge is located slightly anterior to the middle of the orbit and is oriented in a 90 degree angle in relation to the longitudinal axis of the body; the posterior bony bridge is located slightly in advance of the posterior margin of the orbit and is oriented in an angle of approximately 45 degrees in relation to the longitudinal axis; anterior frontal fontanels absent, but bone at the level of the anterior bridge somewhat soft and apparently able to sustain some level of displacement; mesethmoid developed, compressed laterally and projected anteriorly in relation to vomer, a small portion of its posterodorsal region sandwiched between the anterior tips of frontals at the top of the cranium; a pair of lateral processes on the mesethmoid, the anterior one located at the anterior tip of the bone and projecting laterally in approximately a right angle, the posterior one located in the posteroventral region of the mesethmoid, close to the vomer, projected posteroventrally and associated with the premaxilla; nasal and antorbital extremely developed, forming an apparatus that supports the greatly expanded nasal chamber.

Long and narrow gill rakers on first branchial arch, their oral surfaces densely covered with delicate teeth; total number of gill rakers on first branchial arch 49(3), 50(7)*, 51(9), 52(13), 53(23), 54(22), 55(26), 56(16), 57(11), 58(12), 59(7), 60(1), 61(1); number of gill rakers on lower portion of first branchial arch 28(2), 29(8), 30(33)*, 31(38), 32(30), 33(31), 34(7), 35(2); number of gill rakers on upper portion of first branchial arch 19(1), 20(12)*, 21(21), 22(22), 23(30), 24(36), 25(19), 26(6), 27(2), 28(2); about 6 rakers also present at the hind face of the dorsal portion of third branchial arch; rakers absent from hind face of the lower portion of third branchial arch and from both dorsal and ventral portions of more anterior arches; basihyal cartilaginous, reduced, but partially covered by a small tooth plate bearing a few scattered delicate teeth; an apparently single, narrow, continuous tooth plate with delicate teeth extending from the anterior portion of basibranchial 1 to the middle ossified portion of basibranchial 3; tooth plate over basibranchials not expanded laterally over the pair of hypobranchials 2; posterior endochondral tip of basibranchial 3 under anterior portion of a cartilaginous and relatively long basibranchial 4; narrow delicate tooth plates

densely packed with minute teeth arranged in a series at the dorsal (oral) surface of the ventral portion of arches 1 and 2, including lateral margin of the dorsal surface of hypobranchial 2; tooth plates also present on lower portion of third arch (*i.e.*, ceratobranchial 3), not extensively covering the structure; tooth plates absent in the lower portion of fourth arch (*i.e.*, ceratobranchial 4); about 30 conical and developed teeth present on the posterior region of ceratobranchial 5, fused with the underlying bone, teeth at the posterior margin distinctly more developed than teeth at the anterior portion of the bone; anterior elements of upper portion of branchial arches strongly meeting in the midline; gongyloid cartilage reduced, clearly distinct in NPM 1883, apparently reduced in other C&S specimens; small scattered tooth plates present on oral (ventral) surface of upper gill arches, plates associated with infrapharyngobranchials 2-3 fused with the underlying bone; infrapharyngobranchial 3 cartilaginous, but two upper pharyngeal tooth plates present and with well-developed dentition, the more posterior in the shape of a narrow triangle, oriented posterolaterally; epibranchial 4 developed, but epibranchial organ apparently absent or extremely reduced; branchiostegal rays 12 (5 C&S specimens).

Dorsal-fin origin equidistant between anterior border of eye and caudal-fin base; base of dorsal fin lined with small scales; dorsal-fin rays ii(3) or iii(148)*, followed by 9(1), 10(3), 11(22), 12(79)*, 13(42), or 14(4) branched rays; longest dorsal-fin rays reaching to tip of last branched dorsal-fin ray when fin depressed; pectoral-fin rays i(146)*, followed by 10(1), 11(2), 12(23), 13(47), 14(69)* or 15(4); pectoral-fin tip failing to reach pelvic-fin base by almost the eye diameter, or about 27-85% (usually 50%) of pectoral-fin length; axillary scale present, developed, almost equal in length to pectoral fin; pelvic-fin origin slightly in advance of middle distance between pectoral-fin origin and anal-fin origin; pelvic-fin rays i(147)* or ii(1), followed by 5(3), 6(131)* or 7(14) branched rays; last two pelvic-fin rays joined to each other and to the body by a thin membrane for about half their length, a short triangular scale between pelvic fins; axillary scale also present on pelvic-fin, often lost in specimens examined; a single pelvic scute present in front of pelvic-fin base, median keel absent, ascending arms slightly inclined anteriorly, their distal tips reaching about ¼ of body height at that vertical; pre-pelvic and post-pelvic scutes absent; anal-fin origin under or slightly behind vertical through the base of last dorsal-fin ray, slightly nearer to the pelvic-fin origin than to caudal-fin origin; base of caudal-fin lined with small scales; anal-fin rays

ii(2) or iii(146)*, followed by 11(11), 12(59), 13(71) or 14(7)*; caudal fin markedly forked, upper and lower lobes about the same size; 1(6) or 4(5) rudimentary fin rays (*sensu* Grande & Bemis, 1998) on upper lobe of caudal fin, followed by iiii(150), 9(71), 10(63), 11(16) principal (segmented) rays; 1(4) or 4(5) rudimentary fin rays on lower lobe, followed by iiii(150), 9(65), 10(67), 11(18) principal (segmented) rays (rudimentary caudal-fin rays counted only in 5 C&S specimens); bases of middle caudal-fin rays with a "two-peg" arrangement (*sensu* Grande & Nelson, 1985), *i.e*., a single peg present on outer margin of both rays, ventral peg absent in upper middle caudal-fin ray, dorsal peg absent in lower middle caudal-fin ray; a pair of developed alar scales on each lobe of caudal fin, borders delicate and distinctly emarginated in C&S specimens, condition not so evident in alcohol-preserved specimens; outer alar scales more developed, the alar scale associated with upper caudal-fin ray 5 (counting from the first, middle, upper caudal-fin ray) gently curved downwards over the scale associated with upper caudal-fin ray 4, the alar scale associated with lower caudal-fin ray 4 (counting from the first, middle, ventral caudal-fin ray) gently curved upwards over the scale associated with lower caudal-fin ray 3; two epurals, two free uroneurals, six independent hypurals; interlobar notch between hypurals 2 and 3 (Monod's hypural diastema) triangular in shape, somewhat reduced.

Lateral line absent; scales cycloid, often lost; 41(8) or 42(12) transverse series at the longitudinal line; anterior border with distinct "shoulders" and median prominence, unexposed portion of scale with a single complete vertical striation, preceded in the posterior scales by short radial striae; exposed portion of scale with a vertical striation, often curved, the whole area reticulated in posterior scales; scales along dorsal region with 6-7 longitudinal striae [most descriptive information of scales after Whitehead (1973)].

Table 5: Morphometric data of 151 specimens of *Anchoviella cayennensis*, including the type series of *A. sanfranciscana* (SD: Standard Deviation).

	Range	Mean	SD	Mode
SL (mm)	54 – 145.5	100.98	-	-
HL (mm)	13.7 – 32.1	25.472	-	-
Percents of SL				
Body Depth	11.33 – 19.86	17.29	1.64	19.04
Caudal peduncle depth	6.52 – 10.1	7.96	0.56	7.69
Head Length	19.85 – 25	22.73	0.83	22.41
Dorsal-fin base length	8.65 – 15.16	11.87	1.01	11.96
Anal-fin base length	9.36 – 14.35	11.51	0.97	10.52
Pectoral-fin length	12.76 – 19.76	14.99	0.97	14.53
Pelvic-fin length	7.40 – 12.44	9.44	1.18	10
Predorsal length	45.66 - 56.33	52.51	1.98	52.22
Pre-pectoral length	20.16 – 30.32	23.84	1.17	23.60
Prepelvic length	39 – 53	43.24	3.95	44.31
Preanal length	58.71 – 75.68	67.73	2.78	67.95
Pectoral-fin axillary scale length	9.48 – 17.4	14.24	5.6	14.01
Pelvic-fin axillary scale length	7.78 – 11.14	9.3	0.94	9.62
Distance: tip of pectoral-fin, insertion of pelvic-fin	2.88 – 10.02	6.66	1.74	6.66
Distance: tip of pelvic-fin, anal-fin	8.59 – 20.29	14.86	2.21	15.83
Percents of HL				
Snout length	13 – 25	18.73	2.4	20
Upper jaw length	56.12 – 69.42	65.13	1.9	65.38
Upper jaw depth	3.85 – 8.75	5.26	0.67	5
Upper jaw length beyond posterior margin of orbit	13.21 – 25.46	17.23	2.02	17.85
Orbit diameter	27.77 – 37.5	32.34	1.93	33.33
Post-orbital distance	44 – 58.62	52.28	2.49	52
Interorbital width	19.8 – 31.98	24.29	1.61	25

Table 6: Meristic data of specimens of *Anchoviella cayennensis*, including the type series of *A. sanfranciscana* (maximum n=151). Frequency of each count is indicated in parentheses ("i" indicates number of unbranched fin-rays):

Dorsal-fin rays	ii(3), iii(148), 9(1), 10(3), 11(22), 12(79), 13(42), 14(4)
Pectoral-fin rays	i(146), 10(1), 11(2), 12(23), 13(47), 14(69), 15(4)
Pelvic-fin rays	i(147), ii(1), 5(3), 6(131), 7(14)
Anal-fin rays	ii (2) or iii (146), 11(11), 12(59), 13(71), 14(7)
Caudal-fin rays: upper portion	iiii(150), 9(71), 10(63), 11(16)
Caudal-fin rays: lower portion	iiii(150), 9(65), 10(67), 11(18)
Total gill rakers (first branchial arch)	49(3), 50(7), 51(9), 52(13), 53(23), 54(22), 55(26), 56(16), 57(11), 58(12), 59(7), 60(1), 61(1).
Gill rakers, upper portion (first branchial arch)	19(1), 20(12), 21(21), 22(22), 23(30), 24(36), 25(19), 26(6), 27(2), 28(2)
Gill rakers, lower portion (first branchial arch)	28(2), 29(8), 30(33), 31(38), 32(30), 33(31), 34(7), 35(2)
Total vertebrae	41(15), 42(4), 43(3)
Precaudal vertebrae	23(4), 24(18)
Caudal vertebrae	17(15), 18(4), 19 (1), 20(2)
Pre-dorsal bones	10(22)

Coloration in life. [most descriptive information after Puyo (1945, 1949)] Body light brown, small specimens probably translucent; opercular region somewhat darker, with

iridescent reflections, some areas with a metallic blue hue; a well-marked silvery lateral stripe, slightly tapering towards tail, a darker layer of melanophores stripe underneath the guanine layer; posterior third of the body with diffuse transverse silvery streaks projecting from the lateral stripe, directed towards the ventral part of the caudal peduncle; irregularly shaped silvery spots also disposed on the caudal-fin base; dorsal and anal fins hyaline to translucent; pectoral and pelvic fins hyaline; caudal fin with a lighter coloration compared with the body, upper and lower borders of the caudal fin slightly tinged with brown.

Coloration in alcohol. Body brown to yellowish; darker pigments more evident on specimens collected in estuaries, oceanic specimens overall lighter in coloration; silver to pale lateral stripe, often partially or totally absent in preserved specimens, when present extending from the posterior border of the operculum to the caudal peduncle; darker line extending along the dorsal margin of the silver stripe region present in most specimens, even when silver stripe is absent due to guanine layer decay after preservation; largest width of dorsal stripe 1 to 1.5 times orbit diameter; black spots present along the dorsal profile, from the anterior portion of head to the caudal fin, including dorsal-fin base; a distinct somewhat diamond-shaped blackish area present at nape region, anterolaterally limited by the pair of posttemporal bones; top of head in the region posterior to orbit also blackish, a median darker stripe projecting anteriorly up to the tip of the nose; black spots also present on anterior region of anal- and caudal-fin bases; iris and post-orbital, gular and infraorbital regions with some guanine; fins hyaline but some brownish to black dots on alar scales and along caudal-fin rays.

Sexual dimorphism. No sexual dimorphism was observed among specimens examined. However, ripe females collected in estuaries and rivers seem to be overall larger and more robust in terms of abdominal girth.

Geographic distribution. Confirmed records of *A. cayennensis* in Museum Collections (Fig. 11) indicate that the species is distributed in coastal and estuarine environments along the Atlantic coast of South America, from Surinam (Coppename river near Hermina bank; North Atlantic) to the State of Rio de Janeiro (Itaipú beach, Niterói; South Atlantic), southeastern Brazil. More data is needed from northern Brazil, between the States of Piauí and Pernambuco, where the species is also probably present. Confirmed records of both *A. cayennensis* and *A. perfasciata* in this study suggest that

the two species are not sympatric in any portion of their distribution, but more data is needed in northern South America.

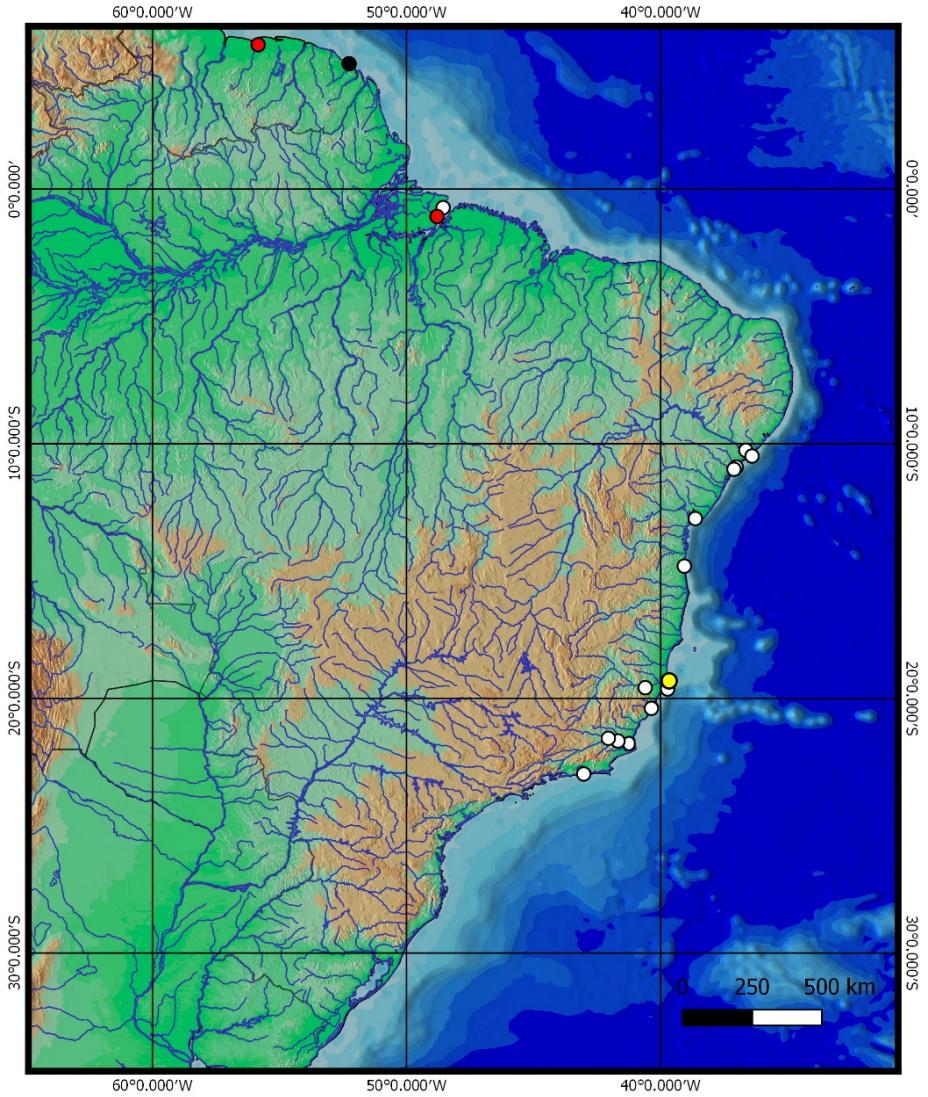

Figure 11. Localities of specimens of *A. cayennensis* examined in the study (white circles: non-type specimens; black circle: type locality), with additional locality information from Whitehead (1973; red circles) and Hildebrand & Carvalho (1948; yellow circles).

Ecological notes. *Anchoviella cayennensis* was described from two specimens collected in the mouth of the Cayenne River, French Guiana. Puyo (1945) reported on additional specimens collected by fishermen in the Mahury and Kourou rivers, also coastal rivers in French Guyana. He apparently regarded the species as not migratory and endemic to estuaries and coastal rivers of the region [“on ne le pêche jamais en mer”; “Cette espèce, à l'encontre des autres *Stolephorus*, doit être sédentaire.” (Puyo, 1945: 103)]. It is interesting to note that more than 70 years later Barbosa *et al*. (2017) also considered

that *A. sanfranciscana*, now under the synonymy of *A. cayennensis* according to the results presented herein, was endemic to the estuary of the São Francisco River, northeastern Brazil. The fact that the type series of both *A. cayennensis* and *A. sanfranciscana* were collected in estuaries might not be just a coincidence; this relatively rare species seems to have a preference for estuaries and lower portions of coastal rivers, judging by the fact that most specimens examined in this study (123 out of 151) were collected in those environments. However, the species is at least occasionally collected in open marine coastal waters. Valentim & Esteves (2018) recently reported that *A. cayennensis* apparently migrate during spawning to the upper section of the lower Paraíba do Sul River in southeastern Brazil. Still according to Valentim & Esteves (2018), the reproductive peak of *A. cayennensis* in the Paraíba do Sul River occurs during the dry season (March-October), when artisanal catches increase significantly. Therefore, and contrary to Puyo's (1945) initial assumption, it seems that *A. cayennensis* is a migratory coastal species, perhaps with a preference for estuaries, but more data on the abundance, frequency and reproduction of *A. cayennensis* is needed, especially in large rivers such as the São Francisco, Amazonas and Cayenne.

Popular names. Cayenne anchovy (English), Manjuba, Manjubinha, Manjuba Perna-de-Moça (Brazilian Portuguese), Anchovieta de Cayena (Spanish), Anchois de Cayenne, Jamais-gouté (French).

Conservation status. Judging by the small size of lots examined (maximum of 23 specimens; MZUSP 60368) and the relatively low total number of specimens identified in ichthyological collections, *A. cayennensis* is apparently naturally rare, especially when compared to more abundant sympatric species of the genus, such as *A. lepidentostole* and *A. guianensis*. The species is also apparently rare in the estuary of the Cayenne river (Tagliarolo, M. and Rousseau, Y. - "Institut Français de Recherche pour l'Exploitation de la Mer - IFREMER Guiane", pers. comm.). Lower portions of coastal rivers and estuaries are highly impacted by several human activities, particularly in the São Francisco river and in other rivers of the central coast of Brazil. The species is now targeted along with *A. lepidentostole* in the Paraíba do Sul river (Valentim & Esteves, 2018), and is also probably fished as by-catch in artisanal fisheries throughout its distributional range. In spite of those possible impacts, the geographic distribution of the species is fairly broad, and at the moment there is no evidence indicating substantial

declines of its population. *Anchoviella cayennensis* was therefore recently assessed as Least Concern (LC) by the "International Union for Conservation of Nature" (IUCN) at the global level (Carpenter, 2015) and also in Brazil (ICMBio/MMA, 2018), which includes most of its distribution. However, giving both its apparent rarity and likely dependence on estuaries and lower portions of coastal rivers for reproduction, the species might be threatened locally. More data is necessary.

Key to marine and estuarine Atlantic species of *Anchoviella*

The identification key presented below for eight coastal and estuarine species of *Anchoviella* was proposed based on the examination of specimens by the authors and information from the literature, including original descriptions, taxonomic revisions, and taxonomic guides, such as Hildebrand (1963), Whitehead (1973), Figueiredo & Menezes (1978), Whitehead *et al*. (1988), Nizinski & Munroe (2003), Loeb (2012, 2013) and Loeb & Figueiredo (2014). *Anchoviella carrikeri, A. jamesi* (Jordan & Seale, 1926), *A. juruasanga* and *A. hernanni* Loeb, Varella & Menezes, 2018 are strictly freshwater species of the genus from the Amazon basin, and also from the Orinoco in the case of *A. jamesi* (Whitehead *et al*., 1988; Loeb, 2012, 2013; Loeb & Figueiredo, 2014; Loeb *et al*., 2018). Their occurrence in estuaries and coastal rivers of the Atlantic coast of South America is highly unlikely, therefore those species are not included in the key presented below. *Anchoviella vaillanti* is an apparently strictly freshwater species endemic to the São Francisco river, northeastern Brazil (Whitehead *et al*., 1988; Loeb & Figueiredo, 2014). Records of the species in the estuary of that river require verification, but the species is included in the taxonomic key presented below. Ongoing studies indicate that *Anchoviella perezi* (Cervigón, 1987) and *A. blackburni* Hildebrand, 1943, which are sometimes recognized as valid (*e.g*., Kullander & Ferraris, 2003; Di Dario et al., 2017; Di Dario, 2018; Fricke *et al*., 2019), are actually junior synonyms of *A. jamesi* and *A. lepidentostole*, respectively (Loeb *et al*., 2018). Therefore, those species are not included in the key. Judging by the number of incorrect identifications of lots examined in this study from collections made in estuaries and coastal rivers of northern South America, it seems that specimens of the relatively more abundant *A. guianensis* (Eigenmann, 1912) are often misidentified as *A. cayennensis* in that region. In addition to the characteristics indicated in the taxonomic key, *A. cayennensis* seems

to attain a fairly larger SL (145.5 mm *vs*. about 70 mm), a condition that may help to properly identify specimens.

1a. Anal-fin origin located at or posterior to the vertical through base of last dorsal-fin ray.....2

1b. Anal-fin origin anterior to the vertical through base of last dorsal-fin ray.....5

2a. Upper-jaw length beyond posterior margin of orbit about up to 9% of HL.....*Anchoviella guianensis*

2b. Upper-jaw length beyond posterior margin of orbit more than 13% of HL.....3

3a. 18-24 rakers on lower portion of first branchial arch; 17-22 branched anal-fin rays.....*Anchoviella vaillanti*

3b. 25-35 rakers on lower portion of first branchial arch; 11-16 branched anal-fin rays.....4

4a. 28-35 rakers on lower portion of first branchial arch; 11-14 branched anal-fin rays; upper jaw 56.12 - 69.42% (usually 65.38%) of HL; reduced basibranchial dentition, consisting of a narrow median tooth plate over basibranchials 1-3, not expanded posteriorly over hypobranchials 2……..……..*Anchoviella cayennensis*

4b. 25-30 rakers on lower portion of first branchial arch; 14-16 branched anal-fin rays; upper jaw 69.23 - 77.30% (usually 74,1%) of HL; developed basibranchial dentition, tooth plate over basibranchials 1-3 wide and expanded posteriorly over hypobranchials 2…….....*Anchoviella perfasciata*

5a. Upper jaw shorter than lower jaw; upper jaw 51-62% of HL.....*Anchoviella brevirostris*

5b. Upper jaw longer than lower jaw; upper jaw 63-80% of HL.....6

6a. Upper-jaw length beyond posterior margin of orbit about up to 5.9% of SL ……..……..……...*Anchoviella manamensis*

6b. Upper-jaw length beyond posterior margin of orbit more than 7.5% of SL……..…….7

7a. "*panamensis*-type" sensory channels over operculum; 10 to 12 branched pectoral-fin rays (Fig. 10a).....*Anchoviella elongata*

7b. "*walkeri*-type" sensory channels over operculum; 12 to 14 branched pectoral-fin rays (Fig. 10b).....*Anchoviella lepidentostole*

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Conclusão

Os resultados obtidos no presente estudo corroboram a hipótese de que *Anchoviella cayennensis* e *A. perfasciata* são espécies válidas. Apesar da sobreposição parcial em três caracteres diagnósticos entre ambas as espécies, as Análises de Componentes Principais (PCA) efetuadas com caracteres morfométricos e dados adicionais oriundos da anatomia interna (dentição dos arcos branquiais) indicam a existência de dois grupos morfologicamente distintos, correspondentes às duas espécies.

As análises efetuadas também indicaram uma grande similaridade morfológica entre os espécimes atribuídos a *Anchoviella cayennensis* e *A. sanfranciscana*. Com isso, é proposto que *A. sanfranciscana* trata-se de um sinônimo júnior de *A. cayennensis*.

Anchoviella cayennensis e *A. perfasciata* também parecem ser espécies relativamente raras entre diversas outras espécies marinhas e estuarinas do gênero. Além disso, ao longo do estudo percebeu-se que existe uma grande quantidade de identificações errôneas de manjubas em Coleções Científicas nacionais e internacionais, ressaltando a necessidade de estudos mais aprofundados na taxonomia e identificação de Engrauloidea como um todo.