



Museu de Zoologia
Universidade de São Paulo

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**Phylogeny of Stromateiformes (Teleostei; Percomorphacea)
based on phenotypic data**

**Relações filogenéticas de Stromateiformes (Teleostei;
Percomorphacea) com base em dados fenotípicos**

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Tese apresentada ao Programa de Pós-Graduação do Museu de Zoologia da Universidade de São Paulo para obtenção do título de Doutor em Ciências (Sistemática, Taxonomia Animal e Biodiversidade).

Orientador: Prof. Dr. Aléssio Datovo

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RESUMO

A divisão Percomorphacea engloba a maior diversidade de peixes vivos, somando mais da metade dos peixes de nadadeiras raiadas e o equivalente a praticamente um quarto de todos os vertebrados atuais. Entretanto, as interações entre a maioria das linhagens de Percomorphacea ainda est longe de uma resolu satisfatria. Dentre as 30 ordens de Percomorphacea reconhecidas atualmente, Stromateiformes agrupa 77 espcies organizadas em 16 gneros e seis famlias – Amarsipidae, Ariommatidae, Centrolophidae, Nomeidae, Stromateidae, e Tetragonuridae. Membros dessa ordem exibem distribu global em guas tropicais e temperadas, tanto em ambientes pelgicos ou costeiros, e so tradicionalmente agrupados por apresentar duas especializaes morfolgicas singulares: a presena de uma bolsa faringeana, e de uma rede de canais subdrmicos sobre a cabea e o tronco. O status filtico de Stromateiformes nunca foi testado de maneira apropriada com base em dados morfolgicos, e seu monofiletismo tem sido rejeitado por diferentes anlises filogenticas pautadas em dados moleculares. Alm disso, anlises morfolgicas e moleculares tm se mostrado indecisivas quanto s relaes de Stromateiformes com outros Percomorphacea. O presente estudo se prop a investigar estas questes e apresentou uma ampla reviso filogentica de Stromateiformes baseada em uma anlise exaustiva de 218 caracteres fenotpicos e 66 txons terminais, o que inclui todos os gneros vlidos de Stromateiformes bem como todas as famlias de Percomorphacea que de alguma maneira j foram alinhadas  ordem. A topologia resultante indica a ordem como monofiltica e suportada por quatro sinapomorfias. Amarsipidae, o nico representante de Stromateiformes a no apresentar uma bolsa faringeana,  posicionado como grupo irmo dos demais membros da ordem. Centrolophidae no  monofiltico, com cinco de seus gneros agrupados em um clado basal, enquanto outros dois aparecem como grupos irmos sucessivos de um clado composto pelas demais famlias de Stromateiformes. Todas estas famlias so recuperadas como monofilticas, arranjas da seguinte maneira: Nomeidae (Stromateidae (Tetragonuridae, Ariommatidae)). Um clado composto por Bramidae e Caristiidae  aqui hipotetizado como sendo o grupo irmo dos Stromateiformes, apesar desse arranjo ser suportado por apenas uma sinapomorfia no ambgua. O presente estudo ainda apresenta uma hiptese de que a relao simbitica singular entre juvenis de Stromateiformes e outros invertebrados gelatinosos (*e.g.* medusas e salpas) est provavelmente associado com a evoluo de algumas das mais notveis especializaes morfolgicas do grupo, tais como os cecos pilricos arranjas numa massa dendrtica, a presena de um plexo de canais subcutneos, e a presena de uma bolsa faringeana.

ABSTRACT

The division Percomorphacea encompasses a major fraction of the extant fish diversity, including over half of all known ray-finned fishes and approximately one fourth of the living vertebrates. The interrelationships among the major percomorphacean lineages are still far from a satisfactory resolution. Among the 30 percomorphacean orders, Stromateiformes encloses 77 extant species distributed into 16 genera and six families – Amarsipidae, Ariommatidae, Centrolophidae, Nomeidae, Stromateidae, and Tetragonuridae. Members of this order are globally distributed in temperate and tropical oceans and exhibit two extraordinary morphological specializations: the presence of a pharyngeal sac and of a subdermal canal plexus over the head and trunk. The phyletic status of Stromateiformes has never been adequately tested on morphological grounds and the monophyly of the order has been recently rejected by multiple molecular analyses. Moreover, stromateiforms have been indecisively aligned with disparate percomorphacean taxa by both morphology- and molecular-based studies. The present work delved into these questions and presented a comprehensive phylogenetic revision of Stromateiformes based on an exhaustive analysis of 218 phenotypic characters and 66 terminal taxa encompassing all valid stromateiform genera, as well as all percomorphacean families somehow aligned with stromateiforms in prior studies. The resulting topology retrieves the order as monophyletic, supported by four unequivocal synapomorphies. Amarsipidae, the only stromateiform lacking a pharyngeal sac, is resolved as the sister group of the remaining members of the order. Centrolophidae is not monophyletic, with five of its genera grouped into a basal clade, whereas the other two appear as successive sister groups of a clade containing the remaining stromateiform families. All these families are recovered as monophyletic with the following cladistic arrangement: Nomeidae (Stromateidae (Tetragonuridae, Ariommatidae)). A clade composed by Bramidae and Caristiidae is herein hypothesized the sister group of stromateiforms, although this arrangement is supported by only a single unequivocal synapomorphy. The present study further hypothesizes that the remarkable symbiotic relationship between juvenile stromateiforms and gelatinous invertebrates (e.g. medusa and salps) is probably associated with the evolution of some of its most remarkable morphological specializations, such as the presence of dendritic pyloric caeca, subcutaneous canal plexuses, and the pharyngeal sac.

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INTRODUCTION

The taxonomy of stromateiformes: an overview

The division Percomorphacea (*sensu* Wiley & Johnson, 2010) encompasses a major fraction of the extant fish diversity, including over half of all known ray-finned fishes and approximately one fourth of the living vertebrates (Nelson, 2006; Van der Laan & Fricke, 2019). Recent classifications based on morphological data organize the 17,000+ known percomorphacean species into 30 distinct order (Wiley & Johnson, 2010). The monophyly of Percomorphacea is supported by studies based on both anatomical (Johnson & Patterson, 1993; Wiley & Johnson, 2010), molecular (Li *et al.*, 2007; Near *et al.*, 2012, 2013; Betancur-R *et al.*, 2013; Betancur-R *et al.* 2017), and combined morphological and molecular data (Mirande, 2016). The internal relationships among the dozens of percomorphacean orders, on the other hand, are still far from a satisfactory resolution. Conflicts between morphology- and DNA-based hypotheses are particularly striking, and the resolution of these discordances represents one of the biggest challenges of the systematics of bony fishes (Johnson & Patterson, 1993; Nelson, 2006, 2016; Wiley & Johnson, 2010).

Among the 30 percomorphacean orders recognized by Wiley & Johnson (2010), Stromateiformes encloses 77 extant species distributed into 16 genera and six families – Amarsipidae, Ariommatidae, Centrolophidae, Nomeidae, Stromateidae, and Tetragonuridae (Van der Laan & Fricke, 2019). Additionally, there is at least one fossil family, Propercarinidae, assigned to Stromateiformes (Bannikov, 1995; Prikryl *et al.* 2014). Members of this order generally exhibit broad geographical distributions in temperate and tropical ocean waters, both in pelagic and coastal environments, and in variable depths (Haedrich, 1967). At least part of the Stromateiformes inhabit deep pelagic waters (*e.g.* some Centrolophidae, Tetragonuridae, and Amarsipidae), a condition that has hampered the sampling and availability of these taxa in scientific collections. Other taxa, instead, inhabit coastal environments and are found in certain abundance in beaches and rocky shores. These species are often used as food resource and some may reach high prices on fish markets (*i.e.* *Peprilus* and *Pampus* spp.). Stromateiformes also exhibit a fair morphological variability, with pelagic taxa usually having shallow, cylindrical body (*i.e.* Tetragonuridae, Amarsipidae, some *Ariomma* species) and those inhabiting the shoreline with deeper and more compressed bodies (*i.e.* Stromateidae).

For over a century, anatomists have unequivocally recognized Stromateiformes as a natural assemblage. Fishes of the order have been traditionally grouped based on the sharing of an extraordinary specialization: the presence of a large and globular pharyngeal sac located on the proximal portion of the esophagus, immediately posterior to the last branchial arch (Günther, 1880;

Regan, 1902; Haedrich, 1967). This sac is covered externally by the *sphincter oesophagi* muscle (Datovo *et al.*, 2014) and internally lined by a series of small teeth-like structures that are covered by a thin epithelial tissue (Günther, 1880; Regan, 1902; Haedrich, 1967). This series of tissue-covered “teeth” are often referred as pharyngeal-sac papillae. Both the pharyngeal-sac dentition and its associated musculature present a notable degree of complexity among the Stromateiformes (Gilchrist, 1922; Buhler, 1930; Isokawa, 1965; Haedrich, 1967; Springer & Johnson, 2004; Datovo *et al.*, 2014) and the anatomical variations in these structures have been used as taxonomic characters (Isokawa, 1965; Haedrich, 1967).

The most important study on the systematics and taxonomy of Stromateiformes was published by Haedrich (1967). This work provided, for the first time, a detailed taxonomic revision of the entire order, identification keys for its families, and diagnosis, descriptions, and lists of synonyms for all its genera. Although presenting his ideas under a pre-cladistic perspective, Haedrich (1967) provided insightful thoughts regarding the interrelationships of the Stromateiformes. According to the author, these fishes could be diagnosed by presenting a “toothed saccular outgrowth in the gullet” (= pharyngeal sac), and small teeth approximately uniserial in the jaws. Within stromateiforms, Centrolophidae and Nomeidae would be “basal” lineages, while Tetragonuridae, Ariommatidae, and Stromateidae represented “specialized” forms (Fig. 1). In addition to the pharyngeal sac and the uniserial teeth, Haedrich (1967) also described an unusual characteristic present in almost all Stromateiformes: a subdermal canal system in the head and trunk, which connects an interdermal space in the skin to the outer surface through minute pores. According to the author, this was an unusual feature of stromateiforms. Indeed, this plexus of subcutaneous canals are only found in some unrelated taxa such as Trachipteridae (Walters, 1963) and some Gempylidae (Bone, 1972). As to the affinities of stromateiforms with other percomorphaceans, the author refrained himself of offering assertive opinions, but briefly stated that Stromateiformes, Kyphosidae, and Carangidae would share an overall similarity.

The taxonomic classification of Stromateiformes have undergone few, but important modifications after the publication of Haedrich’s (1967) seminal study. The main changes were the description two new families and one new genus, and the resurrection of another genus. The first of these was the discovery of *Amarsipus carlsbergi*. This species was described by Haedrich (1969) and placed in a monotypic family – Amarsipidae – just two years after the publication of his systematic revision of Stromateiformes. Curiously, Haedrich (1969) diagnosed *Amarsipus* from all other Stromateiformes by the absence of a pharyngeal sac, *i.e.* one of the two unique character used by himself to diagnose the order (Haedrich, 1967). To justify the placement of *Amarsipus* within

Stromateiformes, the author used a combination of characters shared by the new species and the other members of the order: a “perciform caudal skeleton”, an uniserial jaw teeth, an expanded lacrimal bone, an inflated and protruding top of the head, a bony bridge over the anterior vertical canal of the ear (*i.e.* *pons moultoni sensu* Haedrich, 1971), an overall similarity on external appearance, and the presence of a well-developed subdermal canal system on the head and body. As consequence, Haedrich (1969) implicitly provided a new definition for the order, which was no longer based on the presence of the pharyngeal sac and uniserial teeth, but rather on the combination of several characters.

Since its original description in the late 1920's, the genus *Propercarina* has been indecisively assigned to distinct percomorphacean taxa within Percomorphacea, with an initial suggestion of closer affinity with *Percarina* (Pauca, 1929, 1934), a percid genus from the Black Sea basin. However, subsequent studies rejected that proposition and demonstrated that *Propercarina* should be allocated in Stromateiformes (Bannikov, 1995; Prikryl, 2014). Yet, *Propercarina* species would not fit in any known stromateiform family, and a new family, Propercarinidae, was described to allocate this taxon within the order. As a diagnostic character of Propercarinidae, Bannikov (1995) listed the possession of widely separated dorsal fins and relatively large jaw teeth. Although the interrelationship of the family with the remaining Stromateiformes have not been explicitly tested, the author indicated shared similarities of Propercarinidae with Nomeidae and Amarsipidae in the postcranial skeleton, namely the increased number of vertebrae (about 35), the very slender vertebral spines, and the well-developed parapophyses on the posterior abdominal vertebrae. Moreover, *Propercarina* would share with *Amarsipus* a non-oligomerized caudal skeleton (hypurals free from each other), short-paired fins, most anal-fin rays below the posterior dorsal-fin, absence of pharyngeal sac, and presence of enlarged pharyngeal teeth. Bannikov (1995) listed the latter feature as a possible evidence that propecarinids and amarsipids would form a pre-centrolophid lineage. Propercarinidae was recently focus of a revisionary study, in which an additional species was described from the Oligocene of Romania (*Propercarina problematica*; Prikryl *et al.* 2004). Similar to Bannikov (1995), Prikryl *et al.* (2004) corroborated the affinities of Propercarinidae and Amarsipidae and reaffirmed their allocation within Stromateiformes.

In addition to the aforementioned new stromateiform families, the other two taxonomic novelties within Stromateiformes comprise erection of two new genera to allocate two previously known species of Centrolophidae. Haedrich (1967) considered *Tubbia* a junior synonym of *Schedophilus*. However, in Haedrich & Horn (1972), *T. tasmanica* appears in the key to the species of *Ichthyos*. This arrangement comes with a remark stating that it was provisional since *Tubbia*

tasmanica displayed characters intermediate between the genera *Schedophilus* and *Icichthys* and its position within Stromateiformes would represent an enigma. A few years later, Ahlstrom *et al.* (1976) drew attention to the high supraneural (= predorsal) count in *Icichthys* (up to 12 supraneurals) in contrast with that of *Tubbia* (three). The resurrection of *Tubbia*, however, was only formally made by McDowall (1979) based on a reanalysis of the type of *Tubbia tasmanica* and analysis of three additional specimens captured off the New Zealand coast. McDowall (1979) listed as main diagnostic character of *Tubbia* the distinct number of vertebrae, ranging from 43–44, which was substantially higher than that of *Schedophilus* (25–30), but still significantly lower than *Icichthys* (50–60). More recently, Last *et al.* (2013) described a second species of *Tubbia* and redefined the genus. According to the authors, *Tubbia* was characterized not only by the number of vertebrae, but also the number of fin rays, spines, and several details of the shape of the body, scales, and fins.

The second centrolophid genus described after Haedrich's (1967) study was *Pseudoicichthys*, erected by Parin & Permitin (1969) to allocate *Icichthys australis*. This species was originally described by Haedrich (1966) based on a 77.2 mm SL immature specimen that was placed in *Icichthys* due to its possession of high number of vertebrae (up to 51 bones) and three autogenous haemal spines, both uniquely shared by the other known species of *Icichthys* (*I. lockingtoni*). Other characteristics such as small pelvic fins, soft musculature, poorly calcified skeleton, and an insignificant ventral slit (or groove) were also used to allocate *I. australis* in *Icichthys* (Haedrich, 1966, 1967). However, shortly after its original description, Parin & Permitin (1969) redescribed by and reallocated *Icichthys australis* into a new genus. Based on the analysis of five additional individuals of that species, including adults, Parin & Permitin (1969) concluded that the “differences... are quite sufficient for separate distinction at the generic level” and erected the genus *Pseudoicichthys* to allocate *I. australis*. The authors distinguished the two genera based on the number of epurals (two in *Icichthys* and three in *Pseudoicichthys*), number and shape of pyloric caeca (“few” in *Icichthys*, “numerous” in *Pseudoicichthys*), details on the laterosensory (“seismosensory”) canals of the head, squamation, number of pectoral-fin rays, and body depth. The authors, however, recognized the blatant similarities between *Icichthys* and *Pseudoicichthys* and stated that “the genus *Pseudoicichthys* established by us is undoubtedly extremely close to *Icichthys*”.

The validity of *Pseudoicichthys* has been questioned since its original description. In the same year of the description of the genus, Krefft (1969) pointed out that the diagnostic features of *Pseudoicichthys* also occurred in other closely related genera. He further advocated in favor of a reduction in the number of genera in Centrolophidae and highlighted that most features used to diagnose these taxa were found in varying combinations across the family. Haedrich & Horn (1972)

also rejected the validity of *Pseudoicichthys* as both the taxonomic account of the Centrolophidae (Haedrich & Horn, 1972: p. 2) and the key to the species in *Icichthys* (Haedrich & Horn, 1972: p. 28) considered *I. australis* as belonging to *Icichthys*. McDowall (1982) made the same decision and commented that “*the broad relationships of these strange centrolophid fishes are poorly understood and that the situation is not helped by the proliferation of monotypic genera*”. The genus was also ignored in the phylogenetic studies of Horn (1984), Doiuchi *et al.* (2004), and Doiuchi & Nakabo (2006). Currently the validity of the genus is controversial. Most fish catalogues list it as a junior synonym of *Icichthys*: OBIS (Ocean Biogeographic Information System), WoRMS (World Register of Marine Species; Horton *et al.*, 2019), FishBase (Froese & Pauly, 2019), and FAO Fisheries and Aquaculture Department (Food and Agriculture Organization of the United Nations; Fisher & Bianchi, 1984). Yet, *Pseudoicichthys* is considered a valid genus in the Eschmeyer’s Catalog of Fishes (Fricke *et al.*, 2018), probably because it has never been explicitly synonymized. Taxonomic studies of Stromateiformes point to a split decision favoring its non-validity, with some studies accepting the genus (Rembiszewski, 1981; Haedrich, 1986; Parin & Piotrovstky, 2004; Stewart *et al.*, 2015), and several rejecting or simply ignoring its existence (Krefft, 1969; Haedrich & Horn, 1972; McDowall, 1982; Horn, 1984; Doiuchi *et al.*, 2004; Doiuchi & Nakabo, 2006; Nelson, 2006, 2016).

Phylogeny of Stromateiformes: morphological approaches

The first phylogenetic analysis of Stromateiformes was published by Horn (1984), in a study aiming the ontogeny and phylogeny of the members of the order. The author used 27 characters, examined all 16 stromateiform genera, and corroborated the monophyly of the order including *Amarsipus* as a stromateiform member (Fig. 2A). The monophyly, however, was sustained by characteristics of the head and body squamation (presence and shape of scales on the preopercle and body) and by details of the caudal skeleton (number of hypurals). In the tree obtained by Horn (1984), *Amarsipus* was recovered as the sister-group of all remaining Stromateiformes; Centrolophidae was not monophyletic; and Nomeidae, along with Tetragonuridae, Ariommatidae, and Stromateidae, formed an apical clade. According to this topology, the pharyngeal sac was optimized as a synapomorphy for the non-Amarsipidae Stromateiformes, and no longer considered a synapomorphy for the order as traditionally treated by previous studies (*e.g.* Regan, 1902; Haedrich, 1967). Horn (1984) followed former predictions that Stromateiformes could be related to the Girellidae, Scorpididae, and Kyphosidae, and sampled these taxa as outgroups to his phylogenetic analysis. Kyphosidae was resolved as sister-group to the Stromateiformes, a relationship sustained by aspects of the dentition and color pattern of juveniles.

More recently, a second phylogenetic analysis based on morphological data sampling all stromateiform genera was published by Doiuchi *et al.* (2004). This study investigated 43 characters related to skeleton, muscle, and scales, taken from 17 representatives of the order (all 16 genera, plus a second species of *Psenes*) and two outgroups (Arripidae and Kyphosidae). Similar to Horn (1984), Doiuchi *et al.* (2004) recovered the monophyly of Stromateiformes (Fig. 2B), an arrangement supported by eight synapomorphies (Doiuchi *et al.*, 2004: Char. #7, 11, 20, 21, 22, 31, 40, and 43). Another convergence between these studies was the non-monophyly of Centrolophidae: representatives of this family appeared at a basal polytomy, separated from the other families that were grouped into an apical clade. However, a fundamental difference between the results of Doiuchi *et al.* (2004) and Horn (1984) was the placement of *Amarsipus*. While in Horn (1984) *Amarsipus* was allocated basally in Stromateiformes, figuring as the sister group of all other stromateiforms (Fig. 2A), in Doiuchi *et al.* (2004) the taxon appeared more apically within the order, as the sister-group of a lineage composed by Ariommatidae, Nomeidae, Tetragonuridae, and Stromateidae (Fig. 2B). Such differences implied directly on the interpretation of the pharyngeal-sac evolution in the order. In Horn (1984), the pharyngeal sac was not recovered as a synapomorphy for stromateiforms, but rather as a characteristic acquired after the divergence of *Amarsipus* from the remaining of the lineage. On the other hand, in Doiuchi *et al.* (2004), the pharyngeal sac constituted a synapomorphy for the order, with a secondary loss in *Amarsipus*.

Mentions about the affinity of Stromateiformes to other Percomorphacea are scarce in the anatomical literature. A possible relationship of Stromateiformes with the pelagic *Icosteus aenigmaticus* has been informally suggested by early studies (Jordan & Gilber, 1880; Steindachner, 1881), but basically due to a general external similarity between *Icosteus* and some Centrolophidae, particularly during larval and juvenile stages (Matarese *et al.*, 1984: fig. 306; Horn, 1984: fig. 333). In fact, young *Icosteus* and centrolophids are so similar that a juvenile specimen of *Icosteus* has once been described under the name *Schedophilopsis spinosus* (Steindachner, 1881), and thought to be related to the centrolophid genus *Schedophilus*. Similarly, the original description of *Icichthys lockingtoni* (Jordan & Gilbert, 1880) reveal that the authors believed in a relationship of this taxon with *Icosteus*, and the entire description is dedicated to list similarities and differences between them. However, all subsequent studies failed on finding “special similarities” (= synapomorphies) between Icosteiformes and Stromateiformes, and currently these orders are no longer believed to be closely related (Springer & Johnson, 2004). The alignment of Stromateiformes with pelagic taxa due an overall similarity is not restricted to *Icosteus*. Some other oceanic fishes that were once considered related to Stromateiformes are *Luvarus imperialis* (Luvaridae), *Coryphaena* spp. (Coryphaenidae), and *Gasterochisma melampus* (Scombridae). This grouping was proposed by Le Danois and Le Danois

(1963) as part of their classification of “Scombres”, which was based solely on the presence of two characteristics: hypurostergy (= fusion of hypurals) and erisme (= a bony crest on the skull). However, this hypothesis has received little attention by subsequent studies, possibly due to the common belief that these characteristics are likely convergences associated to the pelagic habit, rather than evidences of a natural assemblage. A more elaborated critic to this hypothesis, and a detailed comparison of *Luvarus* with the Stromateiformes, is provided by Tyler *et al.* (1989).

The latest morphological studies favor a hypothesis of closer relationship of Stromateiformes with the Kyphosidae and Girellidae (Freihofer, 1963; Haedrich, 1967; Johnson & Fritzsche, 1989). Freihofer (1963) offered one of the first mentions of a possible relationship among these taxa in a study dealing about the ramification pattern of a subdivision of the facial nerve, namely the *ramus lateralis accessorius* (RLA), in Teleostei. In a study encompassing 310 species of 130 families and 21 orders, Freihofer identified and described 17 different nerve-branching patterns and suggested several groupings in Teleostei based on the distribution of these patterns. One of those – the RLA pattern 10 – was shared by the Kyphosidae *lato sensu* (*i.e.* Kyphosidae plus Scorpididae, Girellidae, and Microcanthidae), Kuhliidae, Arripidae, Terapontidae, Pomatomidae, Nematistiidae, and all Stromateiformes. Based upon the restrict distribution of this pattern among Teleostei, Freihofer (1963) suggested that some (if not all) these taxa possibly constituted a natural assemblage. The distribution of RLA 10 branching pattern was later reassessed by Johnson & Fritzsche (1989), which tested Freihofer’s (1963) hypothesis on a broader taxon sampling within percomorphaceans. The authors also found an RLA-10 pattern in Oplegnathidae, but disagreed on the presence of this branching pattern in Pomatomidae and Nematistiidae. According to Johnson & Fritzsche (1989), pomatomids and nematistiids would be closely related to Scombriformes (following Johnson, 1986) and Carangiformes (according to Rosenblatt & Bell, 1976), respectively. Apart from these two taxa, Johnson & Fritzsche (1989) agreed with Freihofer (1963) and proposed that the remaining percomorphs with an RLA 10 pattern would form a monophyletic group. The RLA-10 group was later expanded to allocate the family Dichistiidae (Leis & Lingen, 1997), a percomorphacean family endemic to southern African oceans, which was historically related to microcanthids, scorpidids, girellids and kyphosids.

The last study to discuss the Stromateiformes interrelationship was Springer & Johnson (2004). In this study the authors mostly agreed with the monophyletic status of the RLA 10-group. However, the authors revealed that the stromateiform *Amarsipus* – which was not examined in Freihofer (1963) or Johnson & Fritzsche (1989) – lacks an RLA 10 pattern. They described the RLA opercular branch of this taxon as passing parallel to the pterotic and medial to the opercular

musculature, in a fashion that certainly diverges from Freihofer's RLA pattern 10. Based on that evidence, and a reevaluation of several other characters, Springer & Johnson (2004) questioned the inclusion of *Amarsipus* in Stromateiformes, stating that more studies would be needed to determine the allocation of *Amarsipus* within Percomorphacea. In fact, the allocation of *Amarsipus* within Stromateiformes has never been properly tested in a cladistic analysis using morphological data. Both phylogenies involving the Stromateiformes (*i. e.* Horn, 1984, and Doiuchi *et al.* 2004) had as primary objective the study of the intrarelationships among the stromateiform families, and not the monophyly of the order. In such analyses, the inclusion of *Amarsipus* to Stromateiformes could have been a spurious result due to the small outgroup sampling (3 taxa in Horn, 1984; 2 in Doiuchi *et al.* 2004). Until now, only the subdermal canal system can be listed as a strong evidence uniting Amarsipidae to Stromateiformes, even though this characteristic independently appears in unrelated taxa such as the lampridiform Trachipteridae (Walters, 1963) and the gempylid *Ruvettus prestiosus* (Bone, 1972). The other characteristics used to place *Amarsipus* within Stromateiformes (*i.e.* a perciform caudal skeleton, uniserial jaw teeth, expanded lacrimal bone, inflated and protruding top of the head, bony bridge over the anterior vertical canal of the ear) have been demonstrated to be present in a series of percomorphacean families including the Kyphosidae *lato sensu* (Springer & Johnson, 2004), and still await a formal analysis to test their synapomorphic status.

Phylogeny of Stromateiformes: molecular approaches

The first phylogeny of Stromateiformes based on molecular data was conducted by Doiuchi & Nakabo (2006). This analysis did not include *Amarsipus* or tested the monophyly of the order since it used only a single outgroup (*i.e.* the RLA-10 family Arripidae). Nevertheless, the topology obtained by the authors was already strikingly conflicting with the trees resultant from anatomical studies (Fig. 3). For example, their hypothesis presented *Tetragonurus* as the sister group of the remaining Stromateiformes in a parsimony analysis (*vs.* *Amarsipus* in Horn, 1984; Centrolophidae in Doiuchi *et al.* 2004). Moreover, a monophyletic Centrolophidae was obtained by both the parsimony and the maximum likelihood analyses (*vs.* paraphyletic in Horn, 1984 and Doiuchi *et al.*, 2004). Subsequent molecular analyses sampling broader outgroups returned arrangements even more incongruent with preceding morphological hypotheses (Li *et al.*, 2007; Yagishita *et al.*, 2009; Near, 2013; Betancur-R *et al.*, 2013; Miya *et al.*, 2013; Betancur-R *et al.* 2017). Among these, that of Betancur-R *et al.* (2013) deserves special attention. Based on 21 sequences taken from 1410 taxa, which encompasses all orders traditionally recognized in Teleostei, Betancur-R *et al.* (2013) provided an unprecedented phylogenetic classification for bony fishes, redefining many taxa and naming several new others. As a

result, Scombriformes was modified to encompass not only some of the families traditionally assigned to the order (Johnson, 1986; Wiley & Johnson, 2010), but also representatives of Chiasmodontidae, Pomatomidae, Scombrilabracidae, Icosteidae, Caristiidae, Bramidae, and all families composing the Stromateiformes (Betancur-R *et al.*, 2013: fig. 5). The final topology, however, did not recover the monophyly of Stromateiformes, which were divided in three distinct lineages: Centrolophidae, as the sister group of part of the Scombridae; Stromateidae, as the sister group of an assemblage including bramids, caristiids, icosteids and scombrilabracids; and Nomeidae + Ariommatidae as the sister group of a subset of Scombridae. Amarsipidae and Tetragonuridae were not sampled in that study. Although exhibiting strong support for the Scombriformes clade, the authors recognized that the intrarelationships among the taxa composing the clade exhibit low support, and the monophyly of traditional taxa such as the Scombriformes *stricto sensu* would still require further studies (Betancur-R *et al.*, 2013: appendix 2).

Not long after the publication of Betancur-R's *et al.* (2013) phylogenetic classification of bony fishes, Miya *et al.* (2013) published a study on the evolutionary origin of Scombridae (tunas and mackerels). Based on analyses taken from an extensive database (*i.e.* DNA sequence of mitochondrial and nuclear genes of 5367 species allocated in 1558 genera and 215 families of Percomorphacea), the authors supported the existence of a larger clade corresponding to the Scombriformes *sensu* Betancur-R *et al.* (2013). Both the separated analyses for each of the six mitochondrial or three nuclear gene sequences and the combined-data analysis supported the existence of the Scombriformes *lato sensu*. That clade was therein renamed to Pelagia (= Pelagiaria *sensu* Betancur-R *et al.*, 2013). Again, the Stromateiformes (with all families sampled but Amarsipidae) did not result as a monophyletic entity and the members of the order were spread in three different assemblages (Fig. 4). Again, nodes within the Pelagia presented low support.

The first combined analyses of morphological and molecular data sampling Stromateiformes were that of Mirande (2017). The dataset used by the author contained 44 nuclear and mitochondrial markers and 274 morphological characters encompassing representatives of all orders of Actinopterygii. Once again, Stromateiformes was resolved as paraphyletic, with *Tetragonurus* appearing far removed from the remaining stromateiform families and forming a clade with Chiasmodontidae. The remaining stromateiforms formed a clade with Ariommatidae plus Nomeidae, and Centrolophidae plus Stromateidae. The taxon *Amarsipus* was not sampled by Mirande (2017). In fact, the relationships of the genus *Amarsipus* was only recently studied under a phylogenetic perspective using molecular data. That was possible after the discovery of a single fresh specimen at the Nagasaki Fish Market (Japan). According to the analysis of Campbell *et al.* (2018), which used the

datasets of Betancur *et al.* (2013), *Amarsipus* falls deeply nested within the Pelagiaria as the sister group of *Tetragonurus*. Similar to previous studies, the monophyly of Stromateiformes was not recovered and the nodal supports for the subgroups of Pelagiaria were low.

An important outcome from the analyses of Betancur-R *et al.* (2013), Miya *et al.* (2013), Mirande (2017), and Campbell *et al.* (2018), both of which recovering a polyphyletic Stromateiformes, is that complex morphological characters such as the pharyngeal sac or the subdermal canal system, necessarily had to evolve at least two (in Mirande, 2017) or three independent times (in the remaining studies) during the Pelagiaria radiation. In addition, these analyses place Stromateiformes distant from most RLA 10 taxa (*i.e.* Kyphosidae, Scorpididae, Microcanthidae, and Oplegnathidae, among others), which would be the stromateiform sister-group candidate according to some morphological studies (*e.g.* Freihofner, 1963; Johnson & Fritzsche, 1978). Until now, important systematics questions of Stromateiformes, such as its phyletic status, intrarelationships, affinities with enigmatic taxa such as *Amarsipus*, or its relationship with other Percomorphacea remain unsatisfactorily answered. Similarly, the evolution of complex anatomical structures, such as the pharyngeal sac, the subdermal canal system, and the RLA 10 innervation pattern are still unsolved.

DISCUSSION

The phylogeny of the Stromateiformes:

The present study is by far the largest cladistic analysis to test the monophyly, inter- and interrelationships of the Stromateiformes based on phenotypic data. Our final matrix includes 218 phenotypic characters examined in 66 terminal taxa, including 22 stromateiforms and 44 outgroup species that represent 14 orders and 40 families of Acanthopterygii. Previous morphology-based phylogenies of the order analyzed only a small fraction of these characters and taxa (Horn, 1984; Doiuchi *et al.*, 2004). Moreover, none of these studies properly tested the monophyly of the order, as only a few outgroup taxa were included in the analyses. Monophyly of Stromateiformes has been challenged by recent molecular or combined data phylogenies that repeatedly recovered the order as a para- or polyphyletic assemblage (Miya *et al.*, 2013; Betancur-R *et al.*, 2013; Near *et al.*, 2013; Mirande, 2017; Betancur-R *et al.*, 2017; Campbell *et al.*, 2018), as well as by a few morphological studies that questioned the inclusion of Amarsipidae in the order (Springer & Johnson, 2004; Datovo *et al.*, 2014). Our analysis result in one most parsimonious tree (Fig. 68), which supports Stromateiformes as monophyletic, including Amarsipidae and other five families: Ariommatidae, Centrolophidae, Nomeidae, Stromateidae, and Tetragonuridae (Fig. 70). Our study also indicates that a clade formed by the percomorphacean families Bramidae and Caristiidae represents the immediate sister-group of the Stromateiformes (Fig. 68). In the subsequent sections, all 23 resolved clades within Stromateiformes are listed and discussed and a list of unambiguous synapomorphies is offered for each one of them. In addition, further comments on the bramid-caristiids-stromateiform relationship are also provided.

The intrarelationships of Stromateiformes:

Clade A (TNT clade 92) = Order Stromateiformes: *Amarsipus carlsbergi*, *Serirolella violacea*, *Hyperoglyphe perciformis*, *Centrolophus niger*, *Tubbia tasmanica*, *Icichthys lockingtoni*, *Psenopsis anomala*, *Psenopsis cyanea*, *Schedophilus* sp., *Psenes sio*, *Psenes cyanophrys*, *Nomeus gronovii*, *Cubiceps whiteleggii*, *Cubiceps pauciradiatus*, *Tetragonurus cuvieri*, *Ariomma indicum*, *Ariomma bondi*, *Ariomma melanum*, *Stromateus brasiliensis*, *Pampus cinereus*, *Peprilus triacanthus*, *Peprilus paru*.

Synapomorphies: Char. #35 (1>0), Char. #37 (0>1), Char. #85 (0>1), Char. #187 (0>1).

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