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Filogenia de Syngnathidae (Teleostei:  
Syngnathiformes)

Phylogeny of Syngnathidae (Teleostei:  
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## Introduction

The Syngnathidae is a cosmopolitan family of fishes, comprising around one percent of all Teleost diversity, with more than 300 species, including the well-known genus of seahorses (*Hippocampus* Rafinesque 1810), to the less known, albeit more diverse group, pipefishes (Nelson *et al* 2016). Their origins can be traced to the Eocene, on the Tethys Sea (Bannikov 2014, Santaquiteria *et al* 2021), with fossil representatives ranging from the older specimens from Eocene formations on Monte Bolca, Italy, (Bannikov 2014) to the Pliocene formations in California, United States (Frietszche 1980). The most striking characteristic in Syngnathidae is the male parental care, making this the only family of vertebrates in which the male becomes pregnant. Such pregnancy is achieved by incubating the eggs in a ventral brood pouch (Figueiredo and Menezes 1980, Dawson and Vari 1982, Lourie and Randall 2003).

The study of Syngnathidae began with the work of Artedi (1738), with the description of four species of fishes with a tubular snout formed by the fusion of the jaws, hence the name *Syngnathus*, or fused jaws. All four species were from Europe: one seahorse (genus *Hippocampus*), and three pipefishes (genera *Syngnathus* Linnaeus 1758 and *Nerophis* Rafinesque 1810). Along with the fused snout, Artedi (1738) mentioned a geometric shape of the body of syngnathids and body covered by plates, as *Syngnathus* was included in the Malacopterygii.

Linnaeus (1758) included the Syngnathidae in his *Systema Naturae*, placing the family at the Pisces Abdominalis, characterized by a cylindrical snout, opercular opening restricted to a small aperture on the nuchal region, articulated body, absence of pelvic fins and geometric shape of the transversal plane of the body, heptagonal in the trunk region and quadrangular in the tail region. At the tenth edition of his “*Systema Naturae*”, he described seven specimens of Syngnathidae belonging to the genus *Syngnathus* (Linnaeus 1758). Of these, six were pipefishes now belonging to the genera *Syngnathus* and *Nerophis* (Rafinesque 1810), and one seahorse described in the genus *Syngnathus* (*S. hippocampus* Linnaeus 1758).

An insight on the anatomy of Syngnathidae was given by Cuvier (1835), when he placed the genera *Syngnathus* and *Hippocampus* in the Lophobranchiate fishes, noting that the structure of the gills is organized

in lobes, not in filaments as in other teleosts. Cuvier (1837) also provided a brief mention of internal anatomy of Syngnathidae, describing an intestine smooth and indistinct from the stomach.

The first review of Syngnathidae was published by Kaup in 1853 and expanded in 1856, in the “*Übersicht der Lophobranchiate*” or “Review of the Lophobranchiates” which covered three families of fishes: Solenostomidae, Pegasidae and Syngnathidae, the latter included the first use of subfamilies of Syngnathidae, those being the Hippocampinae, Syngnathinae, Doryrhamphinae and Nerophinae. Each subfamily was described, based on the presence of prehensile tail and coronet (i.e., a modification of the nuchal plates), and most importantly the position of the brood pouch and coverage of the eggs in the brood pouch.

Two works further expanded and commented the diversity of syngnathids in 1870 (Duméril and Gunther). Each with different propositions on the relations of syngnathids and their characteristics. Gunther (1870) proposed that Pegasidae should be placed in Acanthopteygii due to the similarities with agonids and absence of lobate gills, while Lophobranchii was comprised only by Solenostomidae and Syngnathidae.

His description of syngnathids was based in the reduced gill opening, one soft dorsal fin, no pelvic fins with the absence of other fins in the fishes of the family. In this work, syngnathids were divided in two groups based on the presence of a caudal fin, the Syngnathina, or the presence of a prehensile tail, the Hippocampina (Gunther 1870). This proposition is the most different for syngnathids because it does not emphasize the brood pouch location and coverage of the eggs as one of the most informative characters in the family (Kaup, 1853, 1856).

Duméril (1870) on the other hand, followed the approach of Kaup (1853, 1856) on his chapter about Lophobranchiate, and used two orders for lophobranchs: the Hypostomidés, with one family, Pegasidae, and the Prostomidés, with two, Solenostomidae and Syngnathidae. The description of Syngnathidae included the same characters of Gunther (1870) and expanded to include: the transversal shape of trunk and tail, size and rays counts of anal fin when present and presence of brood pouch as a protection of the eggs in males.

The division of syngnathids by Duméril (1870) followed the proposal of Kaup (1853, 1856) with four groups: Hippocampini, Syngnathini, Doryrhamphini and Nerophini. The first step in Duméril’s key for subgroups focuses on the presence of pectoral fins and brood

pouch, distinguishing Nerophini from the other groups. While the position of the brood pouch is used to distinguish between Syngnathini and Doryrhamphini.

Contrary to other classifications, Gill (1896) proposed the suborder Syngnathi with two families, the Syngnathidae, divided in four subfamilies, two with abdominal brood pouch and two with caudal brood pouch, and the Hippocampidae, with two subfamilies distinguished by ridge configuration, and presence of a crowning in the back of the head, now known as the coronet. Furthermore, Gill (1896) briefly discussed the osteology of the family regarding the presence of bones of the opercular series (preoperculum and interoperculum) the pectoral girdle, and the absence of the symplectic, the presence of the latter being shown in later studies (Jungersen 1910).

While subfamilies of syngnathids started to have their main characters based on the position of the brood pouch in the previous works (Kaup 1853, 1856, Duméril 1870, Gunther 1870), the consolidation of this feature came in the studies of Duncker (1910 and 1915), with two main subgroups being named: the Gastrophori, genera with the brood pouch located in the trunk, and Urophori, genera with the brood pouch located in the tail.

A tentative proposal on the relationship of syngnathids was published by Herald (1959). In this seminal paper, he combined characters of the brood pouch, bony plates configuration and tail shape to understand the evolutionary history of the group. In this study, Gastrophori is a group composed of three subfamilies: Nerophinae, with the most primitive type of brood pouch with unprotected eggs loosely attached to the ventral region of the abdomen (type B1 of Wilson *et al.* 2001), the next step on brood pouches are found in Syngnathoidinae, with the eggs individually contained in separate membranous compartments, and Doryrhamphinae, with eggs placed into individual compartments either unprotected or protected by pouch plates (types B2 and B3 of Wilson *et al.* 2001, respectively).

The Urophori in Herald's study (1959), on other hand, are more thoroughly described based on brood pouch characters due to their diversity in brood pouch features. With two subfamilies: Solegnathinae, akin to Doryrhamphinae in having the eggs separated by a membranous matrix (type A2 of Wilson *et al.* 2001), and the Syngnathinae (type A4 and A5 of Wilson *et al.* 2001), with a diversity of brood pouch closures, from the semi closed brood pouch in *Corythoichthys* Kaup 1853 to the

sealed brood pouch with the opening restricted to a pore present in *Hippocampus*.

Herald (1959) also raised the question of the hypothetical ancestral pipefish, unknown to this day, a fossil record that could help understand the brood pouch character, if the ancestral state is the brood pouch being located on the abdomen (*Gastrophori sensu* Duncker, 1912) or having the brood pouch in the tail region (*Urophori sensu* Duncker, 1912), as found in Solenostomidae, where the female, not the male as in Syngnathidae, carries the eggs with the help of the pelvic fins (Orr and Fritzsche 1993).

Being published before the translations of the methods of phylogenetic systematics by Hennig in 1966, Herald's (1959) study remains the only morphological study on the relationship of syngnathids. This was not an impediment to be used tentatively as a morphological data to validate molecular studies (Wilson *et al.*, 2001).

The most comprehensive studies on syngnathid taxonomy were made by Dawson (1982, 1985), which shaped the current understanding on the group. Curiously, despite having described and revised almost all the genera in the family, he did not work on the most popular genus of the family, *Hippocampus*, or used the phylogenetic method.

After the works of Dawson, few studies focused on the revision of genera of syngnathids or in large groups geographically correlated species. The only and most recent examples are a molecular and conservation revision on the genus *Hippocampus* (Lourie 2016) and morphological based revisions of the genera *Pseudophallus* (Dallevo-Gomes *et al.*, 2020) and *Urocampus* (Araki and Motomura 2023).

The study of syngnathid osteology had its first major work by Jungersen (1910) in which he described in detail the osteology of eight species of the family from four genera: *Hippocampus*, *Nerophis*, *Phyllopteryx* Swainson 1839 and *Syngnathus*. Following works were mainly divided into two topics: ontogeny of syngnathids, with the only species of the genus *Hippocampus* and *Syngnathus* analysed (Kadam 1958, Azzarello 1990, Silveira 2000a and 2000b, Novelli *et al.*, 2017), and the mechanism of prey capture, with more species being analysed, although only focusing in the head region (Branch 1966, Bergert and Wainwright 1997, Leysen *et al.*, 2010 and 2011, Van Wassenberg *et al.*, 2011 and 2013).

The majority of the osteological data is focused on ontogenetic studies of the two most diverse genera, *Hippocampus* and *Syngnathus* (Kadam 1958, Azzarello 1990, Silveira 2000a and 2000b, Novelli *et al.*



2017), Jungersen (1910) also provided an osteological description of *Nerophis* and *Phyllopteryx*. With these four genera having the most complete source of osteological information, this leaves the other genera of syngnathids in the need for further studies from a morphological perspective.

Additional osteological data can be parsed by consulting studies in functional morphology of syngnathids. Their unique mechanism of prey capture, which is the fastest in all teleosts (Leysen *et al.*, 2010 and 2011, Van Wassenberg *et al.*, 2011 and 2013), provided some data on the morphology of the head in *Corythoichthys*, *Doryrhamphus* Kaup 1856 and *Dunckerocampus* Whitley 1933.

The first attempt of understanding the relations of syngnathids through morphology, in particular, osteological characters, was that from Fritzsche (1980). In this study, 33 species in 20 genera had their branchial skeleton analysed and discussed. The author did not provide explanations on why only the branchial skeleton was used. A second, albeit more limited, use of morphological characters to understand the phylogeny of the group was present in the first molecular study of syngnathids (Wilson *et al.*, 2001). In this study, the brood pouch characters from Herald (1959) were used to describe the family in conjunction with molecular data.

The brood pouch characters were the starting point in the understanding of syngnathids in many molecular studies. After the first study focused on fragments of mitochondrial rDNA genes 12S and 16S, and the complete sequence of cytochrome *b* gene, on a limited number of genera and species, 12 and 34 respectively (Wilson *et al.*, 2001), some relationships were proposed that followed previous studies. Most important is the separation between abdominal brood pouches (*Gastrophori sensu* Duncker, 1912) and caudal brood pouches (*Urophori sensu* Duncker, 1912), which is recovered in all subsequent molecular studies, with one notable exception: *Syngnathoides* is retrieved inside *Urophori* in the study of Wilson and Rouse (2010), this genus is subsequently retrieved inside the *Urophori* clade in later studies (Hamilton *et al.*, 2017, Longo *et al.*, 2017, Santaquiteria *et al.*, 2021 and Stiller *et al.*, 2022).

Subsequent studies were followed by Wilson and colleagues (Wilson *et al.*, 2003 and Wilson and Rouse, 2010), expanding on the genera and species studied, while using the same genes as the first study (Wilson *et al.*, 2001). Contrary to Herald's (1959) relationships, in which *Syngnathus* would be a genus distantly related to *Hippocampus*, the

molecular phylogenies recovered both genera as sister groups. In one study (Wilson *et al.* 2003), *Hippocampus* plus *Hippichthys* Bleeker 1849 form a sister group to *Syngnathus*, and in a latter study (Wilson and Rouse, 2010), *Hippichthys* is the sister group to *Hippocampus* plus *Syngnathus*. In the Gastrophori group, the european pipefishes, with the genera *Nerophis* and *Entelurus* form a monophyletic group (Nerophinae *sensu* Herald 1959) and *Doryrhamphus* (Doryrhamphinae *sensu* Herald 1959) are recovered as monophyletic groups.

The expansion of the molecular phylogenies in Syngnathidae took two paths, the first one through expansion of the genes analyzed, as in Hamilton *et al.* (2017), in which 48 genera and 91 species had four mitochondrial genes (i.e. 12S, 16S, CO1 and ND1) and four nuclear genes (i.e. 18S, Myh6, Tmo4C4, HoxA13a) studied. On the other hand, Longo *et al.* (2017) expanded the molecular phylogeny of Syngnathidae through the analysis of ultraconserved elements, including 24 genera and 59 species. Their results were followed by other studies using ultraconserved elements (Santaquiteria *et al.*, 2021 and Stiller *et al.*, 2022), reaching similar phylogenetic hypotheses. These molecular phylogenies agree with Herald's (1959) hypothesis of separation between brood pouch location, with the notable exception of *Syngnathoides*, which is recovered inside Urophori, despite having an abdominal brood pouch, and even being considered a subfamily by Herald (1959).

With the only study on the relationship of syngnathids being from Herald (1959), and the last morphological characters being proposed more than forty years ago (Fritzsche 1980), no comprehensive morphological phylogenetic studies of Syngnathidae or the proposition of new morphological characters have been made. The understanding of the Syngnathidae has severe gaps in the morphological knowledge, which is paramount to connect the systematics of the group to other areas (e.g. ecology, conservation and biogeography). This study is guided by the words of Gill (1896) "... a close and rigorous comparison of the skeletons of many genera will be requisite before such perfection [of characters] is attainable."

## Conclusions

The phylogeny of Syngnathidae recovered some groups previously not seen and placement of genera among the family. The Nerophinae (*sensu* Stiller et al. 2022) were divided into two lineages among the Syngnathinae (*sensu* Stiller et al. 2022). Pygmy pipehorses (*Acentronura*, *Amphelikturus*, *Cylix* and *Idiotropiscis*) formed a monophyletic group seahorses (*Hippocampus*) and seadragons (*Hallichthys*, *Phycodurus* and *Phyllopteryx*).

## Resumo

A família Syngnathidae, distribuída por todos os oceanos, é composta por mais de 300 espécies de peixes conhecidos como peixes cachimbo, compondo a grande maioria da diversidade da família, e cavalos marinhos, os mais notórios representantes do grupo compreendendo mais de 40 espécies carismáticas. Embora seja um grupo diverso e com uma morfologia bastante peculiar, estudos morfológicos deste grupo são raros e sua classificação é baseada em estudos pré cladísticos que utilizaram exclusivamente caracteres de morfologia externa. Nos últimos anos, estudos moleculares propuseram novas relações entre seus gêneros, porém sem explicitar sinapomorfias morfológicas que sustentassem essas propostas e com alguns táxons não representados, pois de maneira geral não há grande disponibilidade de amostras de tecido para todos os táxons pertinentes. Esta falta de estudos cladísticos com base em caracteres morfológicos também é verificada para famílias relacionadas aos Syngnathidae, com diferentes estudos filogenéticos de cunho molecular propondo diferentes grupos como relacionados aos Syngnathidae. Um estudo filogenético foi realizado com base em caracteres morfológicos, incluindo uma análise de caracteres externos de todos os gêneros de Syngnathidae e caracteres osteológicos de 26 gêneros, gerando 89 caracteres. Uma topologia de consenso foi gerada e analisada, levantando novas informações sobre a história evolutiva do grupo.

## Abstract

The Family Syngnathidae comprises more than 300 species distributed on all oceans, they are mostly known by the charismatic genus of seahorses, *Hippocampus*, and the most diverse group within the family, the pipefishes. Although is a very morphologically peculiar and diverse group, morphological studies of this group are rare and traditionally, their classification is based on pre cladistical studies focused on external morphology. On recent years, molecular studies proposed new relations among the genera of this family, all those new relations are poorly or not supported by morphological characters and lacking a important number of genera, given the lack of available specimens for molecular studies. The lack of cladistics studies based on morphological characters also occurs to related families of syngnathids, with different molecular studies proposing different relationships among syngnathids and other groups. A phylogenetic study was made based on external morphological characters of all genera of Syngnathidae and osteological characters of 26 genera, providing 89 characters. A consensus topology was generated and analised proving new insights on the evolutionary history of the group.

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