



Museu de Zoologia
Universidade de São Paulo

Paulo Presti

**Phylogenetic relationships and evolution of the musculoskeletal system of
Polynemidae (Teleostei: Percomorphacea: Perciformes).**

Relações filogenéticas e evolução do sistema musculoesquelético de Polynemidae (Teleostei:
Percomorphacea: Perciformes)

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Original Version

Dissertation submitted to the Graduate Program of the Museu de Zoologia da Universidade de São Paulo in partial fulfillment of the requirements for the degree of Master of Science (Systematics, Animal Taxonomy and Biodiversity).

Advisor: Prof. Dr. Aléssio Datovo

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ABSTRACT

Polynemidae is a family of primarily marine fishes with eight genera and 42 extant species. The phylogenetic allocation of polynemids within Percomorphacea as well as its internal relationships are uncertain as highly conflicting hypotheses have been proposed in the literature. Many aspects of the polynemid morphology are largely unknown, with little reports in the literature about their osteology, barely any information on their myology, and no studies on the ontogeny of their skeleton. This project aimed to study different aspects of the musculoskeletal system of Polynemidae and understand its internal relationships. The most remarkable feature of polynemids is their pectoral fin divided into an upper, unmodified fin and a lower portion with rays highly modified into specialized filaments. The present analysis reveals that the main *adductor* and *abductor* muscles masses of the pectoral fin involved in such intricate structure are completely divided into two muscle segments that serve separately the pectoral-fin rays, dorsally, and pectoral filaments, ventrally. Interestingly, it is herein demonstrated that the pectoral filaments receive massive nerves specialized in gustatory reception, indicating that the polynemid pectoral filament have not only tactile but also tasting functions. Several unique specializations in the mandibular, hyopalatine and branchial musculature of polynemids are herein reported for the first time. A comprehensive cladistic analysis based on 162 morphological characters and all valid polynemid genera was performed and resulted in fully resolved new hypothesis of relationships. All genera were recovered as monophyletic except *Polydactylus*, which is polyphyletic. Lastly, a survey of the skeletogenesis of polynemids reveals remarkable changes during their ontogeny, such as the shifting in pectoral radial 3 and the expansion of pectoral radial 4, both transformations associated with the differentiation of the pectoral filaments. The saddle-like ossification pattern of vertebral centra 1-4 of polynemids is only shared with sciaenids and additionally supports the hypothesis of a closer relationship between these families.

Keywords: Musculature. Ontogeny. Polynemids. Systematic. Threadfins.

RESUMO

Polynemidae é uma família de peixes primariamente marinhos, com oito gêneros e 42 espécies existentes. Sua posição filogenética dentro de Percomorphacea, bem como suas relações internas, são incertas visto que hipóteses altamente conflitantes foram propostas na literatura. Muitos aspectos da morfologia dos polinemídeos são amplamente desconhecidos, com poucos relatos na literatura sobre sua osteologia, quase nenhuma informação sobre sua miologia e nenhum estudo sobre a ontogenia de seu esqueleto. Este projeto teve como objetivo estudar diferentes aspectos do sistema musculoesquelético de Polynemidae e entender suas relações internas. A característica mais notável destes animais é a presença de uma nadadeira peitoral dividida em uma porção superior não modificada e uma porção inferior composta por raios altamente modificados em filamentos especializados. O presente estudo revelou que as principais massas musculares adutoras e abductoras envolvidas nesta complexa arquitetura peitoral são completamente divididas em dois segmentos musculares, que servem separadamente os raios da nadadeira peitoral, dorsalmente, e os filamentos peitorais, ventralmente. Curiosamente, é aqui demonstrado que os filamentos peitorais recebem nervos maciços especializados em recepção gustativa, indicando que tais filamentos possuem não somente funções táteis, mas também gustativas. Diversas especializações únicas na musculatura mandibular, hiopalatina e branquial dos polinemídeos são relatadas pela primeira vez. Uma análise cladística abrangente, baseada em 162 caracteres morfológicos e em todos os gêneros de polinemídeos válidos, foi realizada e resultou em uma nova hipótese de relacionamento totalmente resolvida. Todos os gêneros foram recuperados como monofiléticos, exceto *Polydactylus*, que foi recuperado como polifilético. Por fim, um levantamento da esqueletogênese dos polinemídeos revela mudanças notáveis durante sua ontogenia, como o deslocamento do terceiro radial e a expansão do quarto radial, ambas transformações associadas à diferenciação dos filamentos peitorais. O padrão de ossificação “saddle-like” dos centros vertebrais 1-4 de polinemídeos é compartilhado apenas com os scianídeos, suportando a hipótese de um relacionamento mais próximo entre essas famílias.

Palavras-chave: Musculatura. Nariz-de-vidro. Ontogenia. Polinemídeos. Sistemática.

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GENERAL INTRODUCTION

The division Percomorphacea (Wiley and Johnson, 2010; Betancur-R *et al.*, 2013) is one of the most diverse lineages of Teleostei, comprising about 17,000 species (Near *et al.*, 2013) and representing over half of bony fishes species and almost a quarter of all living vertebrates (Nelson, 2006). This richness of species is distributed among 30 different orders, 23 of which have contentious phylogenetic allocation, turning Percomorphacea in one of the most daunting challenges of fish systematics (Johnson, 1993; Nelson, 2006; Wiley and Johnson, 2010; Near *et al.*, 2013; Datovo *et al.*, 2014).

The monophyletic status of Percomorphacea has been corroborated by recent literature and, in the past decades, some hypotheses of internal relationships had been proposed for its orders on grounds of molecular (Chen *et al.*, 2003; Miya *et al.*, 2003; Li *et al.*, 2009; Near *et al.*, 2012; Betancur-R *et al.*, 2013; Near *et al.*, 2013; Sanciangco *et al.*, 2015; Hughes *et al.*, 2018) and morphological evidence (Johnson and Patterson, 1993; Springer and Johnson, 2004; Springer and Orrell, 2004; Wiley and Johnson, 2010; Datovo *et al.*, 2014). Nevertheless, morphological- and molecular-based hypotheses are often highly conflicting. Most recent papers regarding percomorphacean systematic are solely based on molecular data and disassociate widely known monophyletic clusters grouped together by anatomical characters (Chen *et al.*, 2003; Miya *et al.*, 2003; Li *et al.*, 2009; Betancur-R *et al.*, 2013). There are only a few morphological studies attempting to address the uncertainties amongst the major lineages of Percomorphacea and, most of them, employ only osteological data. Such analyses hardly dedicate any effort in investigating soft anatomy, despite the demonstrable phylogenetic importance of these systems (Winterbottom, 1974a; b; 1993; Springer and Johnson, 2004; Datovo and Bockmann, 2010; Datovo *et al.*, 2014).

Historically, the most diverse and challenging group within Percomorphacea is the Perciformes, an order that considerably varied along the past decades both in terms of its definition and composition. According to traditional classifications, Perciformes were a non-monophyletic group including many suborders and families with uncertain phylogenetic position, so that the order was the most diverse amongst vertebrates, with around 1500 genera and approximately ten thousand species (Rosen, 1973; Johnson, 1993; Johnson and Patterson, 1993; Nelson, 2006). Later classifications have substantially reduced those

numbers by erecting to the ordinal rank several noticeably monophyletic suborders placed within Perciformes (e.g., Blennioidei, Gobioidae, Carangoidei, etc.; Wiley & Johnson, 2010; Betancur-R et al., 2013). In spite of these changes, in most classification Perciformes remains as a non-monophyletic assemblage that is still one of the largest fish orders that contains a considerable amount of possibly unrelated families.

Polynemidae is one of the dozens families surrounded by systematic uncertainties that is usually allocated within Perciformes. This family is globally distributed and has around 42 species distributed in eight genera: *Eleutheronema*, *Filimanus*, *Galeoides*, *Leptomelanosoma*, *Parapolynemus*, *Pentanemus*, *Polydactylus*, and *Polynemus* (Feltès, 1991; Motomura, 2004; Wiley and Johnson, 2010; Fricke *et al.*, 2019). Polynemids are marine epibenthic animals, inhabiting sandy or muddy bottoms of turbid shallow waters (not exceeding 150 meters of depth). Some species may occur in brackish waters and some might even enter into rivers. These animals have economic value and certain species can reach up to two meters long (De Sylva, 1984; Feltès, 1991; Motomura, 2004; Nelson, 2006).

Polynemids are easily identifiable as a natural group due to their external morphological features, mainly by their distinct pectoral fin which is divided into a dorsal part, with 12 to 19 soft rays united by a membrane, and a ventral portion with around 3 to 16 isolated rays that are usually elongated forming a filament with tactile functions. There are several others characteristics that additionally help to diagnose the family, such as a conic snout with a ventral mouth; adipose eyelid covering the eye; superior lip absent or not well developed; possession of seven branchiostegal rays, where only one ray articulates with the posterior ceratohyal; presence of two well-separated dorsal fins, which the first one has VII to VIII spines and the second one has I spine and around 11 to 18 soft rays; and caudal fin deeply forked (Motomura, 2004; Nelson, 2006).

Polynemidae lacks a consensual phylogenetic position within Percomorphacea and different papers have advanced alternative hypotheses of relationships. Gosline (1962) proposed that polynemids were closely related to Mugilidae and Sphyrænidae due to their sharing of similar vertebral counts, postcleithrum supporting the pelvic girdle, and presence of non-adhesive eggs. The author additionally states that Polynemidae, Mugilidae, Sphyrænidae, Atherinidae and Phallostethoidei were closely related and might be clustered into a newly defined order Mugiliformes. Rosen (1964) defended that Polynemidae,

Mugilidae and Sphyraenidae should not be apart from Perciformes and, in addition, removed Atheriniformes from Mugiloidei. Nevertheless, Gosline (1968; 1971) continued to support the hypothesis of a closer relationship amongst polynemids, sphyraenids, mugilids and atherinoids, based on their lacking of attachment between cleithrum and pelvic girdle.

On the other hand, Johnson (1993) concluded that the characters proposed to support the closer relationship of polynemids with sphyraenids and mugilids were most likely homoplastic. The author suggested that Polynemidae is actually closely related to Sciaenidae due to their shared similarities during larval development, evidence also reported by De Sylva (1984) but that was not considered by most prior systematics in the formulation of hypotheses relationships among perciforms. The phylogeny of the Sciaenidae was the subject of a morphological analysis by Sasaki (1989). In that study, the author proposed 21 synapomorphies for the family, but is inconclusive about the sister group of Sciaenidae. However, Johnson (1993) noticed that, from the 21 synapomorphies for Sciaenidae provided by Sasaki (1989), five are shared by Polynemidae, which are the extension of *epaxialis* onto the frontals, absence of trisegmental pterygiophores, absence of supramaxilla, insertion of a single branchiostegal ray on the posterior ceratohyal, and a medial interdigitation between the quadrate and metapterygoid. Johnson (1993) and also drew attention to the fact that Freihofer (1978) had already pointed out that the two families share a deep and complex membranous prenasal canal extension. Considering all these evidences, Johnson (1993) recognized that more research were necessary to settle these relationships, but believed that Polynemidae and Sciaenidae are indeed sister groups and recommended that both families should be included in a superfamily Polynemoidea. That hypothesis of relationships was contested by Grove and Lavenberg (1997) and by Gusmao-Pompiani *et al.* (2005) based on the otolith structure and on the spermatozoid morphology, respectively.

Molecular analyses, in turn, allocate Polynemidae in positions that are quite contrasting with all prior hypotheses based on morphological evidence. In the study of Betancur-R *et al.* (2013) the family was removed from Perciformes and appeared as sister group of Menidae that, in turn, formed the sister group of Sphyraenidae. Those three families were clustered within Carangimorphariae, one of the nine major lineages of Percomorphacea proposed in that study). Mugilidae, was allocated within Ovalentariae as the sister group of Ambassidae, whereas Sciaenidae was placed in Percomorpharia (yet

outside Perciformes) as sister the group of Emmelichthyidae. In the molecular analysis of Near *et al.* (2013) the authors proposed an alternative hypothesis of placement of polynemids. In that scheme, Polynemidae appears as the sister group of the large lineage that holds Pleuronectiformes and Carangiformes. Also based on molecular data, Polynemidae was placed as the sister group of Menidae and Lactariidae in the study of Sanciangco *et al.* (2015). The analysis of ultraconserved elements recently published by Harrington *et al.* (2016) and Hughes *et al.* (2018) show a different proposal: Polynemidae as the sister group of Pleuronectiformes, only. In conclusion, the phylogenetic position of Polynemidae lack consensual agreement in both molecular morphology-based hypotheses and the family proved to be one of the most recalcitrant groups within the percomorphacean tree.

The intrarelationships of Polynemidae are comparably unclear. Although the polynemid taxonomy had been discussed in important studies (e.g. Motomura, 2004), the relationships among their eight genera have been the subject of only two explicit phylogenetic analyses until now: the unpublished thesis of Feltes (1986) and Kang (2017). The first one did not included all recent genera (*Leptomelanosoma* is lacking) and was based on 55 characters mostly from skeleton, whereas the second phylogeny was proposed based on 64 morphological characters.

It is also surprising the generalized lack of anatomical studies on polynemids, especially considering their highly modified and greatly sophisticated pectoral fins. The ontogeny and evolution of their pectoral filaments is still enigmatic and details of their structural components remains almost completely unknown. The morphological studies about Polynemidae are typically focused in superficial analyses of specific structures, such as vertebrae and pectoral-filament counts (De Sylva, 1984; Motomura, 2002; 2004), caudal fin anatomy (Feltes, 1991) and some cephalic structures (Feltes, 1993; Gosline, 1993). Osteological reports with more detailed analysis (for instance, jaws, neurocranium and shoulder girdle) are found only in a few descriptions of new genera and/or species (Feltes, 1993; Motomura and Iwatsuki, 2000; 2001; Motomura *et al.*, 2002). Knowledge on polynemid myology is even scarcer. There is only one paper superficially reporting the *adductor mandibulae* in *Polydactylus octonemus* (Gosline, 1993) and another that describes the dorsal gill-arch musculature in *Polydactylus oligodon* and *Filimanus xanthonema*

(Springer and Johnson, 2004). More recently, Kang *et al.* (2017) assembled several characteristics for the family, most of which are from osteological nature.

The present study is the major assessment of polynemid morphology done so far, ranging from muscles morphology never surveyed, cladistic analysis to test the family monophyly and to resolve internal relations, and a descriptive osteological study about polynemid development.

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Chapter 1

Cranial and pectoral musculature of Polynemidae

1. INTRODUCTION

The skeletal musculature is a system that has been traditionally neglected in most systematic studies with fishes, and the ones that address muscle morphologies generally have little focus on the muscle homologies across different lineages (Datovo and Rizzato, 2018). Yet, several studies demonstrate the importance of muscles and associated connective tissues to cladistic studies (Winterbottom, 1974b; 1993; Springer and Johnson, 2004; Datovo and Bockmann, 2010; Datovo and Castro, 2012; Datovo and Vari, 2013; 2014; Springer and Johnson, 2015; Datovo and Rizzato, 2018).

In the past decade several studies addressed some specific traits of the polynemid morphology (Feldes, 1991; 1993; Motomura *et al.*, 2000; Motomura and Iwatsuki, 2001; Motomura, 2002; Motomura *et al.*, 2002; Motomura, 2004; Gusmao-Pompiani *et al.*, 2005; Motomura and Tsukawaki, 2006; Chaklader *et al.*, 2015). However, almost all of them depicted only the external morphology of those fishes and a few osteological structures (*e.g.* number of vertebrae, spines, soft rays, and sparse data on the cranium). Myological data available for polynemids are even scarcer. Until recently, only two papers reported isolated data on the *adductor mandibulae* of *Polydactylus octonemus* (Gosline, 1993) and the suprabranchial musculature of *Polydactylus oligodon* and *Filimanus xanthonema* (Springer and Johnson, 2004). More recently, Kang *et al.* (2017) briefly described 14 characters from osteology and 4 from a few cranial and pectoral muscles of Polynemidae. Nevertheless, these myological descriptions are rather superficial and most skeletal muscles were set aside from their analysis and are completely unknown.

The present study describes in detail the musculature of the mandibular arch, hyopalatine arch, opercular series, branchial arches, and pectoral girdle of polynemids and *Cynoscion*, a representative of Sciaenidae, a family often proposed as closely related to Polynemidae. From these descriptions, several new morphological characters were assembled to test the intrarelationships of Polynemidae (see Chapter 2).

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Chapter 2

Phylogenetic relationships within Polynemidae

1. INTRODUCTION

Historically, Polynemidae has been indecisively allocated in incredibly distinct phylogenetic positions within Percomorphacea. Polynemids had been suggested to be closer to Mugilidae and Sphyraenidae (Rosen, 1964); Mugilidae, Sphyraenidae, Atherinidae, and Phallostethoidei (Gosline, 1962; 1968; 1971); and Sciaenidae (De Sylva, 1984; Johnson, 1993; Kang *et al.*, 2017) based on morphological data. Molecular analyses, in turn, alternatively aligned polynemids with Menidae (Betancur-R *et al.*, 2013); Menidae + Lactariidae (Sanciango *et al.*, 2015); Pleuronectiformes + Carangiformes (Near *et al.*, 2013); and Pleuronectiformes (Harrington *et al.*, 2016; Hughes *et al.*, 2018).

Therefore, Polynemidae clearly lacks a consensual phylogenetic allocation in both morphological and molecular approaches. The intrarelationships of Polynemidae are comparably unclear as the only phylogenetic analyses of the family are two unpublished thesis that propose highly divergent hypotheses (Feldes, 1986; Kang, 2017). Both analyses also have a modest amount of phylogenetic characters. Feldes (1986) did not include all genera currently considered valid (*Leptomelanosoma* is lacking) and was based on 55 characters mostly from skeleton (Fig. 1A). The study of Kang (2017) was based on 64 morphological characters and resulted in several polytomies across the tree (Fig. 1B). Recently Kang *et al.* (2017) have assembled several osteological characters and although the authors did not tested those characters in a cladistic analysis, they claimed to had found new synapomorphies for the family.

The present study proposes a new phylogenetic hypothesis for all genera (Fig. 2) of Polynemidae based on the largest morphological matrix ever assembled including more than one hundred new characters from external morphology, squamation, osteology, myology, and laterosensory system.

3.2 Phylogenetic analysis

The 162 morphological characters are herein categorized into 12 quantitatives (counts), 12 from external anatomy, 35 osteological, and 103 myological, which are divided into: 21 from the *adductor mandibulae* complex, seven from the hyopalatine musculature, six from the opercular muscles, 30 from the pectoral girdle musculature, 36 from the branchial arches muscles, and three from axial myology.

The analysis based on all morphological characters in 21 terminal taxa, including 19 polynemid species always recovered a single MPT according to the parameters set (EW or IW with different values of k). The traditional search on TNT without homoplasies weighting parameters (EW) resulted into a topology (Fig. 16) that was consistent to the topology obtained with IW ($k = 7$ to ∞). From $k = 3 - 6$ a different topology was recovered and adopted here as the phylogenetic relationship of Polynemidae (Fig. 17). Moreover, using strong weighting against homoplasies ($k = 1$ and 2) resulted into two new different MPTs.

The MPT obtained with IW ($k = 3 - 6$) was chosen to be the representative topology for the relations within Polynemidae due to its interval, excluding therefore the extreme weightings (too strong: $k = 1$ and 2; and too soft: EW). Nevertheless, the only difference between the topology from $k = 7$ to EW and the one from $k = 3 - 6$ is *Galeoides* and *Polydactylus sextarius* placement.

Intrarelationships of Polynemidae

Clade A (TNT clade 29) = Polynemidae: *Eleutheronema tetradactylum*, *Eleutheronema tridactylum*, *Filimanus similis*, *Filimanus xanthonema*, *Galeoides decadactylus*, *Leptomelanosoma indicum*, *Parapolynemus verekeri*, *Pentanemus quinquarius*, *Polydactylus approximans*, *Polydactylus microstomus*, *Polydactylus octonemus*, *Polydactylus oligodon*, *Polydactylus opercularis*, *Polydactylus plebeius*, *Polydactylus sexfilis*, *Polydactylus sextarius*, *Polydactylus virginicus*, *Polynemus multifilis*, *Polynemus paradiseus*.

Synapomorphies: Char. #1: (12>10); Char. #4: (17>15); Char. #7: (9>11); Char. #9: (9>13-14); Char. #10: (8>12); Char. #11: (22>31-42); Char. #18: (0>1); Char. #31: (0>1); Char. #35: (0>1); Char. #42: (1>0); Char. #43: (0>1); Char. #48: (0>1); Char. #49: (0>1); Char. #52: (0>1); Char.

#74: (0>1); Char. #75: (0>1); Char. #76: (0>1); Char. #77: (0>1); Char. #83: (0>1); Char. #88: (0>1); Char. #93: (0>1); Char. #97: (0>1); Char. #98: (0>1); Char. #101: (0>1); Char. #107: (0>1); Char. #108: (0>1); Char. #109: (0>1) Char. #112: (0>1); Char. #113: (0>1); Char. #121: (0>1); Char. #127: (0>1); Char. #129: (0>1); Char. #136: (0>1); Char. #160: (0>1).

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1. INTRODUCTION

Marine fish eggs and larvae varies drastically and can have several different forms, morphological specializations and pigmentation patterns that act as important characters to identifying them (Moser, 1996). The study of larval ontogeny in systematic research has been a consistent tool to investigate the relationships among fishes and therefore trace homologies between structures (Cubbage and Mabee, 1996; Moser, 1996; Britz and Johnson, 2002; Warth *et al.*, 2017). The morphogenesis of skull, mandibular and hyoid arches are by far the most studied structures in fish development (Arratia and Schultze, 1991; Cubbage and Mabee, 1996; Adriaens and Verraes, 1998; Geerinckx *et al.*, 2005; 2007; Block and Mabee, 2012). Nonetheless, several others papers analyzed other structures such as pectoral girdle and branchial arches (Faustino and Power, 1999; Britz and Johnson, 2002; 2005; Warth *et al.*, 2017). Still, there are a lot of groups lacking information about larval development.

Polynemidae early stages descriptions are rare and can be found, in its majority, in larval identification guides such as Moser *et al.* (1984), Moser (1996), Leis and Carson-Ewart (2000) and Richards (2005). From the few species studied, most Polynemids are considered to be protandrous hermaphrodites, where eggs, larvae and juveniles are pelagic until they reach about 60 mm, in which they began to enter nearshore environments (Santerre and May, 1977; Sandknop and Watson, 1996; Motomura, 2004). In the study of Santerre and May (1977) the authors observed that *Polydactylus sexfilis* matures first as a male with around 200 to 290 mm of length and becomes a female by the time they reach approximately 300 to 400 mm of length. The pelagic eggs are spherical and transparent with approximately 0.79 to 0.99 mm (0.76 mm average) in diameter (De Sylva, 1984; Sandknop and Watson, 1996).

The larvae hatch with around 1.5 to 2 mm in which their mouth is yet not formed, the eye is unpigmented and they bear a large yolk sac ventrally that will nourish them during their early life history (Sandknop and Watson, 1996). The yolk sac is almost fully consumed by the time the larvae reach about 3 mm long (Santerre and May, 1977; Sandknop and Watson, 1996). Polynemidae larvae have a generally large head, with weak spination,

prominent eyes and a rounded snout – characteristic that is distinguishable during the postflexion stage – and a triangular coiled gut that extends about 44 – 62% of body length (Sandknop and Watson, 1996; Leis and Trnski, 2000; Motomura, 2004). During the preflexion stage, the main caudal fin rays are one of the first structures to develop in the larvae body. The flexion regularly occurs at 3.5 to 4.5 mm length, which, early in this stage, the anal and the second dorsal fin rays begin to simultaneously develop with about the same number of rays (Sandknop and Watson, 1996; Leis and Trnski, 2000; Richards, 2005). Small preopercular spines can be seen during flexion which become larger by settlement. These spines will later develop into the serrate preopercular margin of most of the adults (Leis and Trnski, 2000). Furthermore, still during chorda flexion, the pectoral fin rays and the spines of the first dorsal fin start to grow and at the end of the flexion process, pelvic and procurrent caudal fin rays commence to form (Sandknop and Watson, 1996).

Pectoral fin rays are usually leveled with the top of the gut in early flexion and during the postflexion stage they start to migrate ventrally, settling near the ventral margin of body by the time they reach approximately 12 mm, except for *Parapolyneumus* and *Polyneumus* species (Leis and Trnski, 2000; Motomura, 2004). The pectoral rays are added from top to bottom and as it moves, the fin becomes divided into two separate lobes. The lower lobe moves anteroventrally and present thicker rays in comparison to the upper lobe. As they develop, they become longer and the membrane connecting them starts to vanish (Sandknop and Watson, 1996; Leis and Trnski, 2000). The upper lobe rays are fully ossified at 6.5 mm, at which time the lower lobe rays start to ossify. By the time the larvae reach approximately 7 mm, all pectoral structures are ossified and with an extra 0.3 mm in length, all elements of second dorsal and anal fin are complete (Leis and Trnski, 2000; Motomura, 2004).

Larval polynemids are lightly to moderately pigmented, with melanophores distribution and density varying throughout the taxa (Leis and Trnski, 2000). The pigmented areas usually occur along the ventral midline of the tail and gut and on dorsal surfaces of the swimming bladder and head. Melanophores can also be present at the posterior margin of the articular or over the angular bone (Sandknop and Watson, 1996; Leis and Trnski, 2000). Finally, with 15 mm the scales are fully developed and so the adipose eyelid (Leis and Trnski, 2000; Motomura, 2004).

5. CONCLUSIONS

Polynemids certainly present very distinct characteristics in the adult morphology, especially regarding their pectoral girdle, and the ontogeny of these unique morphological specializations has never been described. The study of a developmental series of threadfin larvae reveals ontogenetic patterns behind the formation of such specializations, such as the relatively slow sequence of ossifications of the pectoral radials and the differentiation of the ventralmost pectoral rays into the tactile filaments that have vital functions during the threadfin life, such as foraging and avoiding predators. The late development of supraneurals of polynemids also possibly represents a unique pattern within Teleostei. The saddle-like pattern of ossifications in the first four vertebral centra is apparently only found in polynemids and sciaenids and this shared character may constitute an additional evidence of a closer relationship among these families.

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