Dissertação de Mestrado

Lucas Romero de Oliveira

Anatomia comparada e importância filogenética da musculatura branquial em tubarões da superordem Galeomorphi (Chondrichthyes:Elasmobranchi)

Comparative anatomy and phylogenetic importance of the branchial musculature in sharks of the superorder Galeomorphi (Chondrichthyes:Elasmobranchi)

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Dissertação apresentada ao Instituto de Biociências da Universidade de São Paulo para a obtenção de Título de Mestre em Zoologia, na Área de Anatomia comparada

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Introduction

Extant sharks are currently divided into two monophyletic groups based on morphological (Compagno, 1977; Shirai, 1992a, 1992b, 1996; de Carvalho, 1996; de Carvalho & Maisey, 1996) and molecular (Douady et al., 2003; Winchell et al. 2004; Naylor et al., 2005, 2012; Human et al., 2006; Heinicke et al., 2009)data: Galeomorphi and Squalomorphi. Molecular data support that rays, forming a group named Batoidea, are the sister-group to a clade comprising both galeomorph and squalomorph sharks. Results from many older morphological studies also considered both body plans (sharks and rays) as indicative of monophyletic groups, but some recent works based on morphological data suggested that rays form a monophyletic group nested within squalomorph sharks (Shirai, 1992; de Carvalho & Maisey, 1996; de Carvalho, 1996).

In studies based on both types of dataset, the Galeomorphi comprehend only shark groups. This superorder includes the orders Heterodontiformes, Orectolobiformes, Lamniformes and Carcharhiniformes with approximately 360 species (Ebert et al., 2013). These orders have very distinct representatives, but they are grouped together based on the proximity of the hyomandibular fossa and the orbit in the neurocranium (Compagno, 1984). Galeomorph sharks have several dominant species in epipelagic environments and shallow waters around the globe (Compagno, 1977, 1984, 1988, 1990; Stiassny et al., 2004) and are the most commonly known sharks by the lay public. They have much more complex ecologies than usually assumed, and include mega predators, micro-feeders and feeders on small fishes all within the same order (Lamniformes). They also have many forms of reproduction, including egg laying, egg retention, yolk-sac feeding and even placentary viviparity (Compagno, 1990).

There is some consensus about the relative phylogenetic position of Lamniformes and Carcharhiniformes, which are considered sister-groups by several authors, both morphological (Compagno, 1973; de Carvalho, 1996) and molecularly (Douady et al., 2003; Naylor et al, 2005; Human et al. 2006; Heinicke et al. 2009), but the interrelationships between Orectolobiformes and Heterodontiformes are somewhat ambigous, with characters that suggests them either as sister-groups (Compagno, 1973; Soares & Carvalho, 2013a) or that the Heterodontiformes are the sister-group of all other galeomorph orders with the Orectolobiformes as the sister-group to Lamniformes +

Carcharhiniformes (Shirai, 1992; Carvalho, 1996; Carvalho & Maisey, 1996; Goto, 2001; Naylor et al., 2005; Heinicke et al., 2009). Another hypothesis supported was that the order Heterodontiformes should not be included within the Galeomorphi (Thies & Reif, 1985; summary in Serét, 1986; Douady et al., 2003; Human et al., 2006), but it was not based on strong characters, either morphological or molecular (Shirai, 1992; Carvalho, 1996; Naylor et al., 2012). Recently a paper (Soares, 2013a) proposed two characters of the jaw and hyoid arch musculature that indicate that Heterodontiformes are possibly the sister-group to the Orectolobiformes.

Mickoleit (2004), in a very comprehensive review of the synapomorphies of all vertebrate taxa recognized at the time, listed synapomorphies for a taxon formed by heterodontids and orectolobiforms. They include the nasal capsules expanded caudally and trumpet-like, the size of the mouth gape reduced through the development of the mandibular musculature, the *m. praeorbitalis* strongly expanded inserting, at least in part, on the inferior edge of the mandible and the *m. adductor mandibulae* expanded cranially. Both studies (Soares, 2013a and Mickoleit, 2004) mentioned characters from the musculature associated with the jaws and hyoid arch as indicative of phylogenetic relationships between taxa. So far, characters from the branchial arches were not used in broad systematic studies of elasmobranchs. The visceral arches (jaws, hyoid arch and branchial arches) have been referred as serially homologous structures (Gegenbaur, 1878), which means they have the same basic elements and should, therefore, possess congruent informations about the relationships of different groups.

1. *Musculature associated with the visceral skeleton and its use in systematic studies*

The musculature associated with the visceral arches (jaws, hyoid and branchial arches) is an anatomical complex yet to be fully explored in a phylogenetic context in Chondrichthyes. Many studies have described and analyzed these muscles, but their focus was usually directed towards a better understanding of the feeding and ventilation adaptations (Wilga, 1997, 2008; Motta & Wilga, 2001; Motta et al., 2005; Motta & Huber, 2012; Dolce & Wilga, 2013; Wilga & Ferris, 2016). Some studies from the beginning of the twentieth century provide accurate anatomical descriptions that are useful in phylogenetic analyses, but they are based on different approaches to classification, and

were carried out before the onset of cladistic analysis (Allis Jr., 1917, 1920, 1923; Edgeworth, 1935; Marion, 1905; Vetter, 1874).

A recent work that uses the potential phylogenetic value of visceral musculature is Miyake et al. (1992). Based mostly on the observations made by Edgeworth (1935), Miyake et al. evaluated how the muscles in the ventral region of the gill arches were modified in the evolution of rays, by comparing batoid orders with sharks and with each other. They found important results such as, for example, a muscle called "X" was found only in electric rays (Torpediniformes) and the authors suggested that this would be the same structure Edgeworth called *m. intermandibularis profundus*. Another example is a muscle recognized only in Batoidea, but with uncertain homology among other Chondrichthyes: the *m. spiracularis*. This shows the great unexplored potential this anatomical complex has in helping us to better understand phylogenetic issues. This work also elaborated a list of synonyms for muscles, listing the names of muscles that were thought to be homologous in an attempt to stabilize their nomenclature using both the origin and insertion points and embryonic development to propose homologies. They considered that both insertions and origins are conservative in muscles. They also analyzed some papers that considered other criteria to propose homology, such as the innervation of muscles.

Another study (Soares & Carvalho, 2013b) of the morphology and subsequent description of the musculature associated with the jaws and the hyoid arch allowed a better understanding of the family Chlamydoselachidae, and its sole genus, *Chlamydoselachus*, previously included in the order Hexanchiformes. It was found that this family has no muscular characters in these arches that indicate a closer relationship of the family inside this order as found by previous authors that found this same arrangement based on other characters (Thies, 1987; Shirai, 1992). In another study, the same authors (Soares & Carvalho, 2013a), found evidence from the same muscles that reinforced the hypothesis that Orectolobiformes are the sister-group to Heterodontiformes within Galeomorphi, and not the sister-group of Lamniformes + Carcharhiniformes as previously advocated (Compagno, 1973, Thies & Reif, 1985).

These papers illustrate the diversity of anatomical studies of muscles addressing chondrichthyans. There are more examples if we consider actinopterygians, such as Winterbottom (1974, 1993), Howes (1976), Springer et al. (2004), Datovo & Bockmann

(2010), Wiley & Johnson (2010), Datovo & Vari (2013, 2014), Datovo, de Pinna & Johnson (2014) and Springer & Johnson (2015). All these authors used this anatomical complex to some extent (as the main data set or as additional data) to better understand the interrelationship of groups in different phylogenetic levels. As an exemple, the latter study (Springer & Johnson, 2015) analyzed the branchial musculature of anguilliform taxa. The authors found new characters within this muscles that helped them clarify the relationships of the families within Anguilliformes, as well as new synapomorphies in the branchial arches, both of musculature and osteological nature.

The muscles associated with the branchial region are intimately associated with ventilation and feeding in aquatic vertebrates. Daniel (1934) divided this musculature in three groups among chondrichthyans: the **constrictors** (seven dorsal and seven ventral muscles), the **interarcuals** (named epibranchials by Miyake et al, 1992; Goto, 2001) and the **hypobranchials** (seven muscles). The dorsal and ventral constrictors, as their name indicates, constrict the gill arches, and are always paired structures (one dorsal has a correspondent ventral). The first and second ventral constrictors may have superficial and deep fibers separated by a septum, in which the superficial fibers insert onto the mandibular arch and the deep fibers onto the hyoid arch. The interarcual muscles are composed by the muscles within the same arch and between arches, being divided into dorsal (four muscles) and lateral (five muscles). The hypobranchials consist of the muscles forming the pharynx floor and the floor of the gill pouches. This last group is composed of the *m. coracomandibularis* (associated with the jaw arch), *m. coracohyoideus* (associated with the hyoid arch) and all the *m. coracobranchiales* (associated with the branchial arches). Daniel's (1934) work has been used as one of the primary references in studies of muscles, and his definition of branchial muscles is followed here; therefore, the *m. spinalis* is not described herein, although it does insert onto the first pharyngobranchial.

Objectives

This study aims to describe and analyze, in a phylogenetic context, the visceral musculature associated with the branchial arches in galeomorph sharks, and to present

characters that help to further elucidate the interrelationships of galeomorph orders. This is aimed on the light of the help provided by this musculature on other taxa.

More specific phylogenetic questions include: to verify if characters from the visceral musculature associated with the branchial arches provide evidence that help clarify the phylogenetic relationships between Heterodontiformes and Orectolobiformes with other galeomorph orders and between the Carcharhinidae and Sphyrnidae; to verify if characters of the visceral arch muscles support other, less inclusive galeomorph clades.

A formal cladistic analysis of a data matrix was beyond the scope of the present project. The characters detailed below are inferred to be possible synapomorphies, but further phylogenetic analyzes are necessary to corroborate these conclusions. Yet, the present study suggests that characters from the branchial musculature are useful to help elucidate relationships among galeomorph sharks.

Conclusions

1. Branchial musculature is highly conserved within sharks. *Rhizoprionodon posrosus*, *Eusphyra blochii* and *Prionace glauca* did not present any kind of intraspefcific variations.

2. The orders Carcharhiniformes and Lamniformes have some patterns that suggest they are more closely related to each other than to other orders, which are the divided fifth *m. coracobranchiales* (can also be a convergence, since the basal families are different for each order), the presence of a medial ventral raphe between the two antimeres of the *m. constrictores branchiales superficiales* and the crescent shape of the *m. adductores arcuum branchialium*.

3. Some characters were found to indicate the ancestral morphology of Elasmobranchi and should be investigated in Holocephali and Actinopterygii to acknowledge at which level they originally evolved, if at the elasmobranch, chondrichthyan or gnathostome level, such as the *m. trapezius* possessing two rami (one ramus in Orectolobiformes and Heterodontiformes) and the *m. adductores arcuum branchialium* possessing a triangular shape (crescent shape of these muscles in most carcharhiniform and lamniform families). These features are proposed to be plesiomorphic within elasmobranchs because both groups (Galeomorphi and Squalomorphi) have them, secondarily modified within some families (Carcharhinidae, Sphyrnidae, Hemigaleidae, Leptochariidae and Scyliorhinidae among Carcharhiniformes and Lamnidae and Odontaspididae among Lamniformes have a modified arch adductor and all the families examined within Heterodontiformes, Orectolobiformes and Squaliformes have a modified trapezius).

4. More data is required to assert if Batoidea is a part of the Squalomorphi or a group that branches out before both modern shark groups, since not many representatives of this group was dissected. The presence of a posterior ramus on the *m. arcuales dorsales* in squalomorph sharks (only a single ramus in galeomorph and *Zapteryx*) sustains the monophyly of the squalomorph sharks, as proposed by Shirai (1992).

5. The absence of levator muscles in Elasmobranchi is possibly a characteristic restricted to Chondrichthyes, since neither elasmobranch taxa nor holocephalans,

according to Didier (1995), have this musculature. Teleostei possess this musculature.

6. The abcense of the epibranchial insertion on the *m. trapezius*, the bulkier nature of this muscle and the bulkier and smaller shape of other muscles, with many connective fibers surrounding them, in Heterodontiformes and Orectolobiformes suggests that these orders could be closely related, as suggested by Soares & Carvalho (2013b) based on mandibular and hyoid musculature. This may indicate that these character complexes (musculature of jaws, hyoid and branchial arches) evolved probably as a single anatomical complex. Only one character contradicts this, the presence of the characteristic raphe from carcharhiniform and lamniform taxa in two basal orectoloboid clades.

7. Characters of branchial muscles elucidate to some extent the interrelationships among the families of Carcharhiniformes, largely corroborating the molecular proposal of Naylor et al. (2012) and supporting some observations made by Compagno (1988). The coracobranchial muscles, especially the fifth, and the adductor of the branchial arches are particularly informative in this regard, possessing remarkable differences between families and grouping families as well.

8. The *m. interpharyngobranchiales* present reductions in two orders: parascyllids and orectolobids have the last *interpharyngobranchiales* muscle as a tendinous structure, and *Hemiscyllium* has all three muscles reduced to connective tissue, in Orectolobiformes; and Etmopteridae and Somniosidae have the reduction of the last *interpharyngobranchiales* muscle and Dalatiidae have the reduction of all three muscles to a tendinous structure in Squaliformes. This could suggest a closer relationship of the families within each order. The squaliform families have already been grouped by Shirai (1992) and de Carvalho (1996).

9. The order Lamniformes also have two distinct morphologies of the *m. coracobrachialis* (one or two rami present in the fifth *m. coracobranchialis*) and *m. adductores arcuum branchialium* (crescent or triangular shape). No conclusions can be drawn of the relationships between the lamniform families, aside that Pseudocarchariidae is probably basal within the order, since it has the same features present in basal carcharhiniforms (one ramus and triangular shape). Also, mitsukurinids and alopiids share the crescent shape of the brachial arch adductor and a single trapezial ramus, whereas lamnids and odontaspidis share the

triangular shape of the adductor and two rami on the *m. trapezius*. The proposed interrelationships within lamniforms does not agree with the molecular phylogenetic proposal of Naylor et al. (2012), since it is proposed in this molecular work that Alopiidae is closely related to Pseudocarchariidae and *Odontaspis* (not seen on the present work), whereas Lamnidae is closely related to *Carcharias*. There is also disagreement with the proposal present in the study of Wilga (2005), and no groups proposed in that study is recovered herein.

Resumo

O presente trabalho consiste em uma comparação anatômica da musculatura branquial em Galeomorphi visando determinar se há possíveis padrões que indiquem proximidades filogenéticas, especialmente relacionados com a ordem Heterodontiformes e outras famílias de ordens dentro de Galeomorphi. A análise de musculatura já se provou de grande ajuda para identificar estas questões. Foram observados nove músculos em 44 espécies de todas as ordens Galeomorphi, 13 espécies em duas das cinco ordens de tubarões Squalomorphi (Squaliformes e Hexanchiformes) e um exemplar de Batoidea, totalizando 57 espécies. Os resultados indicam que este complexo anatômico é extremamente conservado e generalizado. Os músculos mais informativos neste contexto foram *m. trapezius*, *m. adductores arcuum branchialium*, *m. coracobranchiales*, em especial o músculo associado ao último arco, e *m. arcuales dorsales*. Outros músculos apresentam variações em poucos ou nenhum grupo. A análise dos padrões das musculaturas indica que Lamniformes é grupo-irmão de Carcharhiniformes e Orectolobiformes é grupo-irmão de Heterodontiformes, indicando este relacionamento próximo entre Orectolobiformes e Heterodontiformes a morfologia do *m. trapezius*, mais maciço e sem divisões, características restritas a ambas as ordens, e as fibras do quinto *m. coracobranchialis* são direcionadas para a frente, enquanto que se dirigem para cima ou obliquamente em outros grupos. Indicam um relacionamento entre Carcharhiniformes e Lamniformes a presença de dois ramos no quinto *m. coracobranchialis*, a forma de meia lua do *m. adductores arcuum branchialium* e a presença de uma rafe entre os antímeros do *m. constrictores branchiales superficiais*, todas características restritas a representantes dessas ordens. Também foi encontrado suporte para a divisão de tubarões em Galeomorphi e Squalomorphi. Esta divisão é indicada principalmente pela presença do ramo posterior do *m. arcuales dorsales* em tubarões do grupo Squalomorphi.

Abstract

The present work consists of an anatomical comparison of the branchial musculature of galeomorph groups in order to search for evidence that could indicate possible phylogenetically relevant patterns, especially related to the Heterodontiformes and other families within the orders of Galeomorphi. Previous studies based on other muscle complexes have contributed with information that helped to address thoses questions (Datavo & Vari, 2014; Soares & Carvalho, 2013a,b). Nine branchial muscles of 44 species among all galeomorph orders, 13 species from two of the five recognized squalomorph shark orders (Squaliformes and Hexanchiformes) and one batoidean were observed, totalizing 57 species. The results indicate a highly conserved anatomy on this anatomical complex, possibly indicating a conservative generalized condition at both chondrichthyan and gnathostomes level. The most informative muscles in this context were the *m. trapezius*, the *m. adductores arcuum branchialium*, the *m. coracobranchiales*, especially the portion associated with the last branchial arch, and the *m. arcuales dorsales*. The other five muscles have little to no variation among different groups. The analysis of the muscular patterns indicates that lamniforms and carcharhiniforms are sister-groups and Orectolobiforms and Heterodontiforems are sister-groups, supported by the *m. trapezius* having a single ramus and absence of the insertion onto the epibranchial only in Orectolobiformes and Heterodontformes, as well as the fifth *m. coracobranchialis* has its fibers oriented forward, when opposed to two rami in the *m. trapezius* in all other orders and fibers of the fifth *m. coracobranchialis* either upwards or obliquely organized. Regarding carcharhiniform and lamniform relatioships, the muscles that provide evidence are the presence of a second ramus on the fifth *m. coracobranchialis*, with a single ramus in all other orders, the crescent shape of the *m. adductores arcuum branchialium*, with triangular shape in other groups, and the presence of a raphe between the antimeres of the *m. constrictores branchiales superficiales*, which are triangular outside this group. Also, it was found support for the division of shark groups between Galeomorphi and Squalomorphi with the presence of a posterior ramus on the *m. arcuales dorsalis* in squalomorph sharks.

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