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

Supervisora: Mônica de Toledo Piza Ragazzo

Instituto de Biociências – Universidade de São Paulo

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A meus pais, amigos e namorada.

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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.

Material and methods

1. Material

The study was based on preserved specimens deposited in collections of five institutions: California Academy of Sciences, San Francisco (CAS), Hokkaido University Museum of Zoology, Sapporo (HUMZ), Museu de Zoologia da Universidade de São Paulo, São Paulo (MZUSP) and National Museum of Natural History - Smithsonian Institution, Washington D.C. (USNM/NMNH-SI), and also from material available for dissection at the Laboratório de Ictiologia - Departamento de Zoologia - Instituto de Biociências - Universidade de São Paulo, São Paulo (IBUSP). Material from the latter institution has no collection number and are cited herein as MZUSP uncat. The material is listed below. Each lot had only one specimen dissected. The informations regarding total length and sex are related to this specimen.

The classification used in this work follows Compagno (1988). The family Pentanchidae was included following our results, that suggests a separation of this group from the rest of the scyliorhinid family.

Among the Galeomorphi, 46 species from 20 of the 24 recognized families of all orders were dissected (five Lamniformes, six Orectolobiformes, three Heterodontiformes and 32 Carcharhiniformes). In addition 10 species of two among the five orders of squalomorph sharks (two Hexanchiformes and eight Squaliformes) and one batoid, *Zapteryx brevirostris* was also dissected.

Carcharhiniformes

Carcharhinidae: *Carcharhinus falciformis* (USNM 196826 6 specimens, female 324mm), *Carcharhinus limbatus* (USNM 196702 7 specimens, male 307mm), *Carcharhinus porosus* (MZUSP 37286 2 specimens, male 335mm), *Galeocerdo cuvier* (USNM 112243 6 specimens, male 510mm), *Loxodon macrorhinus* (USNM

197349 3 specimens, male 531mm), *Nasolamia velox* (USNM 203467 3 specimens, female 529mm), *Negaprion acutidens* (MZUSP uncat. 1 specimen, male 357mm), *Prionace glauca* (USNM 221308 5 specimens, female 368mm; HUMZ 172449 1 specimen, female 675mm), *Rhizoprionodon porosus* (MZUSP 60555 4 specimens, female 355mm), *Rhizoprionodon lalandei* (MZUSP 37300 8 specimens, female 339mm), *Scoliodon laticaudus* (SU 38377 3 specimens, male 392mm), *Triaenodon obesus* (SU 14498 1 specimen, female 480mm)

Hemigaleidae: *Chaenogaleus macrostoma* (NMMBP 6414 1 specimen, female 652mm)

Leptochariidae: *Leptocharias smithii* (USNM 202677 3 specimens, female 578mm)

Pentanchidae: *Apristurus brunneus* (CAS 57475 3 specimens, male 649mm), *Apristurus laurassonii* (USNM 221255 10 specimens, male 345mm), *Galeus arae* (SU 66824 30 specimens, male 262mm), *Galeus melastomus* (USNM 221638 27 specimens, male 232mm), *Parmaturus xaniurus* (CAS 26574 11 specimens, female 249mm)

Proscylliidae: *Eridacnis radcliffei* (CAS 34140 6 specimens, female 230mm)

Scyliorhindae: *Scyliorhinus haeckelii* (MZUSP uncat. 12 specimens, male 168mm), *Schroederichthys maculatus* (USNM 187690 7 specimens, female 312mm)

Sphyrnidae: *Sphyrna tiburo* (MZUSP 37347 3 specimens, female 371mm), *Sphyrna lewini* (MZUSP uncat. 1 specimen, female 497mm), *Sphyrna zygaena* (USNM 190592 3 specimens, female 443 mm), *Eusphyra blochii* (USNM 205342 5 specimens, male 641mm)

Triakidae: *Galeorhinus galeus* (CAS 21347 2 specimens, male 352mm), *Hemitriakis japanica* (USNM 191193 3 specimens, male 649mm), *Mustelus griseus* (MZUSP uncat. 1 specimen, male 298mm), *Mustelus higmani* (CAS sn 1 specimen, female 445mm), *Mustelus schmitti* (MZUSP 37327 4 specimens, female 317mm), *Triakis scyllium* (SU 7257 6 specimens, female 267mm)

Heterodontiformes

Heterodontidae: *Heterodontus portusjacksoni* (USNM 40012 2 specimens, female 248mm), *Heterodontus francisci* (CAS 19176 2 specimens, female 307mm), *Heterodontus zebra* (CAS 29970 4 specimens, female 222mm)

Lamniformes

Alopiidae: *Alopias pelagicus* (USNM 202675 2 specimens, female 751mm)

Lamnidae: *Isurus oxyrhincus* (USNM 201733 1 specimen, female 756mm; USNM 201915 1 specimen, female 925mm)

Mitsukurinidae: *Mitsukurina owstoni* (NMBP 15952 1 specimen, male 1155mm)

Odontaspididae: *Carcharias taurus* (MZUSP 37281 5 specimens, female 335mm)

Pseudocarchariidae: *Pseudocarcharias kamoharai* (MZUSP uncat.1 specimen, only head 269mm)

Orectolobiformes

Ginglymostomatidae: *Ginglymostoma cirratum* (SU 8116 3 specimens, female 271mm)

Hemiscyllidae: *Chiloscyllium punctatum* (USNM 176709 3 specimens, female 729mm), *Hemiscyllium ocellatum* (USNM 176822 3 specimens, female 540mm)

Parascyllidae: *Cirrhoscyllium formosanum* (USNM 395036 4 specimens, female 226mm)

Orectolobidae: *Orectolobus maculatus* (USNM 39999 1 specimen, female 615mm)

Stegostomatidae: *Stegostoma fasciatum* (USNM 138548 1 specimen, male 294mm)

Squaliformes

Centrophoridae: *Centrophorus squamosus* (SU 8582 1 specimen, male 390mm), *Centrophorus uyato* (USNM 220238 3 specimens, female 369mm)

Dalatiidae: *Dalatias licha* (MZUSP uncat. 1 specimen, only head 323mm)

Etmopteriidae: *Centroscyllium nigrum* (USNM 220270 5 specimens, female 367mm), *Etmopterus polli* (CAS 235532 4 specimens, male 205mm)

Somnosidae: *Centroscymnus coelolepis* (USNM 206064 7 specimens, female 588mm), *Scymnodon obscurus* (USNM 220509 5 specimens, male 361mm)

Squalidae: *Squalus albicaudatus* (UERJ 1683 2 specimens, male 485 mm)

Hexanchiformes

Heptranchidae: *Heptranchias perlo* (USNM 220193 2 specimens, male 344mm), *Notorynchus cepedianus* (CAS 39612 1 specimen, female 565mm)

Batoidea

Rhinobatidae: *Zapteryx brevirostris* (MZUSP uncat. 1 specimen, male 476mm)

2. Methods

Branchial muscles were examined through gross dissections of one side of the branchial region, starting with the removal of the skin and subsequent cut through the connective tissue to loosen the muscles from one another. This enabled the observation of the interpharyngobranchial muscles, the dorsal arcual muscles, the coracoarcual muscles, the *m. trapezius*, the constrictor of the oesophagus and the constrictor layer. To observe the musculature associated with the epibranchial-ceratobranchial articulation, the second *m. constrictores branchiales superficiales* (associated with the second branchial arch and third gill opening) were cut to expose these muscles. Only this muscle of the series was chosen after a few dissections because cutting all the constrictor muscles lead to loss of information (all the arches have the same muscular anatomy for the *m. adductor arcuum branchialium* and *m. interbranchiales,* which were the only two muscles in the intertrematic region that required dissection of the constrictor layer to be visible). Also, it was easy to find the

homologous muscle in Hexanchiformes because, despite the larger number of arches the representatives of this order possess, both position and nerve structure support the identification of this constrictor. Notes and photos were taken to help the description of the patterns within each group. All dissections were photographed using a digital camera. Some taxa were illustrated to better demonstrate how the muscles were positioned.

Although this study aims to help understand the evolution of characters, no formal phylogenetic analysis was conducted herein. Therefore, all characters that indicate any kind of relationships between groups should be further studied to evaluate their real phylogenetic value. The characters are listed on the annexes, as well as the groups each state occurs.

The *m. trapezius* was included among the examined branchial muscles because it has a connection with the last branchial arch and is widely considered by some authors (Daniel, 1934; Shirai, 1992; Miyake et al, 1992) as part of the branchial musculature. Although the same could have been applied to the *m. subspinalis*, it is considered by Daniel (1934) and Edgeworth (1935) to be a cranial non-visceral muscle and therefore not considered in this study; this muscle connects the neurocranium to the first pharyngobranchial.

The *m. interbranchiales* was not included on the illustrations because it would be difficult to observe them without making other muscles incomprehensible.

Muscular nomenclature follows Shirai (1992), since it is the most recent work and has very accurate descriptions of each muscle. The adoption of the nomenclature *m. trapezius* instead of *cuccularis* (used in his work) is due to the former being an older name and used in other recent groups, suggesting probable homologies with this muscle outside Chondrichthyes. Additional synonyms are listed on the appendix. The muscles examined are listed on Table 1.

TABLE 1. List of the muscles of the branchial region examined in this study and comments on some their features.

Muscles	**Characteristics**
Constrictor branchiales superficiales	Most superficial muscle; divisions difficult to represent, therefore, no septa between them were represented on the figures. The insertions are on deeper elements, and could not be represented as well.
Trapezius	Muscle connecting the pectoral girdle to the neurocranium; usually divided into two rami.
Adductores arcuum branchialium	Small muscle, each connecting the epibranchial and ceratobranchial of one given arch.
Interpharyngobranchiales	Laminar component that connect two adjacent pharyngobranchial cartilages; these components can be of muscular or connective tissue.
Arcuales dorsales	Muscle that connect the pharyngobranchial and epibranchial of a given arch; in some cases, it also inserts onto the pharyngobranchial of the adjacent arch.
Interbranchiales	Muscle that draw the branchial filaments closer to each other; deeper muscle, was not illustrated on the figures.
Coracoarcualis communis	Posterior region of the *m. rectus-cervicis*; closely related to every muscle that originates on the coracoid bar.
Coracobranchiales	Muscles responsible for expanding the gill chamber.
Constrictor oesophagi	Muscle responsible to direct food to the stomach; associated with the last branchial arch.
Pharyngobranchial n-epibranchial (n+1)	Muscles found only in *Eusphyra blochii* and *Pseudocarcharias kamoharai*; they connect the pharyngobranchial of a given arch with the epibranchial of the adjacent posterior arch.

The abbreviations for the observed structures are as listed below:

aab: *addutores arcuum branchialium*

ad: *arcuales dorsales*

am: *adductor mandibulae*

cac: *coracoarcualis communis*

cbc: ceratobranchial

ch: *coracohyoideus*

cm: *coracomandibularis*

cob 1-5: *coracobranchialis* 1-5

coe: *constrictor oesophagi*

csup 1-4: *constrictores branchiales superficiales* 1-4

ebc: epibranchial

ha: hyoid arch

ib: *interbranchiales*

ipb: *interpharyngobranchiales*

ma: maxillary arch

pg: pectoral girdle

pbc: pharyngobranchial cartilage

po: *preorbitalis*

tr: *trapezius*

Results

1. Heterodontiformes

The muscle that compresses the esophagus and is associated with the last branchial arch covers the exterior surface of the esophagus and has a circular disposition of fibers. No variation in this muscle was observed among the heterodontiform species examined. It is called *m. constrictor oesophagi*.

Heterodontidae

Heterodontus francisci (FIG. 19; CAS 19176, 307mm)

-*m. constrictores branchiales superficiales*: Four pairs of these muscles are present, one pair for each arch, except the fifth arch that lacks this muscle. Laminar muscles that lay immediately beneath the skin in the branchial region, posterior to the first branchial opening. Origin and insertion are through connective tissue, the dorsal origin occurs with a thicker tendon-like aponeurosis, which covers almost all the *m. trapezius*, and the ventral insertion on the lateral region of the *m. coracomandibularis*. The fibers of the portion dorsal to the gill slits are directed in a slightly oblique fashion, anteroventrally in relation to the main axis of the body. The fibers of the portion which forms the wall of the gill pouches pass dorsoventrally with a slight arch accompanying the branchial slit margin. The fibers of the portion ventral to the gill slits are directed posteroventrally in a more oblique way than the dorsal fibers.

-*m. trapezius*: Laminar muscle with a triangular shape due to its insertions. This muscle is restricted to the area of the dorsal portion of the scapular process of the pectoral girdle. Its origin is in an aponeurosis common to the *m. constrictor branchiales superficiales*. Its insertion is on the dorsal surface of the scapular process of the pectoral girdle through a thick layer of dense connective tissue. Fibers are oriented very obliquely to the main axis of the body (between 40°-50°).

-*m. adductores arcuum branchialium*: Five pairs of these muscles are present, one pair for each arch. Small triangular muscles, and restricted to the area of the epibranchial-ceratobranchial articulation. Their origins are on the epibranchial. Their insertions are on the ceratobranchial. The origins and insertions occur without the presence of dense connective tissue. Fibers are oriented downward and slightly divergent.

-*m. interpharyngobranchiales*: Three pairs of these slender, laminar and triangular muscles are present, located between the first and second pharyngobranchials, the second and third pharyngobranchials and the third pharyngobranchial and the fourth pharyngobranchial. Their origins are on the ventroposterior margin of a pharyngobranchial on the half close to the epibranchial through connective tissue. Their insertions are on the anterodorsal margin of the next pharyngobranchial also through connective tissue. Fibers are oriented obliquely to the pharyngobranchial axis (near 15°).

-*m. arcuales dorsales*: Four pairs of these rectangular, somewhat bulky muscles are present, one pair for each arch, except the fifth arch that lacks this muscle. Their origins are on a posteroventral margin on the pharyngobranchial. Their insertions are on the anterodorsal surface of the epibranchial near the articulation with the pharyngobranchial, both through a connective margin. Fibers directed downward.

-*m. interbranchiales*: Four pairs are present, one for each gill arch. They lay within a holobranch on the anterior face of the gill rays. Slender muscle with a semi-elliptical shape, with the thickness of a gill ray. The origins and insertions of the outermost fibers are both on the extrabranchial cartilages (dorsally and ventrally), the origins of the innermost fibers on the arch cartilages (dorsally the epibranchial and ventrally the ceratobranchial) and the insertions on the extrabranchial cartilages, which give these muscles a rather fragile aspect. Fibers have different sizes, the innermost are smaller than the outermost, and are oriented in a semicircular manner, on the posterior surface of the arch. Fibers tightly united, with no spaces between them.

-*m. coracoarcualis communis*: Triangular, bulky muscle with rounded margins. It has a few thin septa which gives it a segmented aspect. Its origin is on the coracoid bar

through a tendon. Its insertion is on an anterior muscle (the *m. coracohyoideus*) through connective tissue. Fibers are oriented anteriorly.

-*m. coracobranchiales*: Five muscles present, one for each branchial arch. The anterior four are small cylindrical muscles (1-4) and the last has a laminar shape. Their origins are on the pericardic membrane. The fifth has fibers that originate on the coracoid bar near the pectoral fin insertion. Their insertions are through a tendon on the 1-3 hypobranchial cartilages, the cardiobranchial and the fifth ceratobranchial, respectively. Fibers are directed anteriorly and slightly upwards when close to the insertion. On the fifth muscle, the fibers are directed anteriorly.

Heterodontus portujacksoni

-*m. constrictores branchiales superficiales*: These muscles are as described in *Heterodontus francisci*, except its origin covers the lower three quarters of the *m. trapezius* and the fibers of the portion ventral to the gill slits are directed posteroventrally in a mirrored fashion as the dorsal fibers.

-*m. trapezius*: These muscles are as described in *Heterodontus francisci*.

-*m. adductores arcuum branchialium*: These muscles are as described in *Heterodontus francisci*.

-*m. interpharyngobranchiales*: These muscles are as described in *Heterodontus francisci*.

-*m. arcuales dorsales*: These muscles are as described in *Heterodontus francisci*.

-*m. interbranchiales*: These muscles are as described in *Heterodontus francisci*.

-*m. coracoarcualis communis*: These muscles are as described in *Heterodontus francisci*, except it does not have the marked septa.

-*m. coracobranchiales*: These muscles are as described in *Heterodontus francisci*.

Heterodontus zebra

-*m. constrictores branchiales superficiales*: These muscles are as described in *Heterodontus portujacksoni*.

-*m. trapezius*: These muscles are as described in *Heterodontus francisci*, except that fibers are oriented very obliquely to the main axis of the body (between 50°-60°).

-*m. adductores arcuum branchialium*: These muscles are as described in *Heterodontus francisci*.

-*m. interpharyngobranchiales*: These muscles are as described in *Heterodontus francisci*.

-*m. arcuales dorsales*: These muscles are as described in *Heterodontus francisci*, except these are slender muscles.

-*m. interbranchiales*: These muscles are as described in *Heterodontus francisci*.

-*m. coracoarcualis communis*: These muscles are as described in *Heterodontus portujacksoni*.

-*m. coracobranchiales*: These muscles are as described in *Heterodontus francisci*.

2. Orectolobiformes

The muscle that compresses the esophagus and is associated with the last branchial arch covers the exterior surface of the esophagus and has a circular disposition of fibers. No variation in this muscle was observed among the orectolobiform species examined. It is called *m. constrictor oesophagi*.

Hemiscyllidae

Chiloscyllium punctatum (FIG. 20; USNM 176709, 729mm)

-*m. constrictores branchiales superficiales*: Four pairs of these muscles are present, one pair for each arch, except the fifth arch that lacks this muscle. Laminar muscles that lay immediately beneath the skin in the branchial region, posterior to the first branchial opening. Origin and insertion are through connective tissue, the dorsal

origin occurs with a thicker tendon-like aponeurosis, which covers the lower theree quarters of the *m. trapezius*, and the ventral insertion on the lateral region of the *m. coracomandibularis*. The fibers of the portion dorsal to the gill slits are directed in a slightly oblique fashion, anteroventrally in relation to the main axis of the body. The fibers of the portion which forms the wall of the gill pouches pass dorsoventrally with a slight arch accompanying the branchial slit margin. The fibers of the portion ventral to the gill slits are directed posteroventrally more oblique than the dorsal fibers.

-*m. trapezius*: Laminar muscle with a triangular shape due to its insertions. The muscle has a triangular shape. Its origin is in an aponeurosis common to the *m. constrictor branchiales superficiales*. Its insertion is on the dorsal surface of the scapular process of the pectoral girdle and the posterior end of the epibranchial-ceratobranchial articulation through a thick layer of dense connective tissue. Fibers are oriented very obliquely to the main axis of the body (between 30°-40°).

-*m. adductores arcuum branchialium*: Five pairs of these muscles are present, one pair for each arch. Small triangular muscles, and restricted to the area of the epibranchial-ceratobranchial articulation. Their origins are on the epibranchial. Their insertions are on the ceratobranchial. The origins and insertions occur without the presence of dense connective tissue. Fibers are oriented downward and slightly divergent.

-*m. interpharyngobranchiales*: Three pairs of these slender, laminar and triangular muscles are present, located between the first and second pharyngobranchials, the second and third pharyngobranchials and the third pharyngobranchial and the fourth pharyngobranchial. Their origins are on the ventroposterior margin of a pharyngobranchial on the half close to the epibranchial through connective tissue. Their insertions are on the anterodorsal margin of the next pharyngobranchial also through connective tissue. Fibers are oriented obliquely to the pharyngobranchial axis (near 15°).

-*m. arcuales dorsales*: Four pairs of these espheric, bulky muscles are present, one pair for each arch, except the fifth arch that lacks this muscle. Their origins are on a posteroventral margin on the pharyngobranchial. Their insertions are on the

anterodorsal surface of the epibranchial near the articulation with the pharyngobranchial, both through a connective margin. Fibers directed downward.

-*m. interbranchiales*: Four pairs are present, one for each gill arch. They lay within a holobranch on the anterior face of the gill rays. Slender muscle with a semi-elliptical shape, with the thickness of a gill ray. The origins and insertions of the outermost fibers are both on the extrabranchial cartilages (dorsally and ventrally), the origins of the innermost fibers on the arch cartilages (dorsally the epibranchial and ventrally the ceratobranchial) and the insertions on the extrabranchial cartilages, which give these muscles a rather fragile aspect. Fibers have different sizes, the innermost are smaller than the outermost, and are oriented in a semicircular manner, on the posterior surface of the arch. Fibers tightly united, with no spaces between them.

-*m. coracoarcualis communis*: Triangular, bulky muscle with rounded margins. It has a few thin septa which gives it a segmented aspect. Its origin is on the coracoid bar through a tendon. Its insertion is on an anterior muscle (the *m. coracohyoideus*) through connective tissue. Fibers are oriented anteriorly.

-*m. coracobranchiales*: Five muscles present, one for each branchial arch. The anterior four are small cylindrical muscles (1-4) and the last has a laminar shape. Their origins are on the *m. coracoarculis communis*. The fifth originates from the coracoid bar near the pectoral fin insertion. Their insertions are through a tendon on the 1-3 hypobranchial cartilages, the cardiobranchial and the fifth ceratobranchial, respectively. Fibers are directed anteriorly and slightly upwards when close to the insertion. On the fifth muscle, the fibers are directed anteriorly.

Hemiscyllium ocellatum

-*m. constrictores branchiales superficiales*: These muscles are as decribed in *Chiloscyllium punctatum*, except its origin covers almost all the *m. trapezius*, the fibers of the portion dorsal to the gill slits are directed downwards and the fibers of the portion ventral to the gill slits are directed posteroventrally slightly oblique.

-*m. trapezius*: This mucle is as described in *Chiloscyllium punctatum*.

-*m. adductores arcuum branchialium*: These muscles are as decribed in *Chiloscyllium punctatum*.

-*m. interpharyngobranchiales*: These muscles are as decribed in *Chiloscyllium punctatum*, except they are composed of connective tissue are present and the fibers are oriented obliquely to the pharyngobranchial axis (near 20°).

-*m. arcuales dorsales*: These muscles are as decribed in *Chiloscyllium punctatum*.

-*m. interbranchiales*: These muscles are as decribed in *Chiloscyllium punctatum*.

-*m. coracoarcualis communis*: This muscle is as decribed in *Chiloscyllium punctatum*.

-*m. coracobranchiales*: These muscles are as decribed in *Chiloscyllium punctatum*.

Parascyllidae

Cirrhoscyllium formosanum (FIG. 21; USNM 395036, 226mm)

-*m. constrictores branchiales superficiales*: Four pairs of these muscles are present, one pair for each arch, except the fifth arch that lacks this muscle. Laminar muscles that lay immediately beneath the skin in the branchial region, posterior to the first branchial opening. Origin and insertion are through connective tissue, the dorsal origin occurs with a thicker tendon-like aponeurosis, which covers almost all the *m. trapezius*, and the ventral insertion occurs lateral to the posterior region of the *m. coracomandibularis* and covers this muscle anteriorly. The fibers of the portion dorsal to the gill slits are directed downwards. The fibers of the portion which forms the wall of the gill pouches pass dorsoventrally with a slight arch accompanying the branchial slit margin. The fibers of the portion ventral to the gill slits are directed posteroventrally slightlyoblique.

-*m. trapezius*: Laminar muscle with a triangular shape due to its insertions. This muscle is restricted to the area of the dorsal portion of the scapular process of the pectoral girdle. Its origin is in an aponeurosis common to the *m. constrictor*

branchiales superficiales. Its insertion is on the dorsal surface of the scapular process of the pectoral girdle and the posterior end of the epibranchial-ceratobranchial articulation through a layer of dense connective tissue. Fibers are oriented very obliquely to the main axis of the body (between 70°-80°).

-*m. adductores arcuum branchialium*: Five pairs of these muscles are present, one pair for each arch, except the fifth arch that lacks this muscle. Small triangular muscles, and restricted to the area of the epibranchial-ceratobranchial articulation. Their origins are on the epibranchial. Their insertions are on the ceratobranchial. The origins and insertions occur without the presence of dense connective tissue. Fibers are oriented downward and slightly divergent.

-*m. interpharyngobranchiales*: Three pairs of these slender, laminar and triangular muscles are present, located between the first and second pharyngobranchials, the second and third pharyngobranchials and the third pharyngobranchial and the fourth pharyngobranchial. The third appears as a connective tendon-like connection between the third and fourth pharyngobranchial. Their origins are on the ventroposterior margin of a pharyngobranchial on the half close to the epibranchial through connective tissue. Their insertions are on the anterodorsal margin of the next pharyngobranchial also through connective tissue. Fibers are oriented obliquely to the pharyngobranchial axis (near 20°).

-*m. arcuales dorsales*: Four pairs of these rectangular, slender muscles are present, one pair for each arch, except the fifth arch that lacks this muscle. Their origins are on a posteroventral margin on the pharyngobranchial. Their insertions are on the anterodorsal surface of the epibranchial near the articulation with the pharyngobranchial, both through a connective margin. Fibers directed downward.

-*m. interbranchiales*: Four pairs are present, one for each gill arch. They lay within a holobranch on the anterior face of the gill rays. Slender muscle with a semi-elliptical shape, with the thickness of a gill ray. The origins and insertions of the outermost fibers are both on the extrabranchial cartilages (dorsally and ventrally), the origins of the innermost fibers on the arch cartilages (dorsally the epibranchial and ventrally the ceratobranchial) and the insertions on the extrabranchial cartilages, which give these muscles a rather fragile aspect. Fibers have different sizes, the innermost are smaller

than the outermost, and are oriented in a semicircular manner, on the posterior surface of the arch. Fibers tightly united, with no spaces between them.

-*m. coracoarcualis communis*: Triangular, bulky muscle with rounded margins. Its origin is on the coracoid bar through a tendon. Its insertion is on an anterior muscle (the *m. coracohyoideus*) through connective tissue. Fibers are oriented anteriorly.

-*m. coracobranchiales*: Five muscles present, one for each branchial arch. The anterior four are small cylindrical muscles (1-4) and the last has a laminar shape. Their origins are on the *m. coracoarculis communis*. The fourth originates from the coracoid bar near the pectoral fin insertion and covers the fifth. Their insertions are through a tendon on the 1-3 hypobranchial cartilages, the cardiobranchial and the fifth ceratobranchial, respectively. Fibers are directed anteriorly and slightly upwards when close to the insertion. On the fifth muscle, the fibers are directed upwards.

Ginglymostomatidae

Ginglymostoma cirratum (FIG. 22; SU 8116, 271mm)

-*m. constrictores branchiales superficiales*: Four pairs of these muscles are present, one pair for each arch, except the fifth arch that lacks this muscle. Laminar muscles that lay immediately beneath the skin in the branchial region, posterior to the first branchial opening. Origin and insertion are through connective tissue, the dorsal origin occurs with a thicker tendon-like aponeurosis, which covers almost all the *m. trapezius*, and the ventral insertion occurs lateral to the posterior region of the *m. coracomandibularis*. The fibers of the portion dorsal to the gill slits are directed in a slightly oblique fashion, anteroventrally in relation to the main axis of the body. The fibers of the portion which forms the wall of the gill pouches pass dorsoventrally with a slight arch accompanying the branchial slit margin. The fibers of the portion ventral to the gill slits are directed posteroventrally more oblique than the dorsal fibers.

-*m. trapezius*: Laminar muscle with a triangular shape due to its insertions. This muscle is restricted to the area of the dorsal portion of the scapular process of the pectoral girdle. Its origin is in an aponeurosis common to the *m. constrictor*

branchiales superficiales. Its insertion is on the dorsal surface of the scapular process of the pectoral girdle through a layer of dense connective tissue. Fibers are oriented nearly transversely to the main axis of the body, slightly oblique (between 75°-85°).

-*m. adductores arcuum branchialium*: Five pairs of these muscles are present, one pair for each arch, except the fifth arch that lacks this muscle. Small triangular muscles, and restricted to the area of the epibranchial-ceratobranchial articulation. Their origins are on the epibranchial. Their insertions are on the ceratobranchial. The origins and insertions occur without the presence of dense connective tissue. Fibers are oriented downward and slightly divergent.

-*m. interpharyngobranchiales*: Three pairs of these slender, laminar and triangular muscles are present, located between the first and second pharyngobranchials, the second and third pharyngobranchials and the third pharyngobranchial and the quarter pharyngobranchial. Their origins are on the ventroposterior margin of a pharyngobranchial on the half close to the epibranchial through connective tissue. Their insertions are on the anterodorsal margin of the next pharyngobranchial also through connective tissue. Fibers are oriented obliquely to the pharyngobranchial axis (near 15°).

-*m. arcuales dorsales*: Four pairs of these rectangular, somewhat bulky muscles are present, one pair for each arch, except the fifth arch that lacks this muscle. Their origins are on a posteroventral margin on the pharyngobranchial. Their insertions are on the anterodorsal surface of the epibranchial near the articulation with the pharyngobranchial, both through a connective margin. Fibers directed downward.

-*m. interbranchiales*: Four pairs are present, one for each gill arch. They lay within a holobranch on the anterior face of the gill rays. Slender muscle with a semi-elliptical shape, with the thickness of a gill ray. The origins and insertions of the outermost fibers are both on the extrabranchial cartilages (dorsally and ventrally), the origins of the innermost fibers on the arch cartilages (dorsally the epibranchial and ventrally the ceratobranchial) and the insertions on the extrabranchial cartilages, which give these muscles a rather fragile aspect. Fibers have different sizes, the innermost are smaller than the outermost, and are oriented in a semicircular manner, on the posterior surface of the arch. Fibers tightly united, with no spaces between them.

-*m. coracoarcualis communis*: Triangular, bulky muscle with rounded margins. It has a few thin septa which gives it a segmented aspect. Its origin is on the coracoid bar through a tendon. Its insertion is on an anterior muscle (the *m. coracohyoideus*) through connective tissue. Fibers are oriented anteriorly.

-*m. coracobranchiales*: Five muscles present, one for each branchial arch. Four small cylindrical muscles (1-4) and the last has a laminar shape. Their origins are on the *m. coracoarculis communis*. The fifth originates from the coracoid bar near the pectoral fin insertion. Their insertions are through a tendon on the 1-3 hypobranchial cartilages, the cardiobranchial and the fifth ceratobranchial, respectively. Fibers are directed anteriorly and slightly upwards when close to the insertion. On the fifth muscle, the fibers are oblique anterodorsally.

Orectolobidae

Orectolobus maculatus (FIG. 23; USNM 39999, 615mm)

-*m. constrictores branchiales superficiales*: Four pairs of these muscles are present, one pair for each arch, except the fifth arch that lacks this muscle. Laminar muscles that lay immediately beneath the skin in the branchial region, posterior to the first branchial opening. Origin and insertion are through connective tissue, the dorsal origin occurs with a thicker tendon-like aponeurosis, which covers almost all the *m. trapezius*, and the ventral insertion occurs lateral to the posterior region of the *m. coracomandibularis* and covers this muscle anteriorly. The fibers of the portion dorsal to the gill slits are directed slightly anteroventrally. The fibers of the portion which forms the wall of the gill pouches pass dorsoventrally with a slight arch accompanying the branchial slit margin. The fibers of the portion ventral to the gill slits are directed ina mirrored fashion as the dorsal.

-*m. trapezius*: Laminar muscle with a triangular shape due to its insertions. Its origin is in an aponeurosis common to the *m. constrictor branchiales superficiales*. Its insertion is on the dorsal surface of the scapular process of the pectoral girdle and the posterior end of the epibranchial-ceratobranchial articulation through a layer of dense

connective tissue. Fibers are oriented obliquely to the main axis of the body (between 60°-70°).

-*m. adductores arcuum branchialium*: Five pairs of these muscles are present, one pair for each arch, except the fifth arch that lacks this muscle. Small triangular muscles, and restricted to the area of the epibranchial-ceratobranchial articulation. Their origins are on the epibranchial. Their insertions are on the ceratobranchial. The origins and insertions occur without the presence of dense connective tissue. Fibers are oriented downward and slightly divergent.

-*m. interpharyngobranchiales*: Three pairs of these slender, laminar and triangular muscles are present, located between the first and second pharyngobranchials, the second and third pharyngobranchials and the third pharyngobranchial and the fourth pharyngobranchial. The third appears as a connective tendon-like connection between the third and fourth pharyngobranchial. Their origins are on the ventroposterior margin of a pharyngobranchial on the half close to the epibranchial through connective tissue. Their insertions are on the anterodorsal margin of the next pharyngobranchial also through connective tissue. Fibers are oriented obliquely to the pharyngobranchial axis (near 20°).

-*m. arcuales dorsales*: Four pairs of these espheric, broad, slender muscles are present, one pair for each arch, except the fifth arch that lacks this muscle. Their origins are on a posteroventral margin on the pharyngobranchial. Their insertions are on the anterodorsal surface of the epibranchial near the articulation with the pharyngobranchial, both through a connective margin. Fibers directed downward.

-*m. interbranchiales*: Four pairs are present, one for each gill arch. They lay within a holobranch on the anterior face of the gill rays. Slender muscle with a semi-elliptical shape, with the thickness of a gill ray. The origins and insertions of the outermost fibers are both on the extrabranchial cartilages (dorsally and ventrally), the origins of the innermost fibers on the arch cartilages (dorsally the epibranchial and ventrally the ceratobranchial) and the insertions on the extrabranchial cartilages, which give these muscles a rather fragile aspect. Fibers have different sizes, the innermost are smaller than the outermost, and are oriented in a semicircular manner, on the posterior surface of the arch. Fibers tightly united, with no spaces between them.

-*m. coracoarcualis communis*: Triangular, bulky muscle with rounded margins. It has a few thin septa which gives it a segmented aspect. Its origin is on the coracoid bar through a tendon. Its insertion is on an anterior muscle (the *m. coracohyoideus*) through connective tissue. Fibers are oriented anteriorly.

-*m. coracobranchiales*: Five muscles present, one for each branchial arch. The anterior four are small cylindrical muscles (1-4) and the last has a laminar shape. Their origins are on the *m. coracoarculis communis*. The fourth originates from the coracoid bar near the pectoral fin insertion and covers the fifth. Their insertions are through a tendon on the 1-3 hypobranchial cartilages, the cardiobranchial and the fifth ceratobranchial, respectively. Fibers are directed anteriorly and slightly upwards when close to the insertion. On the fifth muscle, the fibers are directed upwards.

Stegostomatidae

Stegostoma fasciatum (FIG. 24; USNM 138548, 294mm)

-*m. constrictores branchiales superficiales*: Four pairs of these muscles are present, one pair for each arch, except the fifth arch that lacks this muscle. Laminar muscles that lay immediately beneath the skin in the branchial region, posterior to the first branchial opening. Origin and insertion are through connective tissue, the dorsal origin occurs with a thicker tendon-like aponeurosis, which covers all the *m. trapezius*, and the ventral insertion occurs lateral to the posterior region of the *m. coracomandibularis*. The fibers of the portion dorsal to the gill slits are directed in a slightly oblique fashion, anteroventrally in relation to the main axis of the body. The fibers of the portion which forms the wall of the gill pouches pass dorsoventrally with a slight arch accompanying the branchial slit margin. The fibers of the portion ventral to the gill slits are directed posteroventrally more oblique than the dorsal fibers.

-*m. trapezius*: Laminar muscle with a triangular shape due to its insertions. This muscle is restricted to the area of the dorsal portion of the scapular process of the pectoral girdle. Its origin is in an aponeurosis common to the *m. constrictor branchiales superficiales*. Its insertion is on the dorsal surface of the scapular process

of the pectoral girdle through a layer of dense connective tissue. Fibers are oriented nearly transversely to the main axis of the body, slightly oblique (between 75°-85°).

-*m. adductores arcuum branchialium*: Five pairs of these muscles are present, one pair for each arch, except the fifth arch that lacks this muscle. Small triangular muscles, and restricted to the area of the epibranchial-ceratobranchial articulation. Their origins are on the epibranchial. Their insertions are on the ceratobranchial. The origins and insertions occur without the presence of dense connective tissue. Fibers are oriented downward and slightly divergent.

-*m. interpharyngobranchiales*: Three pairs of these slender, laminar and triangular muscles are present, located between the first and second pharyngobranchials, the second and third pharyngobranchials and the third pharyngobranchial and the quarter pharyngobranchial. Their origins are on the ventroposterior margin of a pharyngobranchial on the half close to the epibranchial through connective tissue. Their insertions are on the anterodorsal margin of the next pharyngobranchial also through connective tissue. Fibers are oriented obliquely to the pharyngobranchial axis (near 15°).

-*m. arcuales dorsales*: Four pairs of these rectangular, slender muscles are present, one pair for each arch, except the fifth arch that lacks this muscle. Their origins are on a posteroventral margin on the pharyngobranchial. Their insertions are on the anterodorsal surface of the epibranchial near the articulation with the pharyngobranchial, both through a connective margin. Fibers directed downward.

-*m. interbranchiales*: Four pairs are present, one for each gill arch. They lay within a holobranch on the anterior face of the gill rays. Slender muscle with a semi-elliptical shape, with the thickness of a gill ray. The origins and insertions of the outermost fibers are both on the extrabranchial cartilages (dorsally and ventrally), the origins of the innermost fibers on the arch cartilages (dorsally the epibranchial and ventrally the ceratobranchial) and the insertions on the extrabranchial cartilages, which give these muscles a rather fragile aspect. Fibers have different sizes, the innermost are smaller than the outermost, and are oriented in a semicircular manner, on the posterior surface of the arch. Fibers tightly united, with no spaces between them.

-*m. coracoarcualis communis*: Triangular, bulky muscle with rounded margins. It has a few thin septa which gives it a segmented aspect. Its origin is on the coracoid bar through a tendon. Its insertion is on an anterior muscle (the *m. coracohyoideus*) through connective tissue. Fibers are oriented anteriorly.

-*m. coracobranchiales*: Five muscles present, one for each branchial arch. The anterior four are small cylindrical muscles (1-4) and the last has a laminar shape. Their origins are on the *m. coracoarculis communis*. The fifth originates from the coracoid bar near the pectoral fin insertion. Their insertions are through a tendon on the 1-3 hypobranchial cartilages, the cardiobranchial and the fifth ceratobranchial, respectively. Fibers are directed anteriorly and slightly upwards when close to the insertion. On the fifth muscle, the fibers are oblique anterodorsally.

3. Lamniformes

The muscle that compresses the esophagus and is associated with the last branchial arch covers the exterior surface of the esophagus and has a circular disposition of fibers. One variation was observed in *Mitsukurina owstoni*, which has this muscle slightly reduced and less volumous. It is called *m. constrictor oesophagi*.

Odontaspididae

Carcharias Taurus (FIG. 14; MZUSP 37281, 335mm)

-*m. constrictores branchiales superficiales*: Four pairs of these muscles are present, one pair for each arch, except the fifth arch that lacks this muscle. Laminar muscles that lay immediately beneath the skin in the branchial region, posterior to the first branchial opening. Origin and insertion are through connective tissue, the dorsal origin occurs with a thicker tendon-like aponeurosis, which covers all the *m. trapezius*, and the ventral insertion occurs lateral to the posterior region of the *m. coracomandibularis* and covers this muscle anteriorly. The fibers of the portion dorsal to the gill slits are directed in an oblique fashion, anteroventrally in relation to the main axis of the body. The fibers of the portion which forms the wall of the gill pouches pass dorsoventrally with a slight arch accompanying the branchial slit

margin. The fibers of the portion ventral to the gill slits are directed posteroventrally in a more oblique way than the dorsal fibers.

-*m. trapezius*: Laminar muscle with a triangular shape due to its insertions. The muscle has a cleavage which divides it into two portions, one anterior and one posterior. The anterior portion has a triangular shape and is three quarters the size of the posterior portion, which also has a triangular shape. Its origin is in an aponeurosis common to the *m. constrictor branchiales superficiales*. Its insertions are on two distinct points (also called a digastric muscle), the dorsal surface of the scapular process of the pectoral girdle through a layer of dense connective tissue, and the dorsal surface of the fifth epibranchial through connective tissue. Fibers are oriented nearly transversely to the main axis of the body (between 70°-80° posteriorly).

-*m. adductores arcuum branchialium*: Five pairs of these muscles are present, one pair for each arch. Small, triangular-shaped muscles, and restricted to the area of the epibranchial-ceratobranchial articulation. Their origins are on the epibranchial. Their insertions are on the ceratobranchial. The origins and insertions occur without the presence of dense connective tissue. Fibers are oriented downward.

-*m. interpharyngobranchiales*: Three pairs of these slender, laminar and rectangular muscles are present, between the first and second pharyngobranchials, the second and third pharyngobranchials and the third pharyngobranchial and the gill pickaxe. Their origins are on the ventroposterior margin of a pharyngobranchial on the half close to the epibranchial through connective tissue. Their insertions are on the anterodorsal margin of the next pharyngobranchial also through connective tissue. Fibers are oriented obliquely to the pharyngobranchial axis (near 15°).

-*m. arcuales dorsales*: Four pairs of these rectangular, slender muscles are present, one pair for each arch, except the fifth arch that lacks this muscle. Their origins are on a posteroventral groove on the pharyngobranchial. Their insertions are on the anterodorsal surface of the epibranchial near the articulation with the pharyngobranchial, both through a connective margin. Fibers directed downward.

-*m. interbranchiales*: Four pairs are present, one for each gill arch. They lay within a holobranch on the anterior face of the gill rays. Slender muscle with a semi-elliptical

shape, with the thickness of a gill ray. The origins and insertions of the outermost fibers are both on the extrabranchial cartilages (dorsally and ventrally), the origins of the innermost fibers on the arch cartilages (dorsally the epibranchial and ventrally the ceratobranchial) and the insertions on the extrabranchial cartilages, which give these muscles a rather fragile aspect. Fibers have different sizes, the innermost are smaller than the outermost, and are oriented in a semicircular manner, on the posterior surface of the arch. Fibers tightly united, with no spaces between them.

-*m. coracoarcualis communis*: Triangular, bulky muscle with rounded margins. It has a few septa which gives a segmented aspect. Its origin is on the coracoid bar through a tendon. Its insertion is on an anterior muscle (the *m. coracohyoideus*) through connective tissue. Fibers are oriented anteriorly.

-*m. coracobranchiales*: Five muscles present, one for each branchial arch. The anterior four are small compressed muscles (1-4) and the last has a digastric laminar shape. Their origins are on the pericardic membrane. Their insertions are through a tendon on the 1-3 hypobranchial cartilages, the cardiobranchial and the fifth ceratobranchial, respectively. The fifth *m. coracobranchial* (also called a digastric muscle) has two points of insertions on the ceratobranchial, the anterior one trapezoidal and covering roughly 70% of the ventral surface and the posterior one triangular-shaped and covering the remaining 30%. Fibers are directed anteriorly and slightly upwards when close to the insertion. On the fifth muscle, the anterior fibers are oblique, anterodorsally oriented, whereas the posterior fibers are nearly upward. The fifth muscle has a connective raphe between the anterior and posterior portions.

Lamnidae

Isurus oxyrinchus (FIG. 15; USNM 201733, 756mm)

-*m. constrictores branchiales superficiales*: Four pairs of these muscles are present, one pair for each arch, except the fifth arch that lacks this muscle. Laminar muscles that lay immediately beneath the skin in the branchial region, posterior to the first

branchial opening. Origin and insertion are through connective tissue, the dorsal origin occurs with a thicker tendon-like aponeurosis, which covers all the *m. trapezius*, and the ventral insertion occurs lateral to the posterior region of the *m. coracomandibularis* and covers this muscle anteriorly. The fibers of the portion dorsal to the gill slits are directed in an oblique fashion, anteroventrally in relation to the main axis of the body. The fibers of the portion which forms the wall of the gill pouches pass dorsoventrally with a slight arch accompanying the branchial slit margin. The fibers of the portion ventral to the gill slits are directed posteroventrally in a more oblique way than the dorsal fibers.

-*m. trapezius*: Laminar muscle with a triangular shape due to its insertions. The muscle has a cleavage which divides it into two portions, one anterior and one posterior. The anterior portion has a triangular shape and is three quarters the size of the posterior portion, which also has a triangular shape. Its origin is in an aponeurosis common to the *m. constrictor branchiales superficiales*. Its insertions are on two distinct points (also called a digastric muscle), the dorsal surface of the scapular process of the pectoral girdle through a layer of dense connective tissue, and the dorsal surface of the fifth epibranchial through connective tissue. Fibers are oriented nearly transversely to the main axis of the body (between 70°-80° posteriorly).

-*m. adductores arcuum branchialium*: Four pairs of these muscles are present, one pair for each arch, except the fifth arch that lacks this muscle. Small, triangular-shaped muscles with a slight curve at midlength, and restricted to the area of the epibranchial-ceratobranchial articulation. Their origins are on the epibranchial. Their insertions are on the ceratobranchial. The origins and insertions occur without the presence of dense connective tissue. Fibers are oriented downward.

-*m. interpharyngobranchiales*: Three pairs of these slender, laminar and rectangular muscles are present, between the first and second pharyngobranchials, the second and third pharyngobranchials and the third pharyngobranchial and the gill pickaxe. Their origins are on the ventroposterior margin of a pharyngobranchial on the half close to the epibranchial through connective tissue. Their insertions are on the anterodorsal margin of the next pharyngobranchial also through connective tissue. Fibers are oriented obliquely to the pharyngobranchial axis (near 15°).

-*m. arcuales dorsales*: Four pairs of these rectangular, slender muscles are present, one pair for each arch, except the fifth arch that lacks this muscle. Their origins are on a posteroventral groove on the pharyngobranchial. Their insertions are on the anterodorsal surface of the epibranchial near the articulation with the pharyngobranchial, both through a connective margin. Fibers directed downward.

-*m. interbranchiales*: Four pairs are present, one for each gill arch. They lay within a holobranch on the anterior face of the gill rays. Slender muscle with a semi-elliptical shape, with the thickness of a gill ray. The origins and insertions of the outermost fibers are both on the extrabranchial cartilages (dorsally and ventrally), the origins of the innermost fibers on the arch cartilages (dorsally the epibranchial and ventrally the ceratobranchial) and the insertions on the extrabranchial cartilages, which give these muscles a rather fragile aspect. Fibers have different sizes, the innermost are smaller than the outermost, and are oriented in a semicircular manner, on the posterior surface of the arch. Fibers tightly united, with no spaces between them.

-*m. coracoarcualis communis*: Triangular, bulky muscle with rounded margins. It has a few septa which gives a segmented aspect. Its origin is on the coracoid bar through a tendon. Its insertion is on an anterior muscle (the *m. coracohyoideus*) through connective tissue. Fibers are oriented anteriorly.

-*m. coracobranchiales*: Five muscles present, one for each branchial arch. Four small compressed muscles (1-4) and the last has a digastric shape. Their origins are on the pericardic membrane. Their insertions are through a tendon on the 1-3 hypobranchial cartilages, the cardiobranchial and the fifth ceratobranchial, respectively. The fifth *m. coracobranchial* (also called a digastric muscle) has two points of insertions on the ceratobranchial, the anterior one trapezoidal and covering roughly 80% of the ventral surface and the posterior one triangular-shaped and covering the remaining 20%. Fibers are directed anteriorly and slightly upwards when close to the insertion. On the fifth muscle, the anterior fibers are oblique, anterodorsally oriented, whereas the posterior fibers are nearly upward. The fifth muscle has a connective raphe between the anterior and posterior portions.

Mitsukurinidae

Mitsukurina owstoni (FIG. 16; NMBP 15952, 1155mm)

-*m. constrictores branchiales superficiales*: Four pairs of these muscles are present, one pair for each arch, except the fifth arch that lacks this muscle. Laminar muscles that lay immediately beneath the skin in the branchial region, posterior to the first branchial opening. Origin and insertion are through connective tissue, the dorsal origin occurs with a thicker tendon-like aponeurosis, which covers the anterior quarter of the *m. trapezius*, and the ventral insertion occurs lateral to the posterior region of the *m. coracomandibularis* and covers this muscle anteriorly. The fibers of the portion dorsal to the gill slits are directed in a slightly oblique fashion, anteroventrally in relation to the main axis of the body. The fibers of the portion which forms the wall of the gill pouches pass dorsoventrally with a slight arch where it meets the dorsal and ventral portions of the muscle. The fibers of the portion ventral to the gill slits are directed posteroventrally, almost transversal on the anterior portion, in a less oblique fashion that the dorsal fibers.

-*m. trapezius*: Laminar muscle with a triangular shape due to its insertions. The muscle has a cleavage which divides it into two portions, one anterior and one posterior. The anterior portion has a triangular shape and is the same size as the posterior portion, which also has a triangular shape. Its origin is in an aponeurosis common to the *m. constrictor branchiales superficiales*. Its insertions are on two distinct points (also called a digastric muscle), the dorsal surface of the scapular process of the pectoral girdle through a layer of dense connective tissue, and the dorsal surface of the fifth epibranchial through connective tissue. Fibers are oriented nearly transversely to the main axis of the body, slightly oblique (between 15°-25° posteriorly).

-*m. adductores arcuum branchialium*: Four pairs of these muscles are present, one pair for each arch, except the fifth arch that lacks this muscle. Small, crescent-shaped muscles with a slight curve at midlength, and restricted to the area of the epibranchial-ceratobranchial articulation. Their origins are on the epibranchial. Their insertions are

on the ceratobranchial. The origins and insertions occur without the presence of dense connective tissue. Fibers are oriented downward curving slightly towards insertions.

-*m. interpharyngobranchiales*: Three pairs of these slender, laminar and triangular muscles are present, between the first and second pharyngobranchials, the second and third pharyngobranchials and the third pharyngobranchial and the gill pickaxe. Their origins are on the ventroposterior margin of a pharyngobranchial on the half close to the epibranchial through connective tissue. Their insertions are on the anterodorsal margin of the next pharyngobranchial also through connective tissue. Fibers are oriented obliquely to the pharyngobranchial axis (near 15°).

-*m. arcuales dorsales*: Four pairs of these rectangular, slender muscles are present, one pair for each arch, except the fifth arch that lacks this muscle. Their origins are on a posteroventral groove on the pharyngobranchial. Their insertions are on the anterodorsal surface of the epibranchial near the articulation with the pharyngobranchial, both through a connective margin. Fibers directed downward.

-*m. interbranchiales*: Four pairs are present, one for each gill arch. They lay within a holobranch on the anterior face of the gill rays. Slender muscle with a semi-elliptical shape, with the thickness of a gill ray. The origins and insertions of the outermost fibers are both on the extrabranchial cartilages (dorsally and ventrally), the origins of the innermost fibers on the arch cartilages (dorsally the epibranchial and ventrally the ceratobranchial) and the insertions on the extrabranchial cartilages, which give these muscles a rather fragile aspect. Fibers have different sizes, the innermost are smaller than the outermost, and are oriented in a semicircular manner, on the posterior surface of the arch. Fibers tightly united, with no spaces between them.

-*m. coracoarcualis communis*: Triangular, bulky muscle with rounded margins. Its origin is on the coracoid bar through a tendon. Its insertion is on an anterior muscle (the *m. coracohyoideus*) through connective tissue. Fibers are oriented anteriorly.

-*m. coracobranchiales*: Five muscles present, one for each branchial arch. The anterior four are small cylindrical muscles (1-4) and the last has a laminar shape. The fifith coracobranchial muscle has loose fibers. Their origins are on the pericardic membrane. Their insertions are through a tendon on the 1-3 hypobranchial cartilages,

the cardiobranchial and the fifth ceratobranchial, respectively. Fibers are directed anteriorly and slightly upwards when close to the insertion. On the fifth muscle, the fibers are oblique, anterodorsally oriented on their whole length.

Pseudocarchariidae

Pseudocarcharias kamoharai (FIG. 17; MZUSP uncat., 269mm)

-*m. constrictores branchiales superficiales*: Four pairs of these muscles are present, one pair for each arch, except the fifth arch that lacks this muscle. Laminar muscles that lay immediately beneath the skin in the branchial region, posterior to the first branchial opening. Origin and insertion are through connective tissue, the dorsal origin occurs with a thicker tendon-like aponeurosis, which covers almost all the *m. trapezius*, and the ventral insertion occurs lateral to the posterior region of the *m. coracomandibularis* and covers this muscle anteriorly. The fibers of the portion dorsal to the gill slits are directed in a slightly oblique fashion, anteroventrally in relation to the main axis of the body. The fibers of the portion which forms the wall of the gill pouches pass dorsoventrally with a slight arch accompanying the branchial slit margin. The fibers of the portion ventral to the gill slits are directed posteroventrally as oblique as the dorsal fibers.

-*m. trapezius*: Laminar muscle with a triangular shape due to its insertions. The muscle has a cleavage which divides it into two portions, one anterior and one posterior. The anterior portion has a triangular shape and is one third the size of the posterior portion, which also has a triangular shape. Its origin is in an aponeurosis common to the *m. constrictor branchiales superficiales*. Its insertions are on two distinct points (also called a digastric muscle), the dorsal surface of the scapular process of the pectoral girdle through a layer of dense connective tissue, and the dorsal surface of the fifth epibranchial through connective tissue. Fibers are oriented nearly transversely to the main axis of the body (between 75°-85° posteriorly).

-*m. adductores arcuum branchialium*: Four pairs of these muscles are present, one pair for each arch, except the fifth arch that lacks this muscle. Small, crescent-shaped

muscles with a slight curve at midlength, and restricted to the area of the epibranchial-ceratobranchial articulation. Their origins are on the epibranchial. Their insertions are on the ceratobranchial. The origins and insertions occur without the presence of dense connective tissue. Fibers are oriented downward with slight curves towards the insertions.

-*m. interpharyngobranchiales*: Three pairs of these slender, laminar and triangular muscles are present, located between the first and second pharyngobranchials, the second and third pharyngobranchials and the third pharyngobranchial and the gill pickaxe. Their origins are on the ventroposterior margin of a pharyngobranchial on the half close to the epibranchial through connective tissue. Their insertions are on the anterodorsal margin of the next pharyngobranchial also through connective tissue. Fibers are oriented obliquely to the pharyngobranchial axis (near 20°).

-*m. arcuales dorsales*: Four pairs of these rectangular, slender muscles are present, one pair for each arch, except the fifth arch that lacks this muscle. Their origins are on a posteroventral groove on the pharyngobranchial. Their insertions are on the anterodorsal surface of the epibranchial near the articulation with the pharyngobranchial, both through a connective margin. Fibers directed downward.

-*m. pharyngobranchiales 1-epibranchiales 2*: Triangular, slender muscle. Its origin is on the same point of origin from the *m. interpharyngobranchiales* on the pharyngobranchial 1. Its insertion is on the dorsal surface of the epibranchial 2 at midlength, both insertion and origin through a connective margin. Fibers directed downward.

-*m. pharyngobranchiales 2-epibranchiales 3*: Triangular, slender muscle. Its origin is on the same point of origin from the *m. interpharyngobranchiales* on the pharyngobranchial 3. Its insertion is on the dorsal surface of the epibranchial 3 at midlength, both insertion and origin through a connective margin. Fibers directed downward.

-*m. pharyngobranchiales 3-epibranchiales 4*: Triangular, slender muscle. Its origin is on the same point of origin from the *m. interpharyngobranchiales* on the pharyngobranchial 3. Its insertion is on the dorsal surface of the epibranchial 4 at

midlength, both insertion and origin through a connective margin. Fibers directed downward.

-*m. interbranchiales*: Four pairs are present, one for each gill arch. They lay within a holobranch on the anterior face of the gill rays. Slender muscle with a semi-elliptical shape, with the thickness of a gill ray. The origins and insertions of the outermost fibers are both on the extrabranchial cartilages (dorsally and ventrally), the origins of the innermost fibers on the arch cartilages (dorsally the epibranchial and ventrally the ceratobranchial) and the insertions on the extrabranchial cartilages, which give these muscles a rather fragile aspect. Fibers have different sizes, the innermost are smaller than the outermost, and are oriented in a semicircular manner, on the posterior surface of the arch. Fibers tightly united, with no spaces between them.

-*m. coracoarcualis communis*: Triangular, bulky muscle with rounded margins. It has a few thin septa which gives it a segmented aspect. Its origin is on the coracoid bar through a tendon. Its insertion is on an anterior muscle (the *m. coracohyoideus*) through connective tissue. Fibers are oriented anteriorly.

-*m. coracobranchiales*: Five muscles present, one for each branchial arch. The anterior four are small cylindrical muscles (1-4) and the last has a digastric laminar shape. Their origins are on the pericardic membrane. Their insertions are through a tendon on the 1-3 hypobranchial cartilages, the cardiobranchial and the fifth ceratobranchial, respectively. The fifth *m. coracobranchial* (also called a digastric muscle) has two points of insertions on the ceratobranchial, the anterior one trapezoidal and covering roughly 70% of the ventral surface and the posterior one rectangular and covering the remaining 30%. Fibers are directed anteriorly and slightly upwards when close to the insertion. On the fifth muscle, the anterior fibers are oblique, anterodorsally oriented, whereas the posterior fibers are near upward. The fifth muscle has a connective raphe between the anterior and posterior portions.

Alopiidae

Alopias pelagicus (FIG. 18; USNM 202675, 751mm)

-*m. constrictores branchiales superficiales*: Four pairs of these muscles are present, one pair for each arch, except the fifth arch that lacks this muscle. Laminar muscles that lay immediately beneath the skin in the branchial region, posterior to the first branchial opening. Origin and insertion are through connective tissue, the dorsal origin occurs with a thicker tendon-like aponeurosis, which covers almost all the *m. trapezius*, and the ventral insertion occurs lateral to the posterior region of the *m. coracomandibularis* and covers this muscle anteriorly. The fibers of the portion dorsal to the gill slits are directed in a slightly oblique fashion, anteroventrally in relation to the main axis of the body. The fibers of the portion which forms the wall of the gill pouches pass dorsoventrally with a slight arch accompanying the branchial slit margin. The fibers of the portion ventral to the gill slits are directed posteroventrally slightly more oblique than the dorsal fibers.

-*m. trapezius*: Laminar muscle with a triangular shape due to its insertions. The muscle has a cleavage which divides it into two portions, one anterior and one posterior. The anterior portion has a triangular shape and is one quarter the size of the posterior portion, which also has a triangular shape. Its origin is in an aponeurosis common to the *m. constrictor branchiales superficiales*. Its insertions are on two distinct points (also called a digastric muscle), the dorsal surface of the ventral end of the scapular process of the pectoral girdle through a layer of dense connective tissue, and the dorsal surface of the fifth epibranchial through connective tissue. Fibers are oriented nearly transversely to the main axis of the body, slightly oblique (between 20°-30° posteriorly on the anterior portion and between 5°-15° anteriorly on the posterior portion, with some convergent anterior fibers on the latter).

-*m. adductores arcuum branchialium*: Five pairs of these muscles are present, one pair for each arch, except the fifth arch that lacks this muscle. Small, crescent-shaped muscles with a slight curve at midlength, and restricted to the area of the epibranchial-ceratobranchial articulation. Their origins are on the epibranchial. Their insertions are on the ceratobranchial. The origins and insertions occur without the presence of dense connective tissue. Fibers are oriented posteriorly curving slightly downwards towards insertions.

-*m. interpharyngobranchiales*: Three pairs of these slender, laminar and triangular muscles are present, located between the first and second pharyngobranchials, the second and third pharyngobranchials and the third pharyngobranchial and the gill pickaxe. Their origins are on the ventroposterior margin of a pharyngobranchial on the half close to the epibranchial through connective tissue. Their insertions are on the anterodorsal margin of the next pharyngobranchial also through connective tissue. Fibers are oriented obliquely to the pharyngobranchial axis (near 20°).

-*m. arcuales dorsales*: Four pairs of these trapezoid, slender muscles are present, one pair for each arch, except the fifth arch that lacks this muscle. Their origins are on a posteroventral groove on the pharyngobranchial. Their insertions are on the anterodorsal surface of the epibranchial near the articulation with the pharyngobranchial, both through a connective margin. Fibers directed downward.

-*m. interbranchiales*: Four pairs are present, one for each gill arch. They lay within a holobranch on the anterior face of the gill rays. Slender muscle with a semi-elliptical shape, with the thickness of a gill ray. The origins and insertions of the outermost fibers are both on the extrabranchial cartilages (dorsally and ventrally), the origins of the innermost fibers on the arch cartilages (dorsally the epibranchial and ventrally the ceratobranchial) and the insertions on the extrabranchial cartilages, which give these muscles a rather fragile aspect. Fibers have different sizes, the innermost are smaller than the outermost, and are oriented in a semicircular manner, on the posterior surface of the arch. Fibers tightly united, with no spaces between them.

-*m. coracoarcualis communis*: Triangular, bulky muscle with rounded margins. It has a few thin septa which gives it a segmented aspect. Its origin is on the coracoid bar through a tendon. Its insertion is on an anterior muscle (the *m. coracohyoideus*) through connective tissue. Fibers are oriented anteriorly.

-*m. coracobranchiales*: Five muscles present, one for each branchial arch. The anterior four are small cylindrical muscles (1-4) and the last has a laminar shape. Their origins are on the pericardic membrane. Their insertions are through a tendon on the 1-3 hypobranchial cartilages, the cardiobranchial and the fifth ceratobranchial, respectively. The fifth *m. coracobranchial* has its insertion on the ventral surface of

the ceratobranchial. Fibers are directed anteriorly and slightly upwards when close to the insertion. On the fifth muscle, the fibers are oblique, anterodorsally oriented.

4. Carcharhiniformes

The muscle that compresses the esophagus and is associated with the last branchial arch covers the exterior surface of the esophagus and has a circular disposition of fibers. No variation in this muscle was observed among the carcharhiniform species examined. It is called *m. constrictor oesophagi*.

Carcharhinidae

Carcharhinus porosus (FIG. 1; MZUSP 37286, 335mm)

-*m. constrictores branchiales superficiales*: Four pairs of these muscles are present, one pair for each arch, except the fifth arch that lacks this muscle. Laminar muscles that lay immediately beneath the skin in the branchial region, posterior to the first branchial opening. Origin and insertion are through connective tissue, the dorsal origin occurs with a thicker tendon-like aponeurosis, which covers the anterior fourth the *m. trapezius*, and the ventral insertion occurs lateral to the posterior region of the *m. coracomandibularis* and covers this muscle anteriorly. The fibers of the portion dorsal to the gill slits are directed in a slightly oblique fashion, anteroventrally in relation to the main axis of the body. The fibers of the portion which forms the wall of the gill pouches pass dorsoventrally with a slight arch where it meets the dorsal and ventral portions of the muscle. The fibers of the portion ventral to the gill slits are directed posteroventrally in a more oblique fashion than the dorsal fibers.

-*m. trapezius*: Laminar muscle with a triangular shape due to its insertions. The muscle has a cleavage which divides it into two portions, one anterior and one posterior. The anterior portion has a triangular shape and is half the size of the posterior portion, which also has a triangular shape. Its origin is in an aponeurosis

common to the *m. constrictor branchiales superficiales*. Its insertions are on two distinct points (also called a digastric muscle), the dorsal surface of the scapular process of the pectoral girdle through a thick layer of dense connective tissue, and the dorsal surface of the fifth epibranchial through connective tissue. Fibers are oriented nearly transversely to the main axis of the body (between 75°-85° posteriorly on both parts, anterior and posterior).

-*m. adductores arcuum branchialium*: -*m. adductores arcuum branchialium*: Five pairs of these muscles are present, one pair for each arch. Small, crescent-shaped muscles with a sharp curve at midlength and restricted to the area of the epibranchial-ceratobranchial articulation. Their origins are on the epibranchial. Their insertions are on the ceratobranchial. The origins and insertions occur without the presence of dense connective tissue. Fibers are oriented downward curving slightly towards insertions.

-*m. interpharyngobranchiales*: Three pairs of slender, laminar and triangular muscles are present, located between the first and second pharyngobranchials, the second and third pharyngobranchials and the third pharyngobranchial and the gill pickaxe. Their origins are on the ventroposterior margin of a pharyngobranchial, on the half close to the epibranchial, through connective tissue. Their insertions are on the anterodorsal margin of the next pharyngobranchial also through connective tissue. Fibers are oriented obliquely to the pharyngobranchial axis (near 20°).

-*m. arcuales dorsales*: Four pairs of these rectangular, slender muscles are present, one pair for each arch, except the fifth arch that lacks this muscle. Their origins are on a posteroventral groove on the pharyngobranchial. Their insertions are on the posterodorsal surface of the epibranchial near the articulation with the pharyngobranchial, origins and insertions through a connective margin. Fibers directed downward.

-*m. interbranchiales*: Four pairs are present, one for each gill arch. They lay within a holobranch on the anterior face of the gill rays. Slender muscle with a semi-elliptical shape, with the thickness of a gill ray. The origins and insertions of the outermost fibers are both on the extrabranchial cartilages (dorsally and ventrally), the origins of the innermost fibers on the arch cartilages (dorsally the epibranchial and ventrally the ceratobranchial) and the insertions on the extrabranchial cartilages, which give these

muscles a rather fragile aspect. Fibers have different sizes, the innermost are smaller than the outermost, and are oriented in a semicircular manner, on the posterior surface of the arch. Fibers tightly united, with no spaces between them.

-*m. coracoarcualis communis*: Triangular, bulky muscle with rounded margins. It possess some septa that gives Its origin is on the coracoid bar through a tendon. Its insertion is on an anterior muscle (the *m. coracohyoideus*) through connective tissue. Fibers are oriented anteriorly.

-*m. coracobranchiales*: Five muscles present, one for each branchial arch. The anterior four are small cyllindrical muscles (1-4) and the last has a laminar shape. Their origins are on the pericardic membrane. Their insertions are through a tendon on the 1-3 hypobranchial cartilages, the cardiobranchial and the fifth ceratobranchial, respectively. The fifth *m. coracobranchial* has two points of insertions on the ceratobranchial (also called a digastric muscle), the anterior one trapezoidal and covering roughly 80% of the ventral surface and the posterior one rectangular and covering the remaining 20%. Fibers are directed anteriorly and slightly upwards when close to the insertion. On the fifth muscle, the anterior fibers are oblique, anterodorsally oriented, whereas the posterior fibers are nearly upward oriented.

Carcharhinus falciformis

-*m. constrictores branchiales superficiales*: These muscles are as described in *Carcharhinus porosus*, except that the origin covers almost all the *m. trapezius*.

-*m. trapezius*: This muscle is as described in *Carcharhinus porosus*, except that the anterior portion has a triangular shape and is one third the size of the posterior portion, which also has a triangular shape.

-*m. adductores arcuum branchialium*: These muscles are as described in *Carcharhinus porosus*.

-*m. interpharyngobranchiales*: These muscles are as described in *Carcharhinus porosus*.

-*m. arcuales dorsales*: These muscles are as described in *Carcharhinus porosus*.

-*m. interbranchiales*: These muscles are as described in *Carcharhinus porosus*.

-*m. coracoarcualis communis*: This muscle is as described in *Carcharhinus porosus*, except it doen not have marked septa.

-*m. coracobranchiales*: These muscles are as described in *Carcharhinus porosus*, except that the fifth *m. coracobranchial* has two points of insertions on the ceratobranchial, the anterior one trapezoidal and covering roughly 80% of the ventral surface and the posterior one rectangular and covering the other 20%.

Carcharhinus limbatus

-*m. constrictores branchiales superficiales*: These muscles are as described in *Carcharhinus porosus*, except that its origin covers the anterior two thirds of the *m. trapezius*.

-*m. trapezius* This muscle is as described in *Carcharhinus porosus*.

-*m. adductores arcuum branchialium*: These muscles are as described in *Carcharhinus porosus*.

-*m. interpharyngobranchiales*: These muscles are as described in *Carcharhinus porosus*, except that fibers are oriented obliquely to the pharyngobranchial axis (near 10°).

-*m. arcuales dorsales*: These muscles are as described in *Carcharhinus porosus*.

-*m. interbranchiales*: These muscles are as described in *Carcharhinus porosus*.

-*m. coracoarcualis communis*: This muscle is as described in *Carcharhinus porosus*.

-*m. coracobranchiales*: These muscles are as described in *Carcharhinus falciformis*.

Galeocerdo cuvier (FIG. 2; USNM 112243, 510mm)

-*m. constrictores branchiales superficiales*: These muscles are as described in *Carcharhinus porosus*, except that the fibers of the portion ventral to the gill slits are directed posteroventrally in an as oblique fashion as the dorsal fibers.

-*m. trapezius*: This muscle is as described in *Carcharhinus porosus*, except that fibers are oriented downwards to oblique anteriorventrally to the main axis of the body (between 75°-80°).

-*m. adductores arcuum branchialium*: These muscles are as described in *Carcharhinus*, except for the triangular-shape of the muscles, as well as fibers oriented downward.

-*m. interpharyngobranchiales*: These muscles are as described in *Carcharhinus porosus*.

-*m. arcuales dorsales*: These muscles are as described in *Carcharhinus*.

-*m. interbranchiales*: These muscles are as described in *Carcharhinus*.

-*m. coracoarcualis communis*: This muscle is as described in *Carcharhinus falciformis.*

-*m. ccoracobranchiales*: These muscles are as described in *Carcharhinus porosus*, except the first muscle has three distinct fiber groups, easily seen without a microscope.

Loxodon macrorhinus

-*m. constrictores branchiales superficiales*: These muscles are as described in *Carcharhinus*, except its origin covers the *m. trapezius*

-*m. trapezius*: These muscles are as described in *Carcharhinus falciformis*, except that fibers are oriented oblique anteriorventrally to the main axis of the body (between 75°-80°).

-*m. adductores arcuum branchialium*: These muscles are as described in *Galeocerdo*.

-*m. interpharyngobranchiales*: These muscles are as described in *Carcharhinus limbatus*.

-*m. arcuales dorsales*: These muscles are as described in *Carcharhinus*, except for the round margins of these muscles.

-*m. interbranchiales*: These muscles are as described in *Carcharhinus*.

-*m. coracoarcualis communis*: This muscle is as described in *Carcharhinus porosus*.

-*m. coracobranchiales*: These muscles are as described in *Galeocerdo*.

Nasolamia velox (FIG. 3; USNM 203467, 529mm)

-*m. constrictores branchiales superficiales*: These muscles are as described in *Carcharhinus falciformes*, except its origin covers almost all the *m. trapezius*.

-*m. trapezius*: This muscle is as described in *Carcharhinus falciformis*, except that fibers are oriented oblique posteriorventrally to the main axis of the body (the anterior portion between 55°-70°, the posterior portion between 70°-80°).

-*m. adductores arcuum branchialium*: These muscles are as described in *Carcharhinus*, except that fibers are oriented downward.

-*m. interpharyngobranchiales*: These muscles are as described in *Carcharhinus limbatus*.

-*m. arcuales dorsales*: These muscles are as described in *Loxodon*.

-*m. interbranchiales*: These muscles are as described in *Carcharhinus*.

-*m. coracoarcualis communis*: This muscle is as described in *Carcharhinus porosus*.

-*m. coracobranchiales*: These muscles are as described in *Galeocerdo*, except on the fifth muscle, the anterior fibers are oblique, anterodorsally oriented, whereas the posterior fibers are upward.

Negaprion acutidens (FIG. 4; MZUSP uncat., 357mm)

-*m. constrictores branchiales superficiales*: These muscles are as described in *Nasolamia*.

-*m. trapezius*: This muscle is as described in *Carcharhinus falciformis*, except that fibers are oriented nearly transversely to the main axis of the body (between 75°-85° anteriorly on the posterior part and between 65°-80° posteriorly on the anterior part).

-*m. adductores arcuum branchialium*: These muscles are as described in *Carcharhinus*, except that fibers are directed downards

-*m. interpharyngobranchiales*: These muscles are as described in *Carcharhinus limbatus*.

-*m. arcuales dorsales*: These muscles are as described in *Carcharhinus*.

-*m. interbranchiales*: These muscles are as described in *Carcharhinus*.

-*m. coracoarcualis communis*: This muscle is as described in *Carcharhinus porosus*.

-*m. coracobranchiales*: These muscles are as described in *Carcharhinus porosus*.

Prionace glauca

-*m. constrictores branchiales superficiales:* These muscles are as described in *Carcharhinus porosus*.

-*m. trapezius*: This muscle is as described in *Negaprion*.

-*m. adductores arcuum branchialium*: These muscles are as described in *Carcharhinus*, except for the crescent-shape of the muscles with no sharp curve at midlength.

-*m. interpharyngobranchiales*: These muscles are as described in *Carcharhinus limbatus*.

-*m. arcuales dorsales*: These muscles are as described in *Carcharhinus*.

-*m. interbranchiales*: These muscles are as described in *Carcharhinus*.

-*m. coracoarcualis communis*: This muscle is as described in *Carcharhinus porosus*.

-*m. coracobranchiales*: These muscles are as described in *Carcharhinus*, except the fifth *m. coracobranchial* has two points of insertions on the ceratobranchial, the anterior one trapezoidal and covering roughly 50% of the ventral surface and the posterior one rectangular and covering the other 50%.

Rhizoprionodon porosus

-*m. constrictores branchiales superficiales*: These muscles are as described in *Carcharhinus porosus*.

-*m. trapezius*: This muscle is as described in *Negaprion*.

-*m. adductores arcuum branchialium*: These muscles are as described in *Negaprion*.

-*m. interpharyngobranchiales*: These muscles are as described in *Carcharhinus limbatus*.

-*m. arcuales dorsales*: These muscles are as described in *Carcharhinus*.

-*m. interbranchiales*: These muscles are as described in *Carcharhinus*.

-*m. coracoarcualis communis*: This muscle is as described in *Carcharhinus porosus*.

-*m. coracobranchiales*: These muscles are as described in *Carcharhinus porosus*.

Rhizoprionodon lalandei

-*m. constrictores branchiales superficiales*: These muscles are as described in *Carcharhinus porosus*.

-*m. trapezius*: This muscle is as described in *Negaprion*, except that the anterior portion has a triangular shape and is one quarter the size of the posterior portion, which has a triangular shape.

-*m. adductores arcuum branchialium*: These muscles are as described in *Carcharhinus*.

-*m. interpharyngobranchiales*: These muscles are as described in *Carcharhinus limbatus*.

-*m. arcuales dorsales*: These muscles are as described in *Carcharhinus*.

-*m. interbranchiales*: These muscles are as described in *Carcharhinus*.

-*m. coracoarcualis communis*: This muscle is as described in *Carcharhinus porosus*.

-*m. coracobranchiales*: These muscles are as described in *Carcharhinus porosus*.

Scoliodon laticaudus

-*m. constrictores branchiales superficiales*: These muscles are as described in *Carcharhinus falciformis*.

-*m. trapezius*: This muscle is as described in *Carcharhinus porosus*, except that fibers are oriented nearly transversely to the main axis of the body (between 85°-95° anteriorly on the posterior part and between 85°-95° posteriorly on the anterior part).

-*m. adductores arcuum branchialium*: These muscles are as described in *Carcharhinus*.

-*m. interpharyngobranchiales*: These muscles are as described in *Carcharhinus limbatus*.

-*m. arcuales dorsales*: These muscles are as described in *Carcharhinus*.

-*m. interbranchiales*: These muscles are as described in *Carcharhinus*.

-*m. coracoarcualis communis*: This muscle is as described in *Carcharhinus porosus*.

-*m. coracobranchiales*: These muscles are as described in *Carcharhinus porosus*.

Triaenodon obesus

-*m. constrictores branchiales superficiales*: These muscles are as described in *Galeocerdo*.

-*m. trapezius*: This muscle is as described in *Carcharhinus*, except that the anterior portion has a triangular shape and about the same size as the posterior portion, which also has a triangular shape and the fibers are oriented obliquely to the main axis of the body (the anterior portion between 55°-70° posteriorly, the posterior portion in a triangular way between 80°-90° anteriorly and 70°-80° posteriorly).

-*m. adductores arcuum branchialium*: These muscles are as described in *Nasolamia*.

-*m. interpharyngobranchiales*: These muscles are as described in *Carcharhinus*, except that fibers are oriented nearly parallel to the pharyngobranchial axis (near 5°).

-*m. arcuales dorsales*: These muscles are as described in *Loxodon*.

-*m. interbranchiales*: These muscles are as described in *Carcharhinus*.

-*m. coracoarcualis communis*: This muscle is as described in *Carcharhinus porosus*.

-*m. coracobranchiales*: These muscles are as described in *Nasolamia*.

Sphyrnidae

Eusphyra blochii (FIG. 5; USNM 205342, 641mm)

-*m. constrictores branchiales superficiales*: Four pairs of these muscles are present, one pair for each arch, except the fifth arch that lacks this muscle. Laminar muscles that lay immediately beneath the skin in the branchial region, posterior to the first branchial opening. Origin and insertion are through connective tissue, the dorsal origin occurs with a thicker tendon-like aponeurosis, which covers almost all the *m. trapezius*, and the ventral insertion occurs lateral to the posterior region of the *m. coracomandibularis* and the two more anterior muscles cover the coracomandibular anteriorly. The fibers of the portion dorsal to the gill slits are directed in a slightly oblique fashion, anteroventrally in relation to the main axis of the body. The fibers of the portion which forms the wall of the gill pouches pass dorsoventrally forming a

slight arch. The fibers of the portion ventral to the gill slits are directed posteroventrally in a more oblique fashion than the dorsal fibers.

-*m. trapezius*: Laminar muscle with a triangular shape due to its insertions. This muscle has a cleavage which divides it into two portions, one anterior and one posterior. The anterior portion has a triangular shape and is the same size as the posterior portion, which has a trapezoid shape with rounded margins. Its origin is in an aponeurosis common to the *m. constrictor branchiales superficiales*. Its insertions are on two distinct points (also called a digastric muscle), the dorsal surface of the scapular process of the pectoral girdle near the articulation of the pectoral fin through a thin layer of dense connective tissue, and the dorsal surface of the fifth epibranchial through connective tissue, expanding on the dorsal inner surface of the branchial cavaity until the region of the sendo pharyngobranchial. Fibers are oriented nearly transversely to the main axis of the body (between 75°-85° posteriorly on the posterior part and between 70°-80° posteriorly on the anterior part).

-*m. adductores arcuum branchialium*: Five pairs of these muscles are present, one pair for each arch, except the fifth arch that lacks this muscle. Small, triangular-shaped muscles and restricted to the area of the epibranchial-ceratobranchial articulation. Their origins are on the epibranchial. Their insertions are on the ceratobranchial. The origins and insertions occur without the presence of dense connective tissue. Fibers are oriented downward curving slightly anteriorly towards insertion.

-*m. interpharyngobranchiales*: Three pairs of these slender, laminar and triangular muscles are present, located between the first and second pharyngobranchials, the second and third pharyngobranchials and the third pharyngobranchial and the gill pickaxe. Their origins are on the ventroposterior margin of a pharyngobranchial, on the half close to the epibranchial, through connective tissue. Their insertions are on the anterodorsal margin of the next pharyngobranchial also through connective tissue. Fibers are oriented obliquely to the pharyngobranchial axis (near 10°).

-*m. arcuales dorsales*: Four pairs of these square-shaped, slender muscles are present, one pair for each arch, except the fifth arch that lacks this muscle. Their origins are on a posteroventral groove on the pharyngobranchial. Their insertions are on the

anterodorsal surface of the epibranchial near the articulation with the pharyngobranchial, both through a connective margin. Fibers directed downward.

-*m. pharyngobranchiales 1-epibranchiales 2*: Triangular, slender muscle. Its origin is on the same origin from the *m. interpharyngobranchiales* on the pharyngobranchial 1. Its insertion is on the dorsal surface of the epibranchial 2 at midlength, both insertion and origin through a connective margin. Fibers directed downward.

-*m. interbranchiales*: Four pairs are present, one for each gill arch. They lay within a holobranch on the anterior face of the gill rays. Slender muscle with a semi-elliptical shape, with the thickness of a gill ray. The origins and insertions of the outermost fibers are both on the extrabranchial cartilages (dorsally and ventrally), the origins of the innermost fibers on the arch cartilages (dorsally the epibranchial and ventrally the ceratobranchial) and the insertions on the extrabranchial cartilages, which give these muscles a rather fragile aspect. Fibers have different sizes, the innermost are smaller than the outermost, and are oriented in a semicircular manner, on the posterior surface of the arch. Fibers tightly united, with no spaces between them.

-*m. coracoarcualis communis*: Triangular, bulky muscle with rounded margins. It has a few thin septa which gives it a segmented aspect. Its origin is on the coracoid bar through a tendon. Its insertion is on an anterior muscle (the *m. coracohyoideus*) through connective tissue. Fibers are oriented anteriorly.

-*m. coracobranchiales*: Five muscles present, one for each branchial arch. The anterior four are small cylindrical muscles (1-4) and the last has a laminar shape. Their origins are on the pericardic membrane. Their insertions are through a tendon on the 1-3 hypobranchial cartilages, the cardiobranchial and the fifth ceratobranchial, respectively. The fifth *m. coracobranchial* has two points of insertions on the ceratobranchial (also called a digastric muscle), the anterior one trapezoidal and covering roughly 70% of the ventral surface and the posterior one rectangular and covering the remaining 30%. Fibers are directed anteriorly and slightly upwards when close to the insertion. On the fifth muscle, the anterior fibers are oblique, anterodorsally oriented, whereas the posterior fibers are slightly oblique, posterodorsally oriented.

Sphyrna lewini

-*m. constrictores branchiales superficiales*: These muscles are as described in *Eusphyra*, except its origin covers the anterior three quarters of the *m. trapezius*, and the three more anterior muscles cover the coracomandibular anteriorly on the insertion.

-*m. trapezius*: These muscles are as described in *Eusphyra*, except the anterior portion has a triangular shape and is one third the size of the posterior portion, which has a semi-elliptic shape and the fibers are oriented nearly transversely to the main axis of the body (between 75°-85° posteriorly on the posterior part and between 65°-80° posteriorly on the anterior part).

-*m. adductores arcuum branchialium*: These muscles are as described in *Eusphyra*, except the crescent-shape of the muscles with a sharp curve at midlength.

-*m. interpharyngobranchiales*: These muscles are as described in *Eusphyra*.

-*m. arcuales dorsales*: These muscles are as described in *Eusphyra*.

-*m. interbranchiales*: These muscles are as described in *Eusphyra*.

-*m. coracoarcualis communis*: These muscles are as described in *Eusphyra*.

-*m. coracobranchiales*: These muscles are as described in *Eusphyra*, except the fifth *m. coracobranchial* has two points of insertions on the ceratobranchial, the anterior one trapezoidal and covering roughly 80% of the ventral surface and the posterior one rectangular and covering the other 20% and on the fifth muscle, the anterior fibers are oblique, anterodorsally oriented, whereas the posterior fibers are near upward.

Sphyrna tiburo (FIG. 6; MZUSP 37347, 371mm)

-*m. constrictores branchiales superficiales*: These muscles are as described in *Eusphyra*, except its origin covers the anterior quarter of the *m. trapezius*, and the insertion covers the *m. coracomandibularis* anteriorly.

-*m. trapezius*: These muscles are as described in *Sphyrna lewini*.

-*m. adductores arcuum branchialium*: These muscles are as described in *Sphyrna lewini*.

-*m. interpharyngobranchiales*: These muscles are as described in *Eusphyra*.

-*m. arcuales dorsales*: These muscles are as described in *Eusphyra*.

-*m. interbranchiales*: These muscles are as described in *Eusphyra*.

-*m. coracoarcualis communis*: These muscles are as described in *Eusphyra*.

-*m. coracobranchiales*: These muscles are as described in *Sphyrna lewini*.

Sphyrna zygaena

-*m. constrictores branchiales superficiales*: These muscles are as described in *Sphyrna tiburo*.

-*m. trapezius*: These muscles are as described in *Sphyrna lewini*.

-*m. adductores arcuum branchialium*: These muscles are as described in *Sphyrna lewini*.

-*m. interpharyngobranchiales*: These muscles are as described in *Eusphyra*.

-*m. arcuales dorsales*: These muscles are as described in *Eusphyra*.

-*m. interbranchiales*: These muscles are as described in *Eusphyra*.

-*m. coracoarcualis communis*: These muscles are as described in *Eusphyra*.

-*m. coracobranchiales*: These muscles are as described in *Sphyrna lewini*.

Hemigaleidae

Chaenogaleus macrostoma (FIG. 7; NMMBP 6414, 652mm)

-*m. constrictores branchiales superficiales*: Four pairs of these muscles are present, one pair for each arch, except the fifth arch that lacks this muscle. Laminar muscles that lay beneath the skin in the branchial region, posterior to the first branchial opening. Origin and insertion are through an aponeurosis, the dorsal origin occurs with a thicker tendon-like aponeurotic layer, which covers almost all the *m. trapezius*, and the ventral insertion occurs lateral to the posterior region of the *m. coracomandibularis* and covers this muscle anteriorly. The fibers of the portion dorsal to the gill slits are directed obliquely, anteroventrally in relation to the main axis of the body. The fibers of the portion which forms the wall of the gill pouches pass dorsoventrally with a slight arch where it meets the dorsal and ventral portions of the muscle. The fibers of the portion ventral to the gill slits are directed posteroventrally in a mirrored fashion to the dorsal fibers.

-*m. trapezius*: Laminar muscle with a triangular shape due to its insertions. This muscle has a cleavage which divides it into two portions, one anterior and one posterior. The anterior portion has a trapezoidal shape and is half the size of the posterior portion, which has a triangular shape. Its origin is in an aponeurosis common anteriorly to the *m. constrictor branchiales superficiales*. Its insertions are on two distinct points (also called a digastric muscle), the dorsal surface of the scapular process of the pectoral girdle through a tendon, and the dorsal surface of the fifth epibranchial through connective tissue. Fibers are oriented nearly transversely to the main axis of the body (between 75°-85° posteriorly).

-*m. adductores arcuum branchialium*: Five pairs of these muscles are present, one pair for each arch. Small crescent-shaped muscles, and restricted to the area of the epibranchial-ceratobranchial articulation. Their origins are on the epibranchial. Their insertions are on the ceratobranchial. The origins and insertions occur without the presence of dense connective tissue. Fibers are oriented downward curving slightly towards insertions.

-*m. interpharingobranchiales*: Three pairs of these slender, laminar muscles are present, between the first and second pharyngobranchials, the second and third pharyngobranchials and the third pharyngobranchial and the gill pickaxe. Their origins are on the ventroposterior margin of a pharyngobranchial through connective

tissue. Their insertions are on the anterodorsal margin of the next pharyngobranchial also through connective tissue. Fibers are oriented slightly obliquely to the pharyngobranchial axis (around 10°).

-*m. arcuales dorsales*: Four pairs of these rectangular, slender muscles are present, one pair for each arch, except the fifth arch that lacks this muscle. Their origins are on a posteroventral groove on the pharyngobranchial. Their insertions are on the anterodorsal surface of the epibranchial on the dorsal third, both through a connective margin. Fibers directed downward.

-*m. interbranchiales*: Four pairs are present, one for each gill arch. They lay within a holobranch on the anterior face of the gill rays. Slender muscle with a semi-elliptical shape, with the thickness of a gill ray. The origins and insertions of the outermost fibers are both on the extrabranchial cartilages (dorsally and ventrally), the origins of the innermost fibers on the arch cartilages (dorsally the epibranchial and ventrally the ceratobranchial) and the insertions on the extrabranchial cartilages, which give these muscles a rather fragile aspect. Fibers have different sizes, the innermost are smaller than the outermost, and are oriented in a semicircular manner, on the posterior surface of the arch. Fibers tightly united, with no spaces between them.

-*m. coracoarcualis communis*: Triangular, bulky muscle with rounded margins. It has a few thin septa which gives it a segmented aspect. Its origin is on the coracoid bar through a tendon. Its insertion is on an anterior muscle (the *m. coracohyoideus*) through connective tissue. Fibers are oriented anteriorly.

-*m. coracobranchiales*: Five muscles present, one for each branchial arch. The anterior four are small cyllindrical muscles (1-4) and the last has a laminar shape. Their origins are on the pericardic membrane. Their insertions are through a tendon on the 1-3 hypobranchial cartilages, the cardiobranchial and the fifth ceratobranchial, respectively. The fifth *m. coracobranchial* (also called a digastric muscle) has two points of insertions on the ceratobranchial, the anterior one trapezoidal and covering roughly 80% of the ventral surface and the posterior one rectangular and covering the remaining 20%. Fibers are directed anteriorly and slightly upwards when close to the insertion. On the fifth muscle, the anterior fibers are oblique, anterodorsally oriented, whereas the posterior fibers are nearly upward oriented.

Leptochariidae

Leptocharias smithii (FIG. 8; USNM 202677, 578mm)

-*m. constrictores branchiales superficiales*: Four pairs of these muscles are present, one pair for each arch, except the fifth arch that lacks this muscle. Laminar muscles that lay beneath the skin in the branchial region, posterior to the first branchial opening. Origin and insertion are through aponeurosis, the dorsal origin occurs with a thicker tendon-like aponeurotic layer, which covers almost all the *m. trapezius*, and the ventral insertion occurs lateral to the posterior region of the *m. coracomandibularis* and covers this muscle anteriorly. The fibers of the portion dorsal to the gill slits are directed obliquely, anteroventrally in relation to the main axis of the body. The fibers of the portion which forms the wall of the gill pouches pass dorsoventrally with a slight arch where it meets the dorsal and ventral portions of the muscle. The fibers of the portion ventral to the gill slits are directed posteroventrally in a mirrored fashion to the dorsal fibers.

-*m. trapezius*: Laminar muscle with a triangular shape due to its insertions. The muscle has a cleavage which divides it into two portions, one anterior and one posterior. The anterior portion has a trapezoidal shape and is half the size of the posterior portion, which has a triangular shape. Its origin is in an aponeurosis common anteriorly to the *m. constrictor branchiales superficiales*. Its insertions are on two distinct points (also called a digastric muscle), the dorsal surface of the scapular process of the pectoral girdle through a tendon, and the dorsal surface of the fifth epibranchial through connective tissue. Fibers are oriented nearly transversely to the main axis of the body (between 70°-80° posteriorly).

-*m. adductores arcuum branchialium*: Five pairs of these muscles are present, one pair for each arch. Small crescent-shaped muscles, and restricted to the area of the epibranchial-ceratobranchial articulation. Their origins are on the epibranchial. Their insertions are on the ceratobranchial. The origins and insertions occur without the presence of dense connective tissue. Fibers are oriented downward curving slightly towards insertions.

-*m. interpharingobranchiales*: Three pairs of these slender, laminar muscles are present, between the first and second pharyngobranchials, the second and third pharyngobranchials and the third pharyngobranchial and the gill pickaxe. Their origins are on the ventroposterior margin of a pharyngobranchial through connective tissue. Their insertions are on the anterodorsal margin of the next pharyngobranchial also through connective tissue. Fibers are oriented paralelly to the pharyngobranchial axis.

-*m. arcuales dorsales*: Four pairs of these rectangular, somewhat bulky muscles are present, one pair for each arch, except the fifth arch that lacks this muscle. Their origins are on a posteroventral groove on the pharyngobranchial. Their insertions are on the anterodorsal surface of the epibranchial on the dorsal third, both through a connective margin. Fibers directed downward.

-*m. interbranchiales*: Four pairs are present, one for each gill arch. They lay within a holobranch on the anterior face of the gill rays. Slender muscle with a semi-elliptical shape, with the thickness of a gill ray. The origins and insertions of the outermost fibers are both on the extrabranchial cartilages (dorsally and ventrally), the origins of the innermost fibers on the arch cartilages (dorsally the epibranchial and ventrally the ceratobranchial) and the insertions on the extrabranchial cartilages, which give these muscles a rather fragile aspect. Fibers have different sizes, the innermost are smaller than the outermost, and are oriented in a semicircular manner, on the posterior surface of the arch. Fibers tightly united, with no spaces between them.

-*m. coracoarcualis communis*: Triangular, bulky muscle with rounded margins. It has a few thin septa which gives it a segmented aspect. Its origin is on the coracoid bar through a tendon. Its insertion is on an anterior muscle (the *m. coracohyoideus*) through connective tissue. Fibers are oriented anteriorly.

-*m. coracobranchiales*: Five muscles present, one for each branchial arch. The anterior four are small cylindrical muscles (1-4) and the last has a laminar shape. Their origins are on the pericardic membrane. Their insertions are through a tendon on the 1-3 hypobranchial cartilages, the cardiobranchial and the fifth ceratobranchial, respectively. The fifth *m. coracobranchial* (also called a digastric muscle) has two points of insertions on the ceratobranchial, the anterior one trapezoidal and covering

roughly 80% of the ventral surface and the posterior one rectangular and covering the remaining 20%. Fibers are directed anteriorly and slightly upwards when close to the insertion. On the fifth muscle, the anterior fibers are oblique, anterodorsally oriented, whereas the posterior fibers are nearly upward.

Triakidae

Galeorhinus galeus (FIG. 9; CAS 21347, 352mm)

-*m. constrictores branchiales superficiales*: Four pairs of these muscles are present, one pair for each arch, except the fifth arch that lacks this muscle. Laminar muscles that lay beneath the skin in the branchial region, posterior to the first branchial opening. Origin and insertion are through aponeurosis, the dorsal origin occurs with a thicker tendon-like aponeurotic layer, which covers the anterior two thirds of the *m. trapezius*, and the ventral insertion occurs lateral to the posterior region of the *m. coracomandibularis* and covers this muscle anteriorly. The fibers of the portion dorsal to the gill slits are directed obliquely, anteroventrally in relation to the main axis of the body. The fibers of the portion which forms the wall of the gill pouches pass dorsoventrally with a slight arch where it meets the dorsal and ventral portions of the muscle. The fibers of the portion ventral to the gill slits are directed posteroventrally in a mirrored fashion to the dorsal fibers.

-*m. trapezius*: Laminar muscle with a triangular shape due to its insertions. The muscle has a cleavage which divides it into two portions, one anterior and one posterior. The anterior portion has a triangular shape and is one third the size of the posterior portion, which also has a triangular shape. Its origin is in an aponeurosis common anteriorly to the *m. constrictor branchiales superficiales*. Its insertions are on two distinct points (also called a digastric muscle), the dorsal surface of the scapular process of the pectoral girdle through a tendon, and the dorsal surface of the fifth epibranchial through connective tissue. Fibers are oriented nearly transversely to the main axis of the body, slightly oblique (between 65°-85° posteriorly).

-*m. adductores arcuum branchialium*: Five pairs of these muscles are present, one pair for each arch. Small muscles with a triangular shape, and restricted to the area of the epibranchial-ceratobranchial articulation. Their origins are on the epibranchial. Their insertions are on the ceratobranchial. The origins and insertions occur without the presence of dense connective tissue. Fibers are oriented downward curving slightly towards insertions.

-*m. interpharingobranchiales*: Three pairs of these slender, laminar muscles are present, between the first and second pharyngobranchials, the second and third pharyngobranchials and the third pharyngobranchial and the gill pickaxe. Their origins are on the ventroposterior margin of a pharyngobranchial through connective tissue. Their insertions are on the anterodorsal margin of the next pharyngobranchial also through connective tissue. Fibers are oriented slightly obliquely to the pharyngobranchial axis (near 20°).

-*m. arcuales dorsales*: Four pairs of these rectangular, slender muscles are present, one pair for each arch, except the fifth arch that lacks this muscle. Their origins are on a posteroventral groove on the pharyngobranchial. Their insertions are on the anterodorsal surface of the epibranchial on the dorsal third, both through a connective margin. Fibers directed downward.

-*m. interbranchiales*: Four pairs are present, one for each gill arch. They lay within a holobranch on the anterior face of the gill rays. Slender muscle with a semi-elliptical shape, with the thickness of a gill ray. The origins and insertions of the outermost fibers are both on the extrabranchial cartilages (dorsally and ventrally), the origins of the innermost fibers on the arch cartilages (dorsally the epibranchial and ventrally the ceratobranchial) and the insertions on the extrabranchial cartilages, which give these muscles a rather fragile aspect. Fibers have different sizes, the innermost are smaller than the outermost, and are oriented in a semicircular manner, on the posterior surface of the arch. Fibers tightly united, with no spaces between them.

-*m. coracoarcualis communis*: Triangular, bulky muscle with rounded margins. It has a few thin septa which gives it a segmented aspect. Its origin is on the coracoid bar through a tendon. Its insertion is on an anterior muscle (the *m. coracohyoideus*) through connective tissue. Fibers are oriented anteriorly.

-*m. coracobranchiales*: Five muscles present, one for each branchial arch. The anterior four are small cylindrical muscles (1-4) and the last has a laminar shape. Their origins are on the pericardic membrane. Their insertions are through a tendon on the 1-3 hypobranchial cartilages, the cardiobranchial and the fifth ceratobranchial, respectively. The fifth *m. coracobranchial* (also called a digastric muscle) has two points of insertions on the ceratobranchial, the anterior one trapezoidal and covering roughly 80% of the ventral surface and the posterior one rectangular and covering the remaining 20%, and is divided by a raphe. Fibers are directed anteriorly and slightly upwards when close to the insertion. On the fifth muscle, all fibers are oblique, anterodorsally oriented, the posterior fibers are a little more oblique anterodorsally.

Hemitriakis japanica

-*m. constrictores branchiales superficiales*: These muscles are as described in *Galeorhinus*, except its origin h covers the anterior half of the *m. trapezius* and, and the insertion of the two more anterior muscles cover the *m. coracomandibularis* anteriorly.

-*m. trapezius*: These muscles are as described in *Galeorhinus*, except that the anterior portion has a trapezoidal shape and is half the size of the posterior portion, which has a triangular shape and the fibers are oriented nearly transversely to the main axis of the body, slightly oblique (between 85°-95° posteriorly).

-*m. adductores arcuum branchialium*: These muscles are as described in *Galeorhinus*.

-*m. interpharingobranchiales*: These muscles are as described in *Galeorhinus*, except that fibers are oriented slightly obliquely to the pharyngobranchial axis (near 10°).

-*m. arcuales dorsales*: These muscles are as described in *Galeorhinus*.

-*m. interbranchiales*: These muscles are as described in *Galeorhinus*.

-*m. coracoarcualis communis*: These muscles are as described in *Galeorhinus*.

-*m. coracobranchiales*: These muscles are as described in *Galeorhinus*, except the fifth *m. coracobranchial* has two points of insertions on the ceratobranchial, the

anterior one trapezoidal and covering roughly 60% of the ventral surface and the posterior one rectangular and covering the other 40%, and is divided by a raphe and on the fifth muscle, the anterior fibers are oblique, anterodorsally oriented, whereas the posterior fibers are nearly upward.

Mustelus higmani:

-*m. constrictores branchiales superficiales*: These muscles are as described in *Galeorhinus*, except its origin covers the anterior half of the *m. trapezius*.

-*m. trapezius*: These muscles are as described in *Hemitriakis*, except that the anterior portion has a trapezoidal shape and is one third the size of the posterior portion, which has a triangular shape and the fibers are oriented nearly transversely to the main axis of the body (between 75°-85°).

-*m. adductores arcuum branchialium*: These muscles are as described in *Galeorhinus*.

-*m. interpharingobranchiales*: These muscles are as described in *Hemitriakis*.

-*m. arcuales dorsales*: These muscles are as described in *Galeorhinus*.

-*m. interbranchiales*: These muscles are as described in *Galeorhinus*.

-*m. coracoarcualis communis*: These muscles are as described in *Galeorhinus*.

-*m. coracobranchiales*: These muscles are as described in *Galeorhinus*, except that on the fifth muscle, the anterior fibers are oblique anteroposteriorly and the posterior fibers are nearly upward.

Mustelus griseus:

-*m. constrictores branchiales superficiales*: These muscles are as described in *Galeorhinus*, except its origin covers the *m. trapezius*.

-*m. trapezius*: These muscles are as described in *Hemitriakis*, except that fibers are oriented nearly transversely to the main axis of the body (between 75°-85°).

-*m. adductores arcuum branchialium*: These muscles are as described in *Galeorhinus*.

-*m. interpharingobranchiales*: These muscles are as described in *Galeorhinus*, except that fibers are oriented obliquely to the pharyngobranchial axis (near 30°).

-*m. arcuales dorsales*: These muscles are as described in *Galeorhinus*.

-*m. interbranchiales*: These muscles are as described in *Galeorhinus*.

-*m. coracoarcualis communis*: These muscles are as described in *Galeorhinus*, except it does not have the marked septa.

-*m. coracobranchiales*: These muscles are as described in *Galeorhinus*, except that the fifth *m. coracobranchial* has two points of insertions on the ceratobranchial, the anterior one trapezoidal and covering roughly 90% of the ventral surface and the posterior one rectangular and covering the other 10% and on the fifth muscle, the anterior fibers are more oblique anteroposteriorly than the posterior fibers.

Mustelus schmitti (FIG. 10; MZUSP 37327, 317mm)

-*m. constrictores branchiales superficiales*: These muscles are as described in *Mustelus higmani*.

-*m. trapezius*: These muscles are as described in *Mustelus higmani*, except that the anterior portion has a trapezoidal shape and is one third the size of the posterior portion, which has a triangular shape and the fibers are oriented obliquely to the main axis of the body (between 50°-70° anteriorly on the posterior region and 70°-80° posteriorly on the anterior region).

-*m. adductores arcuum branchialium*: These muscles are as described in *Galeorhinus*.

-*m. interpharingobranchiales*: These muscles are as described in *Hemitriakis*.

-*m. arcuales dorsales*: These muscles are as described in *Galeorhinus*.

-*m. interbranchiales*: These muscles are as described in *Galeorhinus*.

-*m. coracoarcualis communis*: These muscles are as described in *Galeorhinus*.

-*m. coracobranchiales*: These muscles are as described in *Mustelus higmani*.

Triakis scyllium

-*m. constrictores branchiales superficiales*: These muscles are as described in *Galeorhinus*, except the insertion of the two more anterior muscles cover the coracomandibular anteriorly and the fibers of the portion ventral to the gill slits are directed posteroventrally in a less oblique way than the dorsal fibers.

-*m. trapezius*: These muscles are as described in *Hemitriakis*, except the anterior portion has a triangular shape and is one quarter the size of the posterior portion, which has a triangular shape.

-*m. adductores arcuum branchialium*: These muscles are as described in *Galeorhinus*.

-*m. interpharingobranchiales*: These muscles are as described in *Hemitriakis*.

-*m. arcuales dorsales*: These muscles are as described in *Galeorhinus*.

-*m. interbranchiales*: These muscles are as described in *Galeorhinus*.

-*m. coracoarcualis communis*: These muscles are as described in *Galeorhinus*.

-*m. coracobranchiales*: These muscles are as described in *Mustelus higmani*, except the fifth *m. coracobrachialis* has two points of insertions on the ceratobranchial, the anterior one trapezoidal and covering roughly 70% of the ventral surface and the posterior one rectangular and covering the other 30%, and is divided by a raphe.

Proscyllidae

Eridacnis radcliffei (FIG. 11 CAS 34140, 230mm)

-*m. constrictores branchiales superficiales*: Four pairs of these muscles are present, one pair for each arch, except the fifth arch that lacks this muscle. Laminar muscles that lay beneath the skin in the branchial region, posterior to the first branchial opening. Origin and insertion are through aponeurosis, the dorsal origin occurs with a thicker tendon-like aponeurotic layer, which covers the anterior half of the *m.*, and the

ventral insertion occurs lateral to the posterior region of the *m. coracomandibularis* and covers this muscle anteriorly. The fibers of the portion dorsal to the gill slits are directed obliquely, anteroventrally in relation to the main axis of the body. The fibers of the portion which forms the wall of the gill pouches pass dorsoventrally with a slight arch where it meets the dorsal and ventral portions of the muscle. The fibers of the portion ventral to the gill slits are directed downwards.

-*m. trapezius*: Laminar muscle with a triangular shape due to its insertions. This muscle has a cleavage which divides it into two portions, one anterior and one posterior. The anterior portion has a trapezoidal shape and is one third the size of the posterior portion, which has a triangular shape. Its origin is in an aponeurosis common anteriorly to the *m. constrictor branchiales superficiales*. Its insertions are on two distinct points (also called a digastric muscle), the dorsal surface of the scapular process of the pectoral girdle through a tendon, and the dorsal surface of the fifth epibranchial through connective tissue. Fibers are oriented nearly transversely to the main axis of the body, slightly oblique (between 70°-80° posteriorly).

-*m. adductores arcuum branchialium*: Five pairs of these muscles are present, one pair for each arch. Small muscles with a triangular shape, which are restricted to the area of the epibranchial-ceratobranchial articulation. Their origins are on the epibranchial. Their insertions are on the ceratobranchial. The origins and insertions occur without the presence of dense connective tissue. Fibers are oriented downward curving slightly towards insertions.

-*m. interpharingobranchiales*: Three pairs of these slender, laminar muscles are present, between the first and second pharyngobranchials, the second and third pharyngobranchials and the third pharyngobranchial and the gill pickaxe. Their origins are on the ventroposterior margin of a pharyngobranchial through connective tissue. Their insertions are on the anterodorsal margin of the next pharyngobranchial also through connective tissue. Fibers are oriented slightly nearly parallel to the pharyngobranchial axis (near 5°).

-*m. arcuales dorsales*: Four pairs of these rectangular, slender muscles are present, one pair for each arch, except the fifth arch that lacks this muscle. Their origins are on a posteroventral groove on the pharyngobranchial. Their insertions are on the

anterodorsal surface of the epibranchial on the dorsal third, both through a connective margin. Fibers directed downward.

-*m. interbranchiales*: Four pairs are present, one for each gill arch. They lay within a holobranch on the anterior face of the gill rays. Slender muscle with a semi-elliptical shape, with the thickness of a gill ray. The origins and insertions of the outermost fibers are both on the extrabranchial cartilages (dorsally and ventrally), the origins of the innermost fibers on the arch cartilages (dorsally the epibranchial and ventrally the ceratobranchial) and the insertions on the extrabranchial cartilages, which give these muscles a rather fragile aspect. Fibers have different sizes, the innermost are smaller than the outermost, and are oriented in a semicircular manner, on the posterior surface of the arch. Fibers tightly united, with no spaces between them.

-*m. coracoarcualis communis*: Triangular, bulky muscle with rounded margins. Its origin is on the coracoid bar through a tendon. Its insertion is on an anterior muscle (the *m. coracohyoideus*) through connective tissue. Fibers are oriented anteriorly.

-*m. coracobranchiales*: Five muscles present, one for each branchial arch. The anterior four are small cylindrical muscles (1-4) and the last has a laminar shape. Their origins are on the pericardic membrane. The fifth has two points of origin, on the pericardic membrane and the coracoid bar. Their insertions are through a tendon on the 1-3 hypobranchial cartilages, the cardiobranchial and the fifth ceratobranchial, respectively. Fibers are directed anteriorly and slightly upwards when close to the insertion. On the fifth muscle, the fibers are oblique, anterodorsally oriented.

Pentanchidae

Apristurus brunneus (FIG. 12; CAS 57475, 649mm)

-*m. constrictores branchiales superficiales*: Four pairs of these muscles are present, one pair for each arch, except the fifth arch that lacks this muscle. Laminar muscles that lay immediately beneath the skin in the branchial region, posterior to the first branchial opening. Origin and insertion are through connective tissue, the dorsal origin with a tendon-like aponeurosis, which originates from the anterior third of the

m. trapezius, and the ventral insertion occurs lateral to the posterior region of the *m. coracomandibularis*. The fibers of the portion dorsal to the gill slits are directed anteriorly in a slightly oblique fashion. The fibers of the portion which forms the wall of the gill pouches pass dorsoventrally with a slight arch where it meets the ventral portion of the muscle. The fibers of the portion ventral to the gill slits are directed downards.

-*m. trapezius*: Laminar muscle with a triangular shape due to its insertions. Ths muscle has a cleavage which divides it into two portions, one anterior and one posterior. The anterior portion has a triangular shape and is one third the size of the posterior portion, which also has a triangular shape. Its origin is in an aponeurosisdorsal to the *m. constrictor branchiales superficiales*. Its insertions are on two distinct points (also called a digastric muscle), the dorsal surface of the scapular process of the pectoral girdle through a layer of dense connective tissue, and the dorsal surface of the fifth epibranchial through connective tissue. Fibers are oriented oblique to the main axis of the body (between 60-70° posteriorly).

-*m. adductores arcuum branchialium*: Five pairs of these muscles are present, one pair for each arch. Small, triangular-shaped muscles with a smooth curve at midlength and restricted to the area of the epibranchial-ceratobranchial articulation. Their origins are on the epibranchial. Their insertions are on the ceratobranchial. The origins and insertions occur without the presence of dense connective tissue. Fibers are oriented downward.

-*m. interpharyngobranchiales*: Three pairs of these slender and triangular muscles are present, located between the first and second pharyngobranchials, the second and third pharyngobranchials and the third pharyngobranchial and the gill pickaxe. Their origins are on the ventroposterior margin of a pharyngobranchial on the half close to the epibranchial through connective tissue. Their insertions are on the anterodorsal margin of the next pharyngobranchial also through connective tissue. Fibers are oriented obliquely to the pharyngobranchial axis (near 10°).

-*m. arcuales dorsales*: Four pairs of these rectangular, somewhat bulky muscles are present, one pair for each arch, except the fifth arch that lacks this muscle. Their origins are on a posteroventral groove on the pharyngobranchial. Their insertions are

on the anterodorsal surface of the epibranchial near the articulation with the pharyngobranchial, both through a connective margin. Fibers directed downward.

-*m. interbranchiales*: Four pairs are present, one for each gill arch. They lay within a holobranch on the anterior face of the gill rays. Slender muscle with a semi-elliptical shape, with the thickness of a gill ray. The origins and insertions of the outermost fibers are both on the extrabranchial cartilages (dorsally and ventrally), the origins of the innermost fibers on the arch cartilages (dorsally the epibranchial and ventrally the ceratobranchial) and the insertions on the extrabranchial cartilages, which give these muscles a rather fragile aspect. Fibers have different sizes, the innermost are smaller than the outermost, and are oriented in a semicircular manner, on the posterior surface of the arch. Fibers loosely united, with small spaces between them.

-*m. coracoarcualis communis*: Triangular, bulky muscle with rounded margins. It has a few thin septa which gives it a segmented aspect. Its origin is on the coracoid bar through a tendon. Its insertion is on an anterior muscle (the *m. coracohyoideus*) through connective tissue. Fibers are oriented anteriorly.

-*m. coracobranchiales*: Five muscles present, one for each branchial arch. The anterior four are small cylindrical muscles (1-4) and the last has a laminar shape. Their origins are on the pericardic membrane. The fifth has two points of origin, the pericardic membrane and the coracoid bar near the pectoral fin insertion. Their insertions are through a tendon on the 1-3 hypobranchial cartilages, the cardiobranchial and the fifth ceratobranchial, respectively. The fifth *m. coracobranchial* has one point of insertion on the ceratobranchial along most of the ventral surface of this element. Fibers are directed anteriorly and slightly upwards when close to the insertion.

Apristurus laurussonii

-*m. constrictores branchiales superficiales*: These muscles are as described in *Apristurus laurassoni*, except its origin covers the anterior fifth of the *m. trapezius*.

-*m. trapezius*: This muscle is as described in *Apristurus brunneus*.

-*m. adductores arcuum branchialium*: These muscles are as described in *Apristurus brunneus*.

-*m. interpharyngobranchiales*: These muscles are as described in *Apristurus brunneus*.

-*m. arcuales dorsales*: These mucles are as described in *Apristurus brunneus*.

-*m. interbranchiales*: These mucles are as described in *Apristurus brunneus*.

-*m. coracoarcualis communis*: This muscle is as decribes in *Apristurus brunneus.*

-*m. coracobranchiales*: These muscles are as described in *Apristurus brunneus*.

Galeus arae

-*m. constrictores branchiales superficiales*: These muscles are as described in *Apristurus brunneus*

-*m. trapezius*: This muscle is as described in *Apristurus*, except the anterior portion has a triangular shape and is half the size of the posterior portion, which also has a triangular shape.

-*m. adductores arcuum branchialium*: These muscles are as described in *Apristurus*.

-*m. interpharyngobranchiales*: These muscles are as described in *Apristurus*, except that fibers are oriented obliquely to the pharyngobranchial axis (near 20°).

-*m. arcuales dorsales*: These muscles are as described in *Apristurus*, except these are slender muscles.

-*m. interbranchiales*: These muscles are as described in *Apristurus*, except that the fibers are loosely united, with no spaces between them.

-*m. coracoarcualis communis*: This muscle is as described in *Apristurus*.

-*m. coracobranchiales*: These muscles are as described in *Apristurus*, except the fifth *m. coracobranchial* has two points of insertions on the ceratobranchial, the anterior one trapezoidal and covering roughly 90% of the ventral surface and the posterior one

rectangular and covering the other 10% and on the fifth muscle, the anterior fibers are oblique, anterodorsally oriented, whereas the posterior fibers are near upward.

Galeus melastomus

-*m. constrictores branchiales superficiales*: These muscles are as described in *Apristurus brunneus*, except its origin covers the anterior half of the *m. trapezius*, the fibers of the portion dorsal to the gill slits are directed downwards and the fibers of the portion ventral to the gill slits are directed posteroventrally in a slightly oblique fashion.

-*m. trapezius*: This muscle is as described in *Apristurus*, except the anterior portion has a triangular shape and is two thirds the size of the posterior portion, which also has a triangular shape.

-*m. adductores arcuum branchialium*: These muscles are as described in *Apristurus*.

-*m. interpharyngobranchiales*: These muscles are as described in *Galeus arae*.

-*m. arcuales dorsales*: These muscles are as described in *Galeus arae*.

-*m. interbranchiales*: These muscles are as described in *Galeus arae*.

-*m. coracoarcualis communis*: This muscle is as described in *Apristurus*.

-*m. coracobranchiales*: These muscles are as described in *Apristurus*, except the fifth has two points of origin, the pericardic membrane and the coracoid bar near the pectoral fin insertion.

Parmaturus xaniurus

-*m. constrictores branchiales superficiales*: These muscles are as described in *Galeus melastomosus*, except its origin covers all the *m. trapezius*.

-*m. trapezius*: This muscle is as described in *Galeus melastomosus*.

-*m. adductores arcuum branchialium*: These muscles are as described in *Apristurus*.

-*m. interpharyngobranchiales*: These muscles are as described in *Apristurus*.

-*m. arcuales dorsales*: These muscles are as described in *Galeus*, except for the square-shape of the muscles.

-*m. interbranchiales*: These muscles are as described in *Apristurus*.

-*m. coracoarcualis communis*: This muscle is as described in *Apristurus*, except it does not have the marked septa.

-*m. coracobranchiales*: These muscles are as described in *Galeus melastomosus*.

Scyliorhinidae

Scyliorhinus haeckelii (FIG. 13; MZUSP uncat., 168mm)

-*m. constrictores branchiales superficiales*: Four pairs of these muscles are present, one pair for each arch, except the fifth arch that lacks this muscle. Laminar muscles that lay immediately beneath the skin in the branchial region, posterior to the first branchial opening. These muscles are especially thin, having a translucent aspect. Origin and insertion are through connective tissue, the dorsal origin with a slender tendon-like aponeurosis, which covers the anterior quarter of the *m. trapezius*, and the ventral insertion occurs lateral to the posterior region of the *m. coracomandibularis* and covers this muscle anteriorly. The fibers of the portion dorsal to the gill slits are directed in a slightly oblique fashion, anteroventrally oriented. The fibers of the portion which forms the wall of the gill pouches pass dorsoventrally with a slight arch where it meets the dorsal and ventral portions of the muscle. The fibers of the portion ventral to the gill slits are directed posteroventrally in a less oblique fashion that the dorsal fibers.

-*m. trapezius*: Laminar muscle with a triangular shape due to its insertions. The muscle has a cleavage which divides it into two portions, one anterior and one posterior. The anterior portion has a triangular shape and is one quarter the size of the posterior portion, which also has a triangular shape. Its origin is in an aponeurosis

common to the *m. constrictor branchiales superficiales*. Its insertions are on two distinct points (also called a digastric muscle), the dorsal surface of the scapular process of the pectoral girdle through a layer of dense connective tissue, and the dorsal surface of the fifth epibranchial through connective tissue. Fibers are oriented nearly transversely to the main axis of the body (between 75°-85° posteriorly). The fibers on the posterior portion are convergent.

-*m. adductores arcuum branchialium*: Four pairs of these muscles are present, one pair for each arch, except the fifth arch that lacks this muscle. Small, crescent-shaped muscles with a sharp curve at midlength, and restricted to the area of the epibranchial-ceratobranchial articulation. Their origins are on the epibranchial. Their insertions are on the ceratobranchial. The origins and insertions occur without the presence of dense connective tissue. Fibers are oriented downward curving slightly towards insertions.

-*m. interpharyngobranchiales*: Three pairs of these slender, laminar and triangular muscles are present, between the first and second pharyngobranchials, the second and third pharyngobranchials and the third pharyngobranchial and the gill pickaxe. Their origins are on the ventroposterior margin of a pharyngobranchial on the half close to the epibranchial through connective tissue. Their insertions are on the anterodorsal margin of the next pharyngobranchial also through connective tissue. Fibers are oriented obliquely to the pharyngobranchial axis (near 20°).

-*m. arcuales dorsales*: Four pairs of these rectangular, slender muscles are present, one pair for each arch, except the fifth arch that lacks this muscle. Their origins are on a posteroventral groove on the pharyngobranchial. Their insertions are on the anterodorsal surface of the epibranchial near the articulation with the pharyngobranchial, both through a connective margin. Fibers directed downward.

-*m. interbranchiales*: Four pairs are present, one for each gill arch. They lay within a holobranch on the anterior face of the gill rays. Slender muscle with a semi-elliptical shape, with the thickness of a gill ray. The origins and insertions of the outermost fibers are both on the extrabranchial cartilages (dorsally and ventrally), the origins of the innermost fibers on the arch cartilages (dorsally the epibranchial and ventrally the ceratobranchial) and the insertions on the extrabranchial cartilages, which give these muscles a rather fragile aspect. Fibers have different sizes, the innermost are smaller

than the outermost, and are oriented in a semicircular manner, on the posterior surface of the arch. Fibers tightly united, with no spaces between them.

-*m. coracoarcualis communis*: Triangular, bulky muscle with rounded margins. Its origin is on the coracoid bar through a tendon. Its insertion is on an anterior muscle (the *m. coracohyoideus*) through connective tissue. Fibers are oriented anteriorly.

-*m. coracobranchiales*: Five muscles present, one for each branchial arch. The anterior four are small cylindrical muscles (1-4) and the last has a laminar shape. Their origins are on the pericardic membrane. The fifth has two points of origin, the pericardic membrane and the coracoid bar near the pectoral fin insertion. Their insertions are through a tendon on the 1-3 hypobranchial cartilages, the cardiobranchial and the fifth ceratobranchial, respectively. The fifth *m. coracobranchial* has one point of insertion on the ceratobranchial along most of the ventral surface of this cartilaginous element. Fibers are directed anteriorly and slightly upwards when close to the insertion.

Schroederichthys maculatus

-*m. constrictores branchiales superficiales*: These muscles are as described in *Scyliorhinus haeckelii*, except this muscle is not translucent as in *Scyliorhinus haeckelii*, its origin covers the anterior 2/5 of the *m. trapezius*, the fibers of the portion dorsal to the gill slits are directed downwards and the fibers of the portion ventral to the gill slits are directed slightly oblique, posteroventrally oriented.

-*m. trapezius*: This muscle is as described in *Scyliorhinus haeckelii*, except that fibers are oriented oblique to the main axis of the body (between 60-70° posteriorly).

-*m. adductores arcuum branchialium*: These muscles are as described in *Scyliorhinus haeckelii*.

-*m. interpharyngobranchiales*: These muscles are as described in *Scyliorhinus haeckelii*.

-*m. arcuales dorsales*: These muscles are as described in *Scyliorhinus haeckelii*.

-*m. interbranchiales*: These muscles are as described in *Scyliorhinus haeckelii*.

-*m. coracoarcualis communis*: This muscle is as described in *Scyliorhinus haeckelii*.

-*m. coracobranchiales*: These muscles are as described in *Scyliorhinus haeckelii*.

5. Squaliformes

The muscle that compresses the esophagus and is associated with the last branchial arch covers the exterior surface of the esophagus and has a circular disposition of fibers. No variation in this muscle was observed among the squaliform species examined. It is called *m. constrictor oesophagi*.

Centrophoridae

Centrophorus squamosus (FIG. 25; SU 8582, 390mm)

-*m. constrictores branchiales superficiales*: Four pairs of these muscles are present, one pair for each arch, except the fifth arch that lacks this muscle. Laminar muscles that lay immediately beneath the skin in the branchial region, posterior to the first branchial opening. Origin and insertion are through connective tissue, the dorsal origin occurs with a thicker tendon-like aponeurosis, which covers the anterior half of the *m. trapezius*, and the ventral insertion occurs lateral to the posterior region of the *m. coracomandibularis*. The fibers of the portion dorsal to the gill slits are directed in a slightly oblique fashion, anteroventrally in relation to the main axis of the body. The fibers of the portion which forms the wall of the gill pouches pass dorsoventrally with a slight arch accompanying the branchial slit margin. The fibers of the portion ventral to the gill slits are directed downwards.

-*m. trapezius*: Laminar muscle with a triangular shape due to its insertions. The muscle has a raphe present which divides it into two portions near the insertions. Its

origin is in an aponeurosis common to the *m. constrictor branchiales superficiales*. Its insertions are on two distinct points (also called a digastric muscle), the dorsal surface of the scapular process of the pectoral girdle through a thick layer of dense connective tissue, and the dorsal surface of the fifth epibranchial through connective tissue. Fibers are oriented oblique posteriorventrally to the main axis of the body (between 75°-85°).

-*m. adductores arcuum branchialium*: Five pairs of these muscles are present, one pair for each arch, except the fifth arch that lacks this muscle. Small triangular muscles, and restricted to the area of the epibranchial-ceratobranchial articulation. Their origins are on the epibranchial. Their insertions are on the ceratobranchial. The origins and insertions occur without the presence of dense connective tissue. Fibers are oriented downward and slightly divergent.

-*m. interpharyngobranchiales*: Three pairs of these slender, laminar and triangular muscles are present, located between the first and second pharyngobranchials, the second and third pharyngobranchials and the third pharyngobranchial and the fourth pharyngobranchial. Their origins are on the ventroposterior margin of a pharyngobranchial on the half close to the epibranchial through connective tissue. Their insertions are on the anterodorsal margin of the next pharyngobranchial also through connective tissue. Fibers are oriented obliquely to the pharyngobranchial axis (near 10°).

-*m. arcuales dorsales*: Four pairs of these rectangular, slender muscles are present, one pair for each arch, except the fifth arch that lacks this muscle. Their origins are on a posteroventral groove on the pharyngobranchial of the arch and the adjacent pharyngobranchial (two origins). Only the fourth has a single origin on the fourth pharyngobranchial and on a posterior process of the same (fifth pharyngobranchial?). Their insertions are on the anterodorsal surface of the epibranchial near the articulation with the pharyngobranchial, both through a connective margin. Fibers directed downward.

-*m. interbranchiales*: Four pairs are present, one for each gill arch. They lay within a holobranch on the anterior face of the gill rays. Slender muscle with a semi-elliptical shape, with the thickness of a gill ray. The origins and insertions of the outermost

fibers are both on the extrabranchial cartilages (dorsally and ventrally), the origins of the innermost fibers on the arch cartilages (dorsally the epibranchial and ventrally the ceratobranchial) and the insertions on the extrabranchial cartilages, which give these muscles a rather fragile aspect. Fibers have different sizes, the innermost are smaller than the outermost, and are oriented in a semicircular manner, on the posterior surface of the arch. Fibers loosely united, with no spaces between them.

-*m. coracoarcualis communis*: Triangular, bulky muscle with rounded margins. Its origin is on the coracoid bar through a tendon. Its insertion is on an anterior muscle (the *m. coracohyoideus*) through connective tissue. Fibers are oriented anteriorly.

-*m. coracobranchiales*: Five muscles present, one for each branchial arch. The anterior four are small cylindrical muscles (1-4) and the last has a laminar shape. Their origins are on the *m. coracoarculis communis*. The fifth originates from the coracoid bar near the pectoral fin insertion and the pericardic membrane. Their insertions are through a tendon on the 1-3 hypobranchial cartilages, the cardiobranchial and the fifth ceratobranchial, respectively. Fibers are directed anteriorly and slightly upwards when close to the insertion. On the fifth muscle, the fibers are oblique anterodorsally.

Centrophorus uyato

-*m. constrictores branchiales superficiales*: These muscles are as described in *Centrophorus squamosus*.

-*m. trapezius*: This muscle is as described in *Centrophorus squamosus*.

-*m. adductores arcuum branchialium*: These muscles are as described in *Centrophorus squamosus*.

-*m. interpharyngobranchiales*: These muscles are as described in *Centrophorus squamosus*.

-*m. arcuales dorsales*: These muscles are as described in *Centrophorus squamosus*.

-*m. interbranchiales*: These muscles are as described in *Centrophorus squamosus*.

-*m. coracoarcualis communis*: This muscle is as described in *Centrophorus squamosus*.

-*m. coracobranchiales*: These muscles are as described in *Centrophorus squamosus*.

Dalatiidae

Dalatias licha (FIG. 26; MZUSP uncat., 323mm)

-*m. constrictores branchiales superficiales*: Four pairs of these muscles are present, one pair for each arch, except the fifth arch that lacks this muscle. Laminar muscles that lay beneath the skin in the branchial region, posterior to the first branchial opening. Origin and insertion are through an aponeurosis, the dorsal origin with an tendon-like aponeurotic layer, which covers the anterior half of the *m. trapezius*, and the ventral insertion occurs lateral to the posterior region of the *m. coracomandibularis*. The fibers of the portion dorsal to the gill slits are directed downwards. The fibers of the portion which forms the wall of the gill pouches pass dorsoventrally with a slight arch where it meets the dorsal and ventral portions of the muscle. The fibers of the portion ventral to the gill slits are directed downwards.

-*m. trapezius*: Laminar muscle with a triangular shape due to its insertions. Its origin is in an aponeurosis common to the *m. constrictor branchiales superficiales*. Its origin is on the Its insertions are on two distinct points (also called a digastric muscle), the dorsal surface of the scapular process of the pectoral girdle through a thick layer of dense connective tissue, and the dorsal surface of the fifth epibranchial through connective tissue. Fibers are oriented oblique posteriorventrally to the main axis of the body (between 50°-60°).

-*m. adductores arcuum branchialium*: Five pairs of these muscles are present, one pair for each arch, except the fifth arch that lacks this muscle. Small, triangular-shaped muscles, which are restricted to the area of the epibranchial-ceratobranchial articulation. Their origins are on the epibranchial. Their insertions are on the ceratobranchial. The origins and insertions occur without the presence of dense

connective tissue. Fibers are oriented downward with a slight curve towards the insertions.

-*m. interpharingobranchiales*: Three pairs of these slender, laminar muscles are present, located between the first and second pharyngobranchials, the second and third pharyngobranchials and the third and fourth pharyngobranchials. All three are connective structures. Their origins are on the ventroposterior margin of a pharyngobranchial through connective tissue. Their insertions are on the anterodorsal margin of the next pharyngobranchial also through connective tissue. Fibers are oriented slightly obliquely to the pharyngobranchial axis (near 20°).

-*m. arcuales dorsales*: Four pairs of these rectangular, somewhat bulky muscles are present, one pair for each arch, except the fifth arch that lacks this muscle. Their origins are on a posteroventral groove on the pharyngobranchial of the arch and the adjacent pharyngobranchial (two origins). Only the fourth has a single origin on the fourth pharyngobranchial and on a posterior process of the same (fifth pharyngobranchial?). Their insertions are on the anterodorsal surface of the epibranchial on the dorsal third, both through a connective margin. Fibers directed downward.

-*m. interbranchiales*: Four pairs are present, one for each gill arch. They lay within a holobranch on the anterior face of the gill rays. Slender muscle with a semi-elliptical shape, with the thickness of a gill ray. The origins and insertions of the outermost fibers are both on the extrabranchial cartilages (dorsally and ventrally), the origins of the innermost fibers on the arch cartilages (dorsally the epibranchial and ventrally the ceratobranchial) and the insertions on the extrabranchial cartilages, which give these muscles a rather fragile aspect. Fibers have different sizes, the innermost are smaller than the outermost, and are oriented in a semicircular manner, on the posterior surface of the arch. Fibers tightly united, with no spaces between them.

-*m. coracoarcualis communis*: Triangular, very bulky muscle with rounded margins. It has a few septa which gives a segmented aspect. Its origin is on the coracoid bar through a tendon. Its insertion is on an anterior muscle (the *m. coracohyoideus*) through connective tissue. Fibers are oriented anteriorly.

-*m. coracobranchiales*: Five muscles present, one for each branchial arch. The anterior four are small cylindrical muscles (1-4) and the last has a laminar shape. Their origins are on the pericardic membrane. The fifth originates from the coracoid bar near the pectoral fin insertion. Their insertions are through a tendon on the 1-3 hypobranchial cartilages, the cardiobranchial and the fifth ceratobranchial, respectively. Only the tips of these muscles are recognizable as individual parts, since the rest of them is finely divided from one another. Fibers are directed anteriorly and slightly upwards when close to the insertion. On the fifth muscle, the fibers are oblique anterodorsally.

Etmopteridae

Centroscyllium nigrum (FIG. 27; USNM 220270, 367mm)

-*m. constrictores branchiales superficiales*: Four pairs of these muscles are present, one pair for each arch, except the fifth which lacks these muscles. Laminar muscles that lay beneath the skin in the branchial region, posterior to the first branchial opening. Origin and insertion are through an aponeurosis, the dorsal origin with a tendon-like aponeurotic layer, which covers the anterior two thirds of the *m. trapezius*, and the ventral insertion occurs lateral to the posterior region of the *m. coracomandibularis*. The fibers of the portion dorsal to the gill slits are directed downwards. The fibers of the portion which forms the wall of the gill pouches pass dorsoventrally with a slight arch where it meets the dorsal and ventral portions of the muscle. The fibers of the portion ventral to the gill slits are directed downwards.

-*m. trapezius*: Laminar muscle with a triangular shape due to its insertions. The muscle has a cleavage which divides it into two portions, one anterior and one posterior. The anterior portion has a triangular shape and is half the size of the posterior portion, which also has a triangular shape. Its origin is in an aponeurosis common to the *m. constrictor branchiales superficiales*. Its insertions are on two distinct points (also called a digastric muscle), the dorsal surface of the scapular process of the pectoral girdle through a thick layer of dense connective tissue, and the

dorsal surface of the fifth epibranchial through connective tissue. Fibers are oriented oblique posteriorventrally to the main axis of the body (between 50°-60°).

-*m. adductores arcuum branchialium*: Five pairs of these muscles are present, one pair for each arch, except the fifth arch that lacks this muscle. Small, triangular-shaped muscles, which are restricted to the area of the epibranchial-ceratobranchial articulation. Their origins are on the epibranchial. Their insertions are on the ceratobranchial. The origins and insertions occur without the presence of dense connective tissue. Fibers are oriented downward with a slight curve towards the insertions.

-*m. interpharingobranchiales*: Three pairs of these slender, laminar muscles are present, located between the first and second pharyngobranchials, the second and third pharyngobranchials and the third and fourth pharyngobranchials. The third is a connective structure. Their origins are on the ventroposterior margin of a pharyngobranchial through connective tissue. Their insertions are on the anterodorsal margin of the next pharyngobranchial also through connective tissue. Fibers are oriented slightly obliquely to the pharyngobranchial axis (near 10°).

-*m. arcuales dorsales*: Four pairs of these rectangular, somewhat bulky muscles are present, one pair for each arch, except the fifth arch that lacks this muscle. Their origins are on a posteroventral groove on the pharyngobranchial of the arch and the adjacent pharyngobranchial (two origins). Only the fourth has a single origin on the fourth pharyngobranchial and on a posterior process of the same (fifth pharyngobranchial?). Their insertions are on the anterodorsal surface of the epibranchial on the dorsal third, both through a connective margin. Fibers directed downward.

-*m. interbranchiales*: Four pairs are present, one for each gill arch. They lay within a holobranch on the anterior face of the gill rays. Slender muscle with a semi-elliptical shape, with the thickness of a gill ray. The origins and insertions of the outermost fibers are both on the extrabranchial cartilages (dorsally and ventrally), the origins of the innermost fibers on the arch cartilages (dorsally the epibranchial and ventrally the ceratobranchial) and the insertions on the extrabranchial cartilages, which give these muscles a rather fragile aspect. Fibers have different sizes, the innermost are smaller

than the outermost, and are oriented in a semicircular manner, on the posterior surface of the arch. Fibers loosely united, with no spaces between them.

-*m. coracoarcualis communis*: Triangular, bulky muscle with rounded margins. It has a few septa which gives a segmented aspect. Its origin is on the coracoid bar through a tendon. Its insertion is on an anterior muscle (the *m. coracohyoideus*) through connective tissue. Fibers are oriented anteriorly.

-*m. coracobranchiales*: Five muscles present, one for each branchial arch. The anterior four are small cylindrical muscles (1-4) and the last has a laminar shape. Their origins are on the pericardic membrane. The fifth originates from the coracoid bar near the pectoral fin insertion. Their insertions are through a tendon on the 1-3 hypobranchial cartilages, the cardiobranchial and the fifth ceratobranchial, respectively. Fibers are directed anteriorly and slightly upwards when close to the insertion. On the fifth muscle, the fibers are oblique anterodorsally.

Etmopterus polli

-*m. constrictores branchiales superficiales*: These muscles are as described in *Centroscyllium nigrum*, except its origin covers the anterior three quarters of the *m. trapezius,* the fibers of the portion dorsal to the gill slits are directed slightly obliquely, anteroventrally in relation to the main axis of the body and the fibers of the portion ventral to the gill slits are directed posteroventrally in a mirrored fashion to the dorsal fibers.

-*m. trapezius*: These muscles are as described in *Centroscyllium nigrum,* except it has a cleavage that divides the muscle in two portions, one anterior with tringular elongated shape that is one third the size of the posterior, also of triagular shap, the insertions are divided by a small raphe and the fibers are oriented obliquely to the main axis of the body (between 45°-55° posteriorly).

-*m. adductores arcuum branchialium*: These muscles are as described in *Centroscyllium nigrum*.

-*m. interpharingobranchiales*: These muscles are as described in *Centroscyllium nigrum*.

-*m. arcuales dorsales*: These muscles are as described in *Centroscyllium nigrum*, except these are very slender muscles.

-*m. interbranchiales*: These muscles are as described in *Centroscyllium nigrum*.

-*m. coracoarcualis communis*: These muscles are as described in *Centroscyllium nigrum*, except it does not have the marked septa.

-*m. coracobranchiales*: These muscles are as described in *Centroscyllium nigrum*, except the fifth originates from the coracoid bar farther of the pectoral fin.

Somniosidae

Centroscymnus coelolepis

-*m. constrictores branchiales superficiales*: Four pairs of these muscles are present, one pair for each arch, except the fifth arch that lacks this muscle. Laminar muscles that lay beneath the skin in the branchial region, posterior to the first branchial opening. Origin and insertion are through an aponeurosis, the dorsal origin with a tendon-lile aponeurotic layer, which covers the lower half of the *m. trapezius*, and the ventral insertion occurs lateral to the posterior region of the *m. coracomandibularis*. The fibers of the portion dorsal to the gill slits are directed obliquely, anteroventrally in relation to the main axis of the body. The fibers of the portion which forms the wall of the gill pouches pass dorsoventrally with a slight arch where it meets the dorsal and ventral portions of the muscle. The fibers of the portion ventral to the gill slits are directed posteroventrally in a mirrored fashion to the dorsal fibers.

-*m. trapezius*: Laminar muscle with a triangular shape due to its insertions. The muscle has a triangular shape. Its origin is in an aponeurosis common anteriorly to the *m. constrictor branchiales superficiales*. Its insertions are on two distinct points (also called a digastric muscle), the dorsal surface of the scapular process of the pectoral

girdle through a tendon, and the dorsal surface of the fifth epibranchial through connective tissue. Fibers are oriented obliquely to the main axis of the body (between 55°-65° posteriorly).

-*m. adductores arcuum branchialium*: Five pairs of these muscles are present, one pair for each arch, except the fifth arch that lacks this muscle. Small, triangular-shaped muscles, which are restricted to the area of the epibranchial-ceratobranchial articulation. Their origins are on the epibranchial. Their insertions are on the ceratobranchial. The origins and insertions occur without the presence of dense connective tissue. Fibers are oriented downward with a slight curve towards the insertions.

-*m. interpharingobranchiales*: Three pairs of these slender, laminar muscles are present, located between the first and second pharyngobranchials, the second and third pharyngobranchials and the third and fourth pharyngobranchials. The third is a connective tendon-like structure. Their origins are on the ventroposterior margin of a pharyngobranchial through connective tissue. Their insertions are on the anterodorsal margin of the next pharyngobranchial also through connective tissue. Fibers are oriented slightly obliquely to the pharyngobranchial axis (near 10°).

-*m. arcuales dorsales*: Four pairs of these rectangular, somewhat bulky muscles are present, one pair for each arch, except the fifth arch that lacks this muscle. Their origins are on a posteroventral groove on the pharyngobranchial of the arch and the adjacent pharyngobranchial (two origins). Only the fourth has a single origin on the fourth pharyngobranchial and on a posterior process of the same (fifth pharyngobranchial?). Their insertions are on the anterodorsal surface of the epibranchial on the dorsal third, both through a connective margin. Fibers directed downward.

-*m. interbranchiales*: Four pairs are present, one for each gill arch. They lay within a holobranch on the anterior face of the gill rays. Slender muscle with a semi-elliptical shape, with the thickness of a gill ray. The origins and insertions of the outermost fibers are both on the extrabranchial cartilages (dorsally and ventrally), the origins of the innermost fibers on the arch cartilages (dorsally the epibranchial and ventrally the ceratobranchial) and the insertions on the extrabranchial cartilages, which give these

muscles a rather fragile aspect. Fibers have different sizes, the innermost are smaller than the outermost, and are oriented in a semicircular manner, on the posterior surface of the arch. Fibers loosely united, with no spaces between them.

-*m. coracoarcualis communis*: Triangular, bulky muscle with rounded margins. It has a few septa which gives a segmented aspect. Its origin is on the coracoid bar through a tendon. Its insertion is on an anterior muscle (the *m. coracohyoideus*) through connective tissue. Fibers are oriented anteriorly.

-*m. coracobranchiales*: Five muscles present, one for each branchial arch. The anterior four are small cylindrical muscles (1-4) and the last has a laminar shape. Their origins are on the pericardic membrane. Their insertions are through a tendon on the 1-3 hypobranchial cartilages, the cardiobranchial and the fifth ceratobranchial, respectively. Fibers are directed anteriorly and slightly upwards when close to the insertion. On the fifth muscle, the fibers are oblique anterodorsally.

Scymnodon obscurus (FIG. 28; USNM 220509, 361mm)

-*m. constrictores branchiales superficiales*: These muscles are as described in *Centroscymnus coelolepis*, except its covers the anterior quarter of the *m. trapezius*.

-*m. trapezius*: This muscle is as described in *Centroscymnus coelolepis*.

-*m. adductores arcuum branchialium*: These muscles are as described in *Centroscymnus coelolepis*.

-*m. interpharingobranchiales*: These muscles are as described in *Centroscymnus coelolepis*.

-*m. arcuales dorsales*: These muscles are as described in *Centroscymnus coelolepis*.

-*m. interbranchiales*: These muscles are as described in *Centroscymnus coelolepis*.

-*m. coracoarcualis communis*: This muscle is as described in *Centroscymnus coelolepis*.

-*m. coracobranchiales*: These muscles are as described in *Centroscymnus coelolepis*, except the fifth originates from the coracoid bar.

Squalidae

Squalus albicaudatus

-*m. constrictores branchiales superficiales*: Four pairs of these muscles are present, one pair for each arch, except the fifth arch that lacks this muscle. Laminar muscles that lay beneath the skin in the branchial region, posterior to the first branchial opening. Origin and insertion are through an aponeurosis, the dorsal origin with a tendon-like aponeurotic layer, which covers the anterior half of the *m. trapezius*, and the ventral insertion occurs lateral to the posterior region of the *m. coracomandibularis* and covers this muscle anteriorly. The fibers of the portion dorsal to the gill slits are directed obliquely, anteroventrally in relation to the main axis of the body. The fibers of the portion which forms the wall of the gill pouches pass dorsoventrally with a slight arch where it meets the dorsal and ventral portions of the muscle. The fibers of the portion ventral to the gill slits are directed posteroventrally in a mirrored fashion to the dorsal fibers.

-*m. trapezius*: Laminar muscle with a triangular shape due to its insertions. The muscle has a triangular shape. Its origin is in an aponeurosis common anteriorly to the *m. constrictor branchiales superficiales*. Its insertions are on two distinct points (also called a digastric muscle), the dorsal surface of the scapular process of the pectoral girdle through a tendon, and the dorsal surface of the fifth epibranchial through connective tissue. Fibers are oriented obliquely to the main axis of the body (between 55°-65° posteriorly).

-*m. adductores arcuum branchialium*: Five pairs of these muscles are present, one pair for each arch. Small, triangular-shaped muscles, which are restricted to the area of the epibranchial-ceratobranchial articulation. Their origins are on the epibranchial. Their insertions are on the ceratobranchial. The origins and insertions occur without the presence of dense connective tissue. Fibers are oriented downward with a slight curve towards the insertions.

-*m. interpharingobranchiales*: Three pairs of these slender, laminar muscles are present, located between the first and second pharyngobranchials, the second and third pharyngobranchials and the third and fourth pharyngobranchials. Their origins are on the ventroposterior margin of a pharyngobranchial through connective tissue. Their insertions are on the anterodorsal margin of the next pharyngobranchial also through connective tissue. Fibers are oriented slightly obliquely to the pharyngobranchial axis (near 10°).

-*m. arcuales dorsales*: Four pairs of these rectangular, somewhat bulky muscles are present, one pair for each arch, except the fifth arch that lacks this muscle. Their origins are on a posteroventral groove on the pharyngobranchial of the arch and the adjacent pharyngobranchial (two origins). Only the fourth has a single origin on the fourth pharyngobranchial and on a posterior process of the same (fifth pharyngobranchial?). Their insertions are on the anterodorsal surface of the epibranchial on the dorsal third, both through a connective margin. Fibers directed downward.

-*m. interbranchiales*: Four pairs are present, one for each gill arch. They lay within a holobranch on the anterior face of the gill rays. Slender muscle with a semi-elliptical shape, with the thickness of a gill ray. The origins and insertions of the outermost fibers are both on the extrabranchial cartilages (dorsally and ventrally), the origins of the innermost fibers on the arch cartilages (dorsally the epibranchial and ventrally the ceratobranchial) and the insertions on the extrabranchial cartilages, which give these muscles a rather fragile aspect. Fibers have different sizes, the innermost are smaller than the outermost, and are oriented in a semicircular manner, on the posterior surface of the arch. Fibers tightly united, with no spaces between them.

-*m. coracoarcualis communis*: Triangular, bulky muscle with rounded margins. It has a few septa which gives a segmented aspect. Its origin is on the coracoid bar through a tendon. Its insertion is on an anterior muscle (the *m. coracohyoideus*) through connective tissue. Fibers are oriented anteriorly.

-*m. coracobranchiales*: Five muscles present, one for each branchial arch. The anterior four are small cylindrical muscles (1-4) and the last has a laminar shape. Their origins are on the pericardic membrane. The fifth originates from the coracoid

bar. Their insertions are through a tendon on the 1-3 hypobranchial cartilages, the cardiobranchial and the fifth ceratobranchial, respectively. Fibers are directed anteriorly and slightly upwards when close to the insertion. On the fifth muscle, the fibers are oblique anterodorsally.

6. Hexanchiformes

The muscle that compresses the esophagus and is associated with the last branchial arch covers the exterior surface of the esophagus and has a circular disposition of fibers. No variation in this muscle was observed among the hexanchiform species examined. It is called *m. constrictor oesophagi*.

Hexanchidae

Heptranchias perlo

-*m. constrictores branchiales superficiales*: Six pairs of these muscles are present, one pair for each arch, except the seventh arch that lacks these muscles. Laminar muscles that lay beneath the skin in the branchial region, posterior to the first branchial opening. Origin and insertion are through an aponeurosis, the dorsal origin with a tendon-like aponeurotic layer, which covers the anterior half of the *m. trapezius*, and the ventral insertion occurs lateral to the posterior region of the *m. coracomandibularis*. The fibers of the portion which forms the wall of the gill pouches pass dorsoventrally with a slight arch where it meets the ventral portion of the muscle. The fibers of the portion ventral to the gill slits are directed downwards. There are no fibers on the dorsal region.

-*m. trapezius*: Laminar muscle with a triangular shape due to its insertions. The muscle has a cleavage which divides it into two portions near the insertion, one anterior and one posterior. The anterior portion has a triangular shape and is one quarter the size of the posterior portion, which has a triangular shape. Its origin is in

an aponeurosis common to the *m. constrictor branchiales superficiales*. Its insertions are on two distinct points (also called a digastric muscle), the dorsal surface of the scapular process of the pectoral girdle near the articulation of the pectoral fin through a thin layer of dense connective tissue, and the dorsal surface of the fifth epibranchial through connective tissue. Fibers are oriented nearly transversely to the main axis of the body (between 75°-85° posteriorly on the anterior part and between 65°-80° posteriorly on the posterior part).

-*m. adductores arcuum branchialium*: Seven pairs of these muscles are present, one pair for each arch. Small, triangular-shaped muscles, which are restricted to the area of the epibranchial-ceratobranchial articulation. Their origins are on the epibranchial. Their insertions are on the ceratobranchial. The origins and insertions occur without the presence of dense connective tissue. Fibers are oriented downward with a slight curve towards the insertions.

-*m. interpharingobranchiales*: Five pairs of these slender, laminar muscles are present, between the first and second pharyngobranchials, the second and third pharyngobranchials, the third and fourth pharyngobranchials, the fourth and fifth pharyngobranchials and the fifth and sixth pharyngobranchials. Their origins are on the ventroposterior margin of a pharyngobranchial through connective tissue. Their insertions are on the anterodorsal margin of the next pharyngobranchial also through connective tissue. Fibers are oriented slightly obliquely to the pharyngobranchial axis (near 10°).

-*m. arcuales dorsales*: Six pairs of these triangular-shaped, slender muscles are present, one pair for each arch, except the fifth arch that lacks this muscle. Their origins are on a posteroventral groove on the pharyngobranchial of the arch and the adjacent pharyngobranchial (two origins). Only the sixth has a single origin on the sixrth pharyngobranchial and on a posterior process of the same (seventh pharyngobranchial?). Their insertions are on the anterodorsal surface of the epibranchial on the dorsal third, both through a connective margin. Fibers directed downward.

-*m. interbranchiales*: Six pairs are present, one for each gill arch. They lay within a holobranch on the anterior face of the gill rays. Slender muscle with a semi-elliptical

shape, with the thickness of a gill ray. The origins and insertions of the outermost fibers are both on the extrabranchial cartilages (dorsally and ventrally), the origins of the innermost fibers on the arch cartilages (dorsally the epibranchial and ventrally the ceratobranchial) and the insertions on the extrabranchial cartilages, which give these muscles a rather fragile aspect. Fibers have different sizes, the innermost are smaller than the outermost, and are oriented in a semicircular manner, on the posterior surface of the arch. Fibers tightly united, with no spaces between them.

-*m. coracoarcualis communis*: Triangular, bulky muscle with rounded margins. It has a few septa which gives a segmented aspect. Its origin is on the coracoid bar through a tendon. Its insertion is on an anterior muscle (the *m. coracohyoideus*) through connective tissue. Fibers are oriented anteriorly.

-*m. coracobranchiales*: Seven muscles present, one for each branchial arch. The anterior six are small cylindrical muscles (1-6) and the last has a laminar shape. Their origins are on the pericardic membrane. The seventh originates from the coracoid bar. Their insertions are through a tendon on the 1-5 hypobranchial cartilages, the cardiobranchial and the seventh ceratobranchial, respectively. Fibers are directed anteriorly and slightly upwards when close to the insertion. On the seventh muscle, the fibers are oblique anterodorsally.

Notorynchus cepedianus (FIG. 29; CAS 39612, 565mm)

-*m. constrictores branchiales superficiales*: These muscles are as decribed in *Heptranchias perlo*, except that the fibers of the portion dorsal to the gill slits are slightly oblique anteroventrally.

-*m. trapezius*: These muscles are as decribed in *Heptranchias perlo*, except that the anterior portion has a triangular shape and is half the size of the posterior portion, which has a triangular shape and the fibers are oriented nearly transversely to the main axis of the body (between 60°-70°).

-*m. adductores arcuum branchialium*: These muscles are as decribed in *Heptranchias perlo*.

-*m. interpharingobranchiales*: These muscles are as decribed in *Heptranchias perlo*.

-*m. arcuales dorsales*: These muscles are as decribed in *Heptranchias perlo*.

-*m. interbranchiales*: These muscles are as decribed in *Heptranchias perlo*.

-*m. coracoarcualis communis*: These muscles are as decribed in *Heptranchias perlo*.

-*m. coracobranchiales*: These muscles are as decribed in *Heptranchias perlo*.

7. Batoidea: Rhinobatiformes

The muscle that compresses the esophagus and is associated with the last branchial arch covers the exterior surface of the esophagus and has a circular disposition of fibers. It is called *m. constrictor oesophagi*.

Zapteryx brevirostris (FIG. 30; MZUSP uncat., 476mm)

-*m. constrictores branchiales superficiales*: Four pairs of these muscles are present, one pair for each arch, except the fifth arch that lacks this muscle. Laminar muscles that lay beneath the skin in the branchial region, posterior to the first branchial opening. Origin and insertion are through an aponeurosis, the dorsal origin with a tendon-like aponeurotic layer, on the anterior branchial arch, and the ventral insertion occurs onto the mid-region of the posterior gill pouch. The muscle extends from the anterior one third of the *m. trapezius* until the lateral margin of the *coracomandibularis*. The fibers of the portion dorsal to the gill slits are directed forwards. The fibers of the portion ventral to the gill slits are directed forwards.

-*m. trapezius*: Laminar muscle with a triangular shape due to its insertions. The muscle has a raphe present which divides it into two portions near the insertions. Its origin is in an aponeurosis common to the *m. constrictor branchiales superficiales*. Its insertions are on two distinct points (also called a digastric muscle), the dorsal surface of the scapular process of the pectoral girdle through a thick layer of dense connective tissue, and the dorsal surface of the fifth epibranchial through connective tissue.

Fibers are oriented oblique posteriorventrally to the main axis of the body (between 75°-85°).

-*m. adductores arcuum branchialium*: Five pairs of these muscles are present, one pair for each arch. Small, triangular-shaped muscles, which are restricted to the area of the epibranchial-ceratobranchial articulation. Their origins are on the epibranchial. Their insertions are on the ceratobranchial. The origins and insertions occur without the presence of dense connective tissue. Fibers are oriented downward with a slight curve towards the insertions.

-*m. interpharingobranchiales*: Three pairs of these muscles are present, located between the first and second pharyngobranchials, the second and third pharyngobranchials and the third and fourth pharyngobranchials. All three are connective structures. Slender, laminar muscles. Their origins are on the ventroposterior margin of a pharyngobranchial through connective tissue. Their insertions are on the anterodorsal margin of the next pharyngobranchial also through connective tissue. Fibers are oriented slightly obliquely to the pharyngobranchial axis (near 20°).

-*m. arcuales dorsales*: Four pairs of these muscles are present, one pair for each arch, except the fifth arch that lacks this muscle. Rectangular, very slender muscles. Their origin is on a posteroventral groove on the pharyngobranchial of the arch and the adjacent pharyngobranchial. Their insertions are on the anterodorsal surface of the epibranchial on the dorsal third, both through a connective margin. Fibers directed downward.

-*m. interbranchiales*: Four pairs are present, one for each gill arch. They lay within a holobranch on the anterior face of the gill rays. Slender muscle with a semi-elliptical shape, with the thickness of a gill ray. The origins and insertions of the outermost fibers are both on the extrabranchial cartilages (dorsally and ventrally), the origins of the innermost fibers on the arch cartilages (dorsally the epibranchial and ventrally the ceratobranchial) and the insertions on the extrabranchial cartilages, which give these muscles a rather fragile aspect. Fibers have different sizes, the innermost are smaller than the outermost, and are oriented in a semicircular manner, on the posterior surface of the arch. Fibers tightly united, with no spaces between them.

-*m. coracoarcualis communis*: Trapezoid, bulky muscle with rounded margins. It has a few septa which gives a segmented aspect. Its origin is on the coracoid bar through a tendon. Its insertion is on an anterior muscle (the *m. coracohyoideus*) through connective tissue. Fibers are oriented anteriorly.

-*m. coracobranchiales*: Five muscles present, one for each branchial arch. The anterior four are small cylindrical muscles (1-4) and the last has a laminar shape. Their origins are on the pericardic membrane. The fifth originates from the coracoid bar near the pectoral fin insertion. Their insertions are through a tendon on the 1-3 hypobranchial cartilages, the cardiobranchial and the fifth ceratobranchial, respectively. Fibers are directed anteriorly and slightly upwards when close to the insertion. On the fifth muscle, the fibers are oblique anterodorsally.

8. Summary of the variations within each muscle

- *m. constrictores branchiales superficiales*: these muscles are delimited ventrally by a medial septum in lamniform and carcharhiniform (except pentanchids) taxa and in parascyllids, orectolobids and squalids, which divides left and right sides. In orectolobiforms (except for parascyllids and orectolobids) and heterodontiforms, the muscle inserts onto the *m. coracomandibularis*, what also means the muscles do not possess the medial septum in these animals, as well as in squalomorph sharks. Although the images are not clear as to the limits of these components on the superficial illustrations, the divisions are quite easy to see in most animals with the specimen on hands.

- *m. trapezius*: this muscle is most commonly slender, divided into two rami, the anterior smaller and triangular, the posterior larger and trapezoidal; the anterior inserts onto the fifth epibranchial and the posterior onto the scapular process of the pectoral girdle. In Squaliformes, the insertions are kept, and the division is lost; this disposition pulls the fifth epibranchial closer to the pectoral girdle. In Orectolobiformes and Heterodontiformes, this muscle has lost the anterior portion, inserting only onto the scapular process. In Sphyrnidae, the posterior part is clearly rounded in its posterodorsal margin.

- *m. adductores arcuum branchialium*: these muscles are most commonly triangular, with their origin on the epibranchial and insertion onto the ceratobranchial. In Carcharhiniformes except for Pentanchidae, Proscyllidae and Scyliorhinidae and in Lamniformes except for Lamnidae and Odontaspididae, these muscles have a crescent shape.

- *m. interpharingobranchiales*: these muscles connect two consecutive pharyngobranchial cartilages and do not vary much in shape, only on the fibers orientation (more oblique or less oblique in relation to the pharyngobranchial axis). In *Dalatias licha* and *Hemiscyllium ocellatum*, all the components of the series are tendinous, with no muscular tissue. In Etmopteridae, *Centroscyllium*, *Orectolobus maculatus* and *Cirrhoscyllium formosanum*, the last component of the series is tendinous, and the other have muscular tissue

- *m. arcuales dorsales*: in galeomorphs, this muscle is a simple slip, slender in lamniforms and carcharhiniforms and bulkier in heterodontiforms and orectolobiforms. In squalomorphs, it is divided in two rami and inserts onto the pharyngobranchial of the same and the next arch, originating from the epibranchial. In *Zapteryx*, it has only a single, slender slip.

- *m. interbranchiales*: these muscles have most commonly tightly united fibers in a semicircular pattern. In pentanchids, centrophorids, etmopterids and somniosids, the fibers are more loosely united, some pentanchids possessing spaces between the fibers.

- *m. coracoarcualis communis*: this muscle has two configurarions: with or without visible septa; both are distributed among all groups observed in this study.

- *m. coracobranchiales 1-5*: these muscles are most commonly cylindrical and the last is slender and laminar; in carcharhiniforms, except scyliorhinids, and in pseudocarchariids and odontaspidids, the fifth muscle has an extra ramus, both rami inserting on the fifth ceratobranchial.

- *m. constrictor oesophagi*: the muscle envelops the oesophagus, the only difference is on *Mitsukurina owstoni*, which has this muscle reduced when compared to the other elasmobranch taxa.

- *m. pharyngobranchiales n-epibranchiales n+1*: only present in two taxa, *Eusphyra blochi* has just the first (*m. pharyngobranchialis 1-epibranchialis 2*) and *Pseudocarcharias kamoharai* has three pairs of these muscles between the pharyngobranchial and the epibranchial of the next arch.

Discussion

The muscles examined in this study were generally conservative among the taxa analyzed, but significant differences were observed. Such differences are present at the level of families and orders, with species and genera being usually similar in overall morphology. This condition is similar to observations made in previous studies (e.g. Soares & Carvalho, 2013a, b). No character was found that suggests a cohese galeomorph group, although some of the characters described below indicate close relationships between orders of this group. The same happens when we consider other studies that evaluated the musculature (Shirai, 1992; Soares & Carvalho, 2013a,b). A formal phylogenetic analisys would be recquired to better assess this question.

1. *Musculi constrictores branchiales superficiales*

The presence of a medial ventral raphe dividind the left and right antimeres of the *m. constrictores branchiales superficiales*, present in all lamniform families and almost all carcharhiniform families, except for pentanchids, supports the closer relationship between these orders (Compagno, 1988; Wilga, 2005; Naylor et al., 2012), since the basal families have the same character state, or a convergence due to the closer habitats both orders live in (Compagno, 1990). All other orders have the condition where the antimeres are well separated in almost all other groups, except for two orectoloboid families (Orectolobidae and Parascyllidae) and squalids. The latter is probably a convergence, since squalids have never been considered as closely related to either Carcharhiniformes or Lamniformes. Concerning the orectoloboid taxa, the presence of the medial raphe is interesting because Goto (2001) suggested that the families presenting the raphe are the basal clades within Orectolobiformes (Fig. 34). If that is the case, the presence of this charater, shared with lamniform and carcharhiniform taxa, could indicate a closer relationship between these three orders when compared to heterodontiforms, the other galeomorph group.

2. *Musculus trapezius*

The *m. trapezius* connects the pectoral girdle to the neurocranium and is a laminar, broad and relatively thin muscle sheet. The most common form of this muscle, found in galeomorph and squalomorph shark alike, is to have two rami, either completely or partially separated, with the anterior ramus inserting onto the fifth epibranchial and the posterior ramus onto the scapular process of the girdle.

This arrangement is found in all studied groups except for Heterodontiformes and Orectolobiformes. In these groups, it was not possible to see any raphe dividing the muscle as in other galeomorph orders. Also, the insertion on the epibranchial is absent in these orders, and the muscle inserted only on the scapular process. Regarding its shape, the *m. trapezius* is bulkier, narrower and thicker in both orders compared to other groups. This supports the idea present in some morphological studies that these orders are closely related (Compagno, 1973; Soares & Carvalho, 2013a). In this case, the evidence would be the convergence in the overall shape of this muscle (smaller and bulkier) and the lack of an insertion onto the epibranchial, both restricted to these two orders. The presence of the two rami in lamniform and carcharhiniforms can be a convergence to the pattern found in Squalomorphi.

Squaliformes also had a different arrangement for this muscle, which was laminar but without the subdivision into two rami. Still they retained the insertion on the epibranchial, with the posterior fibers in close contact to the ones inserting onto the fifth epibranchial. The squaliform families do not have any kind of raphe visible on this muscle as in carcharhiniforms, lamniforms and hexanchiforms. This is the same disposition found by the study of Shirai (1992).

Among the Carcharhiniformes, there is one family that is slightly different. Sphyrnids possess a rather fragile *m. trapezius,* and it was not possible to completely dissect this musculature from the *m. constrictores branchiales superficiales,* whereas all other representatives of the order were relatively easier to dissect. This morphology made it more challenging to observe the overall shape of the muscle, although it is similar to the musculature of other carcharhiniform families.

The batoidean dissected herein, *Zapteryx,* illustrates how this muscle is in rays. Although Miyake et al. (1992) observed this region, the study focused on the ventral region. Therefore, no description of the *m. trapezius* was made, since this is a dorsal muscle.

3. *Musculi adductores arcuum branchialium*

There are two basic shapes of this muscle: crescent-shaped and triangular-shaped. The crescent shape is present only in Carcharhiniformes and Lamniformes but not in all families of these orders. Alopiidae, Mitsukurinidae and Pseudocarchariidae (lamniforms) have the crescent shaped form, and Lamnidae and Odontaspididae have the triangular shaped form. Among Carcharhiniformes, Scyliorhinidae, Leptochariidae, Hemigaleidae, Sphyrnidae (except *Eusphyra blochii*) and Carcharhinidae (except *Galeocerdo cuvier*, *Loxodon macrorhinus* and *Triaenodon obesus*) have the crescent shape, and Pentanchidae, Proscyllidae and Triakidae, with the exceptions in Sphyrnidae and Carcharhinidae, have the triangular shape. Since the crescent shape is restricted to lamniforms and carcharhiniforms, this could also indicate a closer relationship of these orders. This restricted muscular character (crescent-shaped muscles) also corroborates a closer relationship between lamnids and odontaspidids, and indicates a possible closer relationship between pentanchids and proscyllids when compared to scyliorhinids, since all analyzed pentanchids and proscyllids have both triangular shaped muscles and all analyzed scyliorhinids, crescent shaped muscles. This evidence supports the division of Scyliorhinidae *sensu* Compagno (1988) in at least two families, Pentanchidae and Scyliorhinidae *sensu* Naylor et al. (2012). Further data are recquired about the “scyliorhinids” in order to better understand their interrelations within the family and with other families.

4. *Musculi interpharyngobranchiales*

In some shark groups, the muscles that connect two adjacent pharyngobranchial cartilages are tendinous. In *Dalatias licha*, all the three components uniting the pharyngobranchial cartilages are composed of connetive tissue, with no evidence of muscular tissue. In Etmopteridae and *Centroscyllium*, only the third component is made of connective tissue, as in the orectolobiform sharks *Cirrhoscyllium* and *Orectolobus*, which have the third component tendinous. *Hemiscyllium* has all three components observed as in *Dalatias licha*.

The tendinous condition present in some families could indicate a closer relationship between them, the families Dalatiidae, Etmopteridae and Somniosidae among the Squaliformes and between Orectolobidae and Parascylliidae among the Orectolobiformes. This is probable because the limited distribution of this character (tendinous slips between pharyngobranchials). Since *Chiloscyllium* does not have the tendinous condition present in *Hemiscyllium* and both genera compose the family Hemiscylliidae, probably this is an autapomorphy present in *Hemiscyllium* species.

The present description of these muscles agrees with the work of Marion (1905), although he followed Vetter (1874) in calling these muscles *m. interarcuales mediales*. Also, the findings in the present work corroborate those made by Goto (2001) regarding this muscular group, in that orectolobids, parascyllids and hemiscyllids have the description afore-mentioned. Goto also proposes that parascyllids are the sister group to all other orectoloboids, followed by orectolobids as sister group to the other families, then hemiscyllids sister group to a clade composed of ginglymostomatids, *Stegostoma* and *Rhincodon*. Following this proposal (Fig. 34), the loss of the last interpharyngobranchial muscle is probably a synapomorphy of orectolobiform taxa, and its reacquisition is a putative autapomorphy of hemiscyllids and ginglymostomatids + *Stegostoma* + *Rhincodon*. From these latter groups, only *Rhincodon* was not observed on the present study.

5. *Musculi arcuales dorsales*

Shirai (1992a) proposed as one of the synapomorphies of the Squalomorphi, the presence of two rami per dorsal arcual muscle, with the anterior ramus maintaining the original origin (pharyngobranchial of the corresponding arch) and insertion (epibranchial of the corresponding arch), and the posterior ramus originating from the next pharyngobranchial and inserting onto the same place as the anterior. In this study, this condition was observed only in the same groups as originally proposed by Shirai. Galeomorphs have only one ramus present in all representatives analyzed. Therefore, in all observed squalomorph sharks there is a second ramus in this muscle, whereas in all galeomorph sharks there is only one. *Zapteryx brevirostris*, the only batoidean observed in the present work, has only one muscular slip, not two. Although the works of Huber, Soares & Carvalho (2011) and Miyake et al. (1992)

analyzed the same region, they did not comment on the condition of this muscle (the work of Myiake et al. focused on the ventral branchial region, the muscle in question is dorsally placed on the same region). We can conclude that, when sharks are analyzed, only squalomorphs have the second ramus and the batoidean and galeomorph groups have the same morphology, what sustains the proposition made by Shirai (1992) on regard to the observed shark taxa. We had no access to pristiophoriforms and squatiniformes, since they were not on the scope of this work, and further analisys are needed to further investigate the condition on these squalomorph groups and Batoidea.

6. *Musculi coracobranchiales*

Among the squalomorph orders, *Zapteryx* and orectoloboids and heterodontids, there is no significant divergence of the shape of the posteriormost *m. coracobranchialis*. All other observed groups have a single ramus of the last *m. coracobranchialis*, which is also laminar. The only remarkable difference is that Hexanchiformes have a higher number on this muscular series because of their one or two extra gill arches; in all other orders, there are just five muscles. All the other coracobranchial muscles, excluding the posteriormost, are dorsoventrally compressed. The conclusion is that the condition where there is one laminar ramus of the last coracobranchial muscle and the other components of the series are compressed dorsoventrally is the plesiomorphic state for this muscular complex, both because it is more commonly found in elasmobranch groups and because it is found in the groups that are suggested as more basal in elasmobranch phylogenies, both in molecular and morphological studies.

The orders Lamniformes and Carcharhiniformes have one feature of the *m. coracobranchiales* in common: the division of the fifth *m. coracobranchialis*, present in all carcharhiniform families, except for Scyliorhindae, and also present in the lamniform families Odontaspididae, Pseudocarchariidae and Lamnidae (the lamniform families examined in this study that did not have this division are Alopiidae and Mitsukurinidae). This suggests a convergence between the orders, since the families sustained as basal on both families are different (Compagno, 1988; Wilga, 2005; Naylor et al., 2012).

Among the Carcharhiniformes, the same muscle suggests further interrelationships. Pentanchids and proscyllids have in common the presence of a single slip os the fifth *m. coracobranchialis* with double origins and a single insertion. The morphology present in scyliorhinids, with a single origin and insertion, suggests that the three families are either plesiomorphically similar, since all other families have two well separated rami on the fifth *m. coracobranchialis*, or have a reversion to the plesiomorphic state of one ramus present, what would support this clade as monophiletic, as proposed by Compagno (1988). Although the proposal of this cluster was already sustained by Compagno, the differences on the number of origins on the fifth *m. coracobranchialis* suggests a different relationship within this suprafamilial group. Whereas Compagno proposes that Scyliorhinidae and Pentanchidae form a single (although questionable according to his data) group, the numbers of origins on the fifth coracobranchial muscle suggest that proscyllids are more closely related to pentanchids than scyliorhinids. This supports the view of Naylor et al. (2012) (Fig. 32), who named what we call Pentanchidae on this work as Scyliorhinidae I in his study. The dissection made on this study are related to the taxa Scyliorhinidae I (our pentanchids), Scyliorhinidae II (our scyliorhinids) and Proscyllidae II. This study could not access members of Naylor's groups Scyliorhinidae III and Proscyllidae I, but the relatioships among the observed groups follow his results.

The carcharhiniform families Triakidae, Hemigaleidae and Leptochariidae are usually positioned at mid clade within the carcharhiniform phylogeny (Naylor et al., 2012, Fig. 32; on his work in 1988, Compagno proposed a similar tree of interrelationships regarding these families). The fifth coracobranchial muscle in these families is divided into two well-defined rami, same condition present in sphyrnids and carcharhinids. In Sphyrnidae, the fifth coracobranchial muscle is much less developed, being much thiner than in the other families, possessing a translucent region towards the insertion. This is restricted to this family. In Carcharhinidae, the fifth muscle of the series is more markedly divided. *Prionace* diverges from the others carcharhinids regarding the proportion of the two divisions. In all other species analyzed, the anterior portion of the fifth coracobranchial muscle is considerably larger, whereas *Prionace* has both parts (anterior and posterior) with the same size.

Concerning the four anterior coracobranchial muscles there is not much change within carcharhiniforms in all the afore-mentioned families. They are all

cylindrical and dorso-ventrally compressed. The only difference is in Carcharhinidae, where the four anterior are compressed laterally intead of dorso-ventrally. *Nasolamia velox* is the only deviant from this rule, possessing the four anterior coracobranchial muscles more cylindrical and not very compressed. The other difference found among these four anterior muscles is also in the family Carcharhinidae, with representatives that have the first coracobranchial divided in three groups of fibers. The species that have this characteristic are *Galeocerdo cuvier*, *Loxodon macrorhinus* and *Nasolamia velox*. This supports the inclusion of *Galeocerdo cuvier* inside carcharhinids, or at least its close relationship with the other members of the family.

Among the Lamniformes, there are two types of design for the fifth *m. coracobranchialis*. It can be divided into two rami (Odontaspididae, Pseudocarchariidae and Lamnidae) or have a single ramus (Mitsukurinidae and Alopiidae). Proportionally, the posterior region is about one-fourth of the anterior region. The four anterior are compressed dorso-ventrally in Alopiidae, Pseudocarchariidae and Mitsukurinidae and compressed laterally in Lamnidae and Odontaspididae. These characters could indicate a closer relationship between lamnids and odontaspidids, since they share characters on all coracobranchial muscles, differeing from previous proposals (Naylor et al, 2012; Wilga, 2005) (Fig. 32).

7. *Musculus constrictor oesophagi*

Although this muscle is more associated with swallowing food, the anterior region is associated with the last branchial arch. There were no great modifications in this muscle, except for the Mitsukurinidae, which has this muscle reduced.

8. Absence of levator muscles

In the actinopterygian fishes, there is usually a set of muscles that are responsible for lifting the branchial arches (Winterbottom, 1993; Datovo & Bockmann, 2010; Springer & Johnson, 2015). There is no indication of any kind of muscular tissue in the corresponding region of sharks. They possess connective tissue strands in the same region. Didier (1995) did not describe any muscles with this

function for any holocephalans examined, which indicates that it is possible that chondrichthyans never had the levator muscles at all.

9. Galeomorphi and Squalomorphi

There was no indicative of character restricted to Galeomorphi, since the results of this study strongly suggest that Orectolobiformes and Heterodontiformes are sister groups, and the charcaters present in these orders and the other clade, composed of carcharhiniforms and lamniforms, do not have any congruent characters supporting the whole superorder. On the other hand, squalomorph sharks are corroborated by the presence of a second ramus on the *m. arcuales dorsalis*, present only in this superder, and also abset from the batoidean dissected herein. No conclusion can be drawn as to the relationships of rays, since there is not much data on thig group in this study.

10. Relationships among Heterodontiformes and Orectolobiformes

There interrelationships if Orectolobiformes and Heterodontiformes form a monophyletic taxon. Although some authors consider Heterodontiformes and Orectolobiforme to be sister groups based on morphological characters, such as on their unique type of nasal capsule, type of orbital process and its cranial articulation, arrangement of the preorbital muscle on the cranium and jaws, short mouth gape, limited behind by the labial cartilages and jaw muscles, morphology of the pectoral fin skeleton and nostril structure (Compagno, 1973) or based on the presence of the *m. levator labii superioris* (= *m. preorbitalis*) on the orbitonasal lamina, the insertion area of the *m. levator labii superioris* (= *m. preorbitalis*) significantly restricting the mouth gape and the presence of the *m. levator hyomandibulae* well separated from the *m. constrictor hyoideus dorsalis* (Soares & Carvalho, 2013a), none of these works included branchial arch muscle characters. That means there are not many synapomorphies and/or diagnostic characters based on muscles for comparison. The present work has some characters that could support the idea of this heterodontiform + orectolobiform clade. Both orders do not possess the insertion on the last epibranchial of the *m. trapezius* (it was not find the same as Goto in his study in 2001, where it was observed this insertion in all orectolobiforms) and the fifth

coracobranchial has its fibers directed forward, whereas in the other galeomorph orders the *m. trapezius* has the insertion on the epibranchial and the fifth coracobranchial has its fibers directed either upwards or oblique, anterodorsally directed. Also, the presence of more connective tissue over the branchial muscles is conspicuous in these two orders, making the musculature look more protected and stout as well. The only character disagreeing with this proposal of a heterodontid + orectoloboid taxon is the presence os a medial ventral raphe in two orectoloboid families, condition also present in Carcharhiniformes and Lamniformes. Those families are considered by Goto (2001) as the two most basal groups (Fig. 34), and the presence of this raphe could indicate a synapomorphy for a clade composed of Orectolobiformes, Lamniformes and Carcharhiniformes. Since a phylogenetic analysis is beyond the scope of this work, this question remains open.

Goto (2001) proposed the latest anatomically based phylogeny for orectolobiform families (Fig. 34). His conclusions were partially corroborated in the present work. The proximity of *Ginglymostoma* and *Stegostoma* proposed by that author is corroborated by characters of branchial arch muscles, markedly in the *constrictors superficiales*, one of the muscles he found as being similar and derived for these genera. Both genera have a reduced form of these muscles, as well as connective tissue in large dorsolateral strands on them. He followed Applegate (1972) for proposing three groups together: *Stegostoma*, *Rhincodon* and ginglymostomatids. Of these, it was not possible to examine *Rhincodon*. Also, it was not observed any specimen of two ginglymostomatid genera, *Pseudoginglymostoma* and *Nebrius*, the same taxa Goto (2001) also failed to examine among Orectolobiformes. Still the study could access more material concerning the genera it was possible to observe. Therefore, concerning the interrelationships inside this group, the conclusions reached in this work are that these genera are related to some extent, but we had access to less material than Goto. The new evidences gathered in this study that corroborates Goto are: the *m. trapezius* is bulky in orectolobiforms, with the parascyllids having it less developed, suggesting it possess the character present in other orders; the greater distance between the *m. constrictores branchiales superficiales* antimeres, due to the realocation of the insertion os the constrictor muscles to the lateral of the coracomandibular muscle (common to the whole order, but more separated in these two families). The evidences already found in Goto (2001) and recovered here are: the

reduction on the *m. constrictores branchiales superficiales* on S*tegostoma* and *Ginglymostoma*, restricted to these families; the connective nature of the last *m. interpharyngobranchiales* in parascyllids and orectolobids indicates this is either a synapomorphy at orectolobiform level or an autapomorphy for both families.

11. Relationships among the Lamniformes

There are five observed families of Lamniformes on the present work (Alopiidae, Mitsukurinidae, Odontapididae, Lamnidae and Pseudocarchariidae). The two families not observed are Cetorhinidae and Megachasmidae. The general morphology of lamniform sharks suggests they are closely related to carcharhiniforms (Compagno, 1973; de Carvalho, 1996; Douady et al., 2003; Naylor et al, 2005; Human et al. 2006; Heinicke et al. 2009). Some of the similarities indicating this closer relationship are exclusive to these orders, such as the division of the fifth *m. coracobranchialis* and the crescent-shaped *m. adductores arcuum branchialiumi*. There are two major divisions when we see the anatomy of lamniforms. One group comprises lamnids and odontaspidids, which have the general morphology more alike that of carcharhiniforms. The similar anatomy is composed of the presence of a second ramus on the fifth *m. coracobranchialis* and the laterally compressed first four *m. coracobranchiales*, both present in derived carcharhiniforms, and the shape of the *m. adductores arcuum branchialium*, which is triangular, same as in the supposed basal carcharhiniform pentanchids, scyliorhinids and proscyllids. Mitsukurinids and alopiids have more specialized life-styles and are more alike each other. Both families have the crescent-shaped *m. adductores arcuum branchialium*, the dorsoventrally compressed first four *m. coracobranchiales* and the lack of the second ramus on the fifth *m. coracobranchialis*. Pseudocarchariids are a miscelanic group of these two morphologies, possessing some characters of lamnids and odontaspidids (triangular-shaped *m. adductores arcuum branchialium*) and other of mitsukurinids and alopiids (one ramus on the fifth *m. coracobranchialis*, and the dorsoventrally compressed first four *m. coracobranchiales*), as well as autapomorphies of the family (the presence of three muscles connecting pharyngobranchial cartilages of one arch to the epibranchial of the adjacent posterior arch, called on this study as *m. pharyngobranchiales n-epibranchiales n+1*). All characters present in pseudocarchariid are considered herein

as plesiomorphies at the lamniform level. Therefore, the present study suggests that pseudocarchariids are probably in the base of lamniform evolution. This contradicts the proposal made by Naylor et al. (2012) (Fig 32), where mitsukurinids and alopiids are depicted as more basal groups. Some disagreeements are also found with the proposal of Wilga (2005), where also mitsukurinids are depicted as the basal family within Lamniformes and none of the interrelationships found on the present study corroborates any relationships found on the work of 2005.

12. Relationships among the Carcharhiniformes

There is no evidence on the branchial musculature that supports this order, since all character that could show any kind of apomophy is either not restricted to the order, appearing in its sister-group Lamniformes, or is not present on the basal clades. The most recent morphological work (Compagno, 1988) did not analyze any kind of character contained on the branchial musculature, so every character proposed here is new.

The anatomy found on the branchial muscles suggest that the history of Carcharhiniformes is at some extent explained by these muscles. The family Pentanchidae, originally described as a hexanchoid (Smith & Radcliffe, 1912), is considered as a subfamily within scyliorhinids by Compagno (1988). On the present work, one character (common coracoarcual with no septa) was found that suggests that *Scyliorhinus* and *Schroederichthys* are more closely related to the proscyllid *Eridacnis* than to the other scyliorhinid genera *sensu* Compagno (1988). Other characters (*m. adductores arcuum branchialium* trapezoidal, double origin of the fifth coracobranchial muscle, *m. interpharyngobranchialis* with low inclination in comparison to the pharyngobranchial axis) suggest the genera of the subfamily Pentanchinae (*sensu* Compagno, 1988) (*Apristurus*, *Galeus* and *Parmaturus* in this study) appear to be more closely related to the proscyllid observed herein. All these characters point out that these families are closely related and that Scyliorhinidae *sensu* Compagno (1988) could be a non-monophiletic group. This was already found by some authors, particularly with molecular data (Iglesias et al. 2005; Naylor et al., 2012). The material observed herein comprehended some of the species present in study of Naylor et al., restricted to his Scyliorhinidae I and II and Proscyllidae II. We

had no access to the three species present on Scyliorhinidae III neither to the genus *Proscyllium*, proposed in his Proscyllidae I.

Triakids did not show any clear division in any subfamilies, with a myriad of congruencies in members of Triakinae and Galeorhininae. The genus *Mustelus* does not appear as a monophyletic group when we observe the muscles *m. constrictores branchiales superficiales*, *m. trapezius* and *m. corabranchiales*. *Mustelus higmani* and *M. schmitti* appear as more similar to each other. The afore-mentioned muscles in *M. griseus* resemble more strongly the musclulature present in *Galeorhinus galeus* and *Hemitriakis japonica*. The genus Mustelus must be further studied phylogenetically to further elucidate its validity. When compared to the other carcharhiniform families, it showed a composite character state, with some characters resembling scyliorhinids, proscyllids, pentanchids and groups outside the order and others in common with more derived carcharhiniform groups, such as carcharhinids and sphyrnids, indicating this could be a transitional family between crown and basal groups.

Leptochariids and *Chaenogaleus*, the observed hemigaleid herein, were classically placed among the carcharhinid taxa. On the present work, the characters found support the idea they are closely related to charcharinids and sphyrnids but also with each other (Compagno, 1988). The characters found for each family is highly congruent with the other, with few differences (dorsal arcuals bulky on *Leptocharias* and slender on *Chaenogaleus*, interpharyngobranchials with more angulation on *Chaenogaleus* and parallel to the pharyngobranchial axis on *Leptocharias*), usually in muscles that vary a lot within other families. It is concluded that they could be closely related to each other.

Carcharhinids and sphyrnids are very alike each other on this anatomical complex. There are some differences that suggest they are not a single family, or at least sphyrnids are not a group deeply immersed on the carcharhinids, as proposed by Compagno (1973). These differences are the shape of the posterior ramus trapezius muscle (triangular in carcharhinids and rounded in sphyrnids), the rather thin and fragile coracobranchials of sphyrnids and *m. trapezius* and the stout musculature present in all carcharhinids. Among the sphyrnids, *Eusphyra* is different from the others, also because it has an extra muscle set connecting the first pharyngobranchial with the second epibranchial. Such muscle is present only on this genus among all

carcharhiniforms observed, being a possible autapomorphy separating it from the other Sphyrnidae.

Considering only the family Carcharhinidae, there is one possible synapomorphy on the muscles of the branchial arches, which is the laterally compressed first four *m.* coracobranchiales. The genus *Galeocerdo* is not out of the median carcharhinid anatomy in the muscles observed on the present work, also having two genera that share almost all the characters found in the branchial musculature: *Loxodon* and *Triaenodon*. The general morphology of these follows the genus *Carcharhinus*, but there are a few similarities only shared by these three genera. The presence of three groups of fibers, not separated in rami, but still easyly distinguishable, on the first coracobranchial, the disposition of the superficial constrictors and the triangular arch adductors are characters shared exclusively between these genera. All the other genera have the basic morphology more similar to each other. This could suggest a division in two large subfamilies within Carcharhinidae, one including the three genera Galeocrdo, *Loxodon* and *Triaenodon* and another composed of the remaining genera. The size of this family, also the better sampling of it, generated a rather intrincated character complex, in which many characters vary much, such as the trapezius form, and others are almost single-stated, such as the dorsal arcuals.

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 Carcharhinformes 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 superficiales*, 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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Appendices

1. Abbreviations

aab: *addutores arcuum branchialium*

ad: *arcuales dorsales*

am: *adductor mandibulae*

cac: *coracoarcualis communis*

cbc: ceratobranchial

ch: *coracohyoideus*

cm: *coracomandibularis*

cob 1-5: *coracobranchialis* 1-5

coe: *constrictor oesophagi*

csup 1-4: *constrictores branchiales superficiales* 1-4

ebc: epibranchial

ib: *interbranchiales*

ipb: *interpharyngobranchiales*

ma: maxillary arch

pg: pectoral girdle

pbc: pharyngobranchial cartilage

po: *preorbitalis*

tr: *trapezius*

2. Synonymy of muscle names

Some muscles, assumed as homologous on this work, have been described by some authors with more than one name. To make the communication less confusing, here is a list of synonyms* used by the authors cited on this work:

Trapezius (Allis, 1917, 1920, 1923; Marion 1905; Vetter, 1874): as *Cuccularis* in Shirai, 1992; Soares & Carvalho, 2013 a,b, *Protactor pectoralis* in Myiake et al., 1992.

Interpharyngobranchiales (Shirai, 1992): as *Interarcuales dorsales* in Allis Jr., 1917, 1923; Daniel, 1934, *Interarcuales mediales* in Marion, 1905, *Interarcuales* in Vetter, 1874, *Levatores branchiales* in Kesteven, 1942

Arcuales dorsales (Allis, 1917, 1923; Shirai, 1992): as *Interarcuales laterales* in Daniel, 1934; Huber, Soares & Carvalho, 2013 a,b, *Epiarcuales obliqui* in Kesteven, 1942

Coracoarcualis communis (Allis, 1917, 1923; Shirai, 1992): as *Coracobranchialis communis* in Kesteven, 1942, *Coracobranchialis* in Vetter 1874

*the muscles without synonymy were not listed.

3. Images

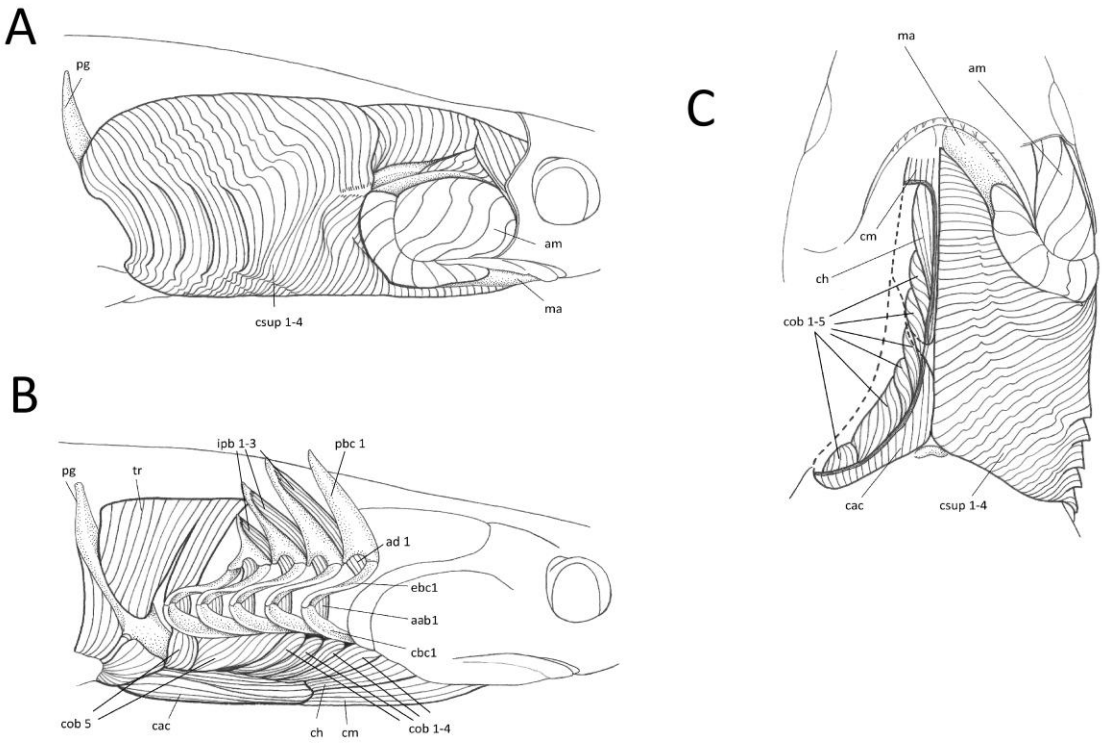

FIGURE 1. *Carcharhinus porosus* (MZUSP 37286, 335mm). Lateral superficial (A) and deep (B) views. (C) Ventral superficial (right) and deep (left) views.

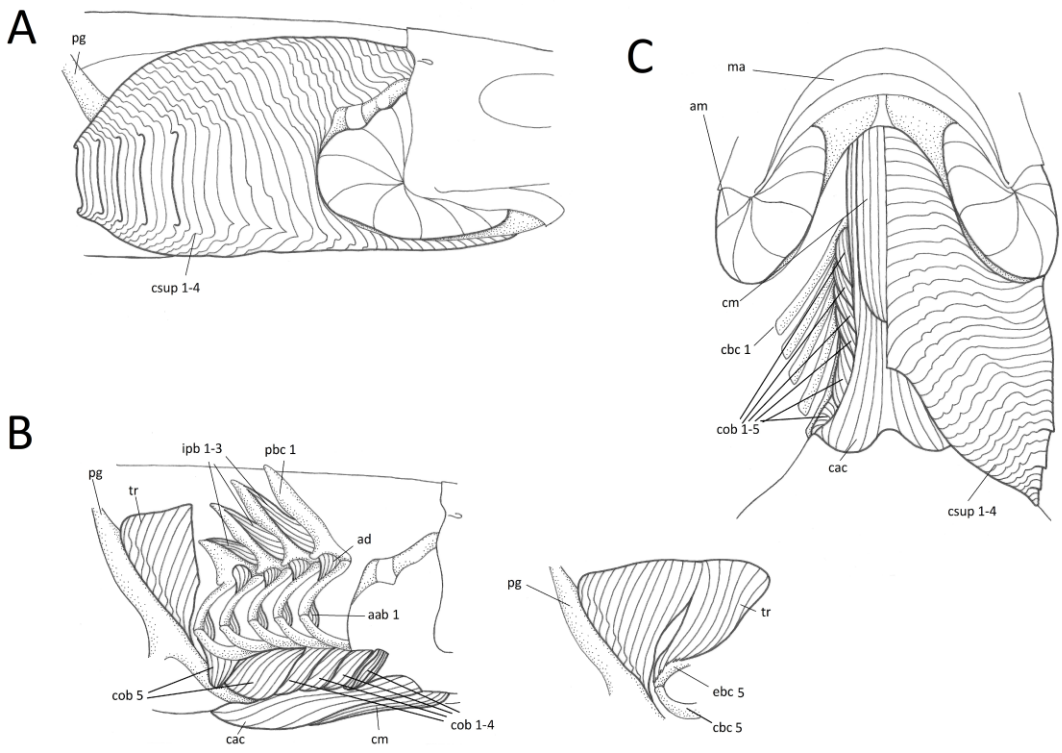

FIGURE 2. *Galeocerdo cuvier* (USNM 112243, 510mm). Lateral superficial (A) and deep (B) views, with a detail on the *m. trapezius*. (C) Ventral superficial (right) and deep (left) views.

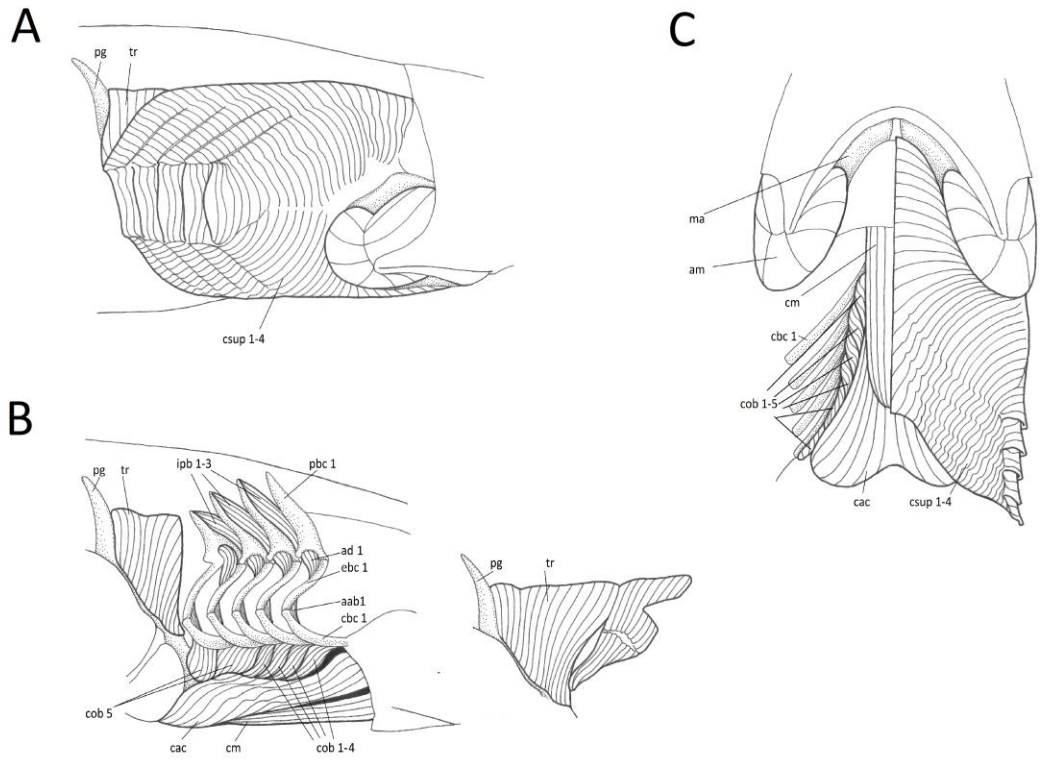

FIGURE 3. *Nasolamia velox* (USNM 203467, 529mm). Lateral superficial (A) and deep (B) views, with a detail on the *m. trapezius*. (C) Ventral superficial (right) and deep (left) views.

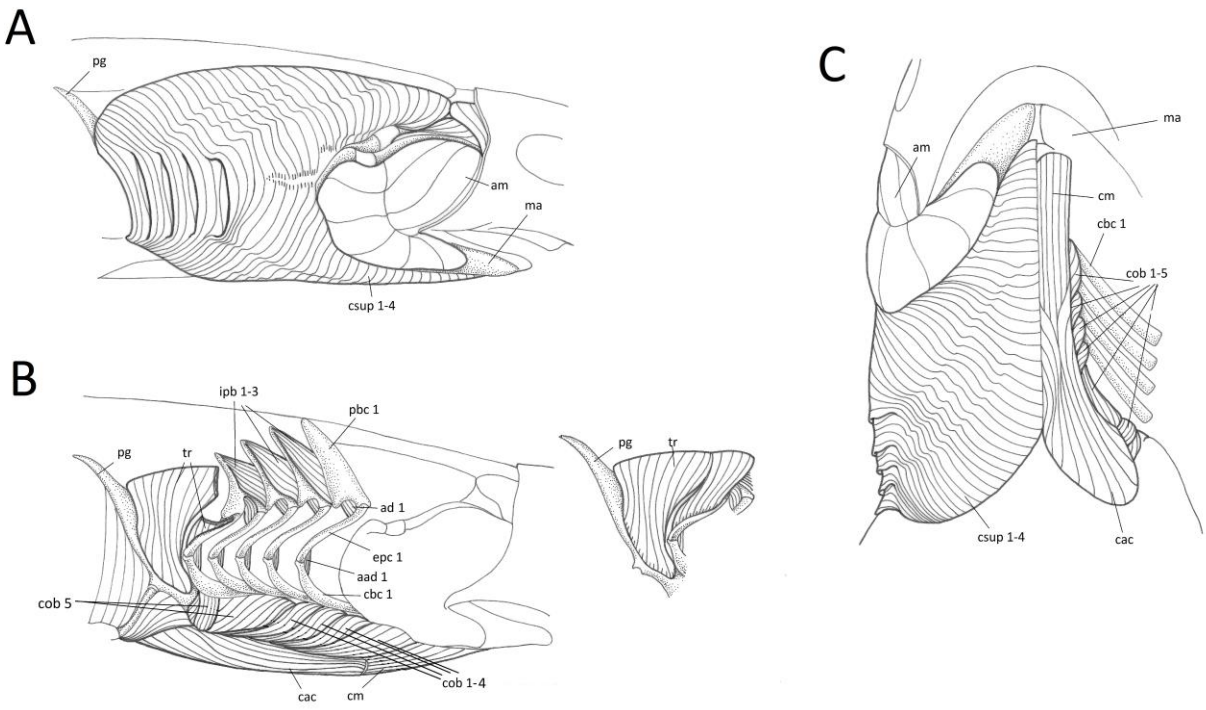

FIGURE 4. *Negaprion acutidens* (MZUSP uncat., 357mm). Lateral superficial (A) and deep (B) views, with a detail on the *m. trapezius*. (C) Ventral superficial (right) and deep (left) views.

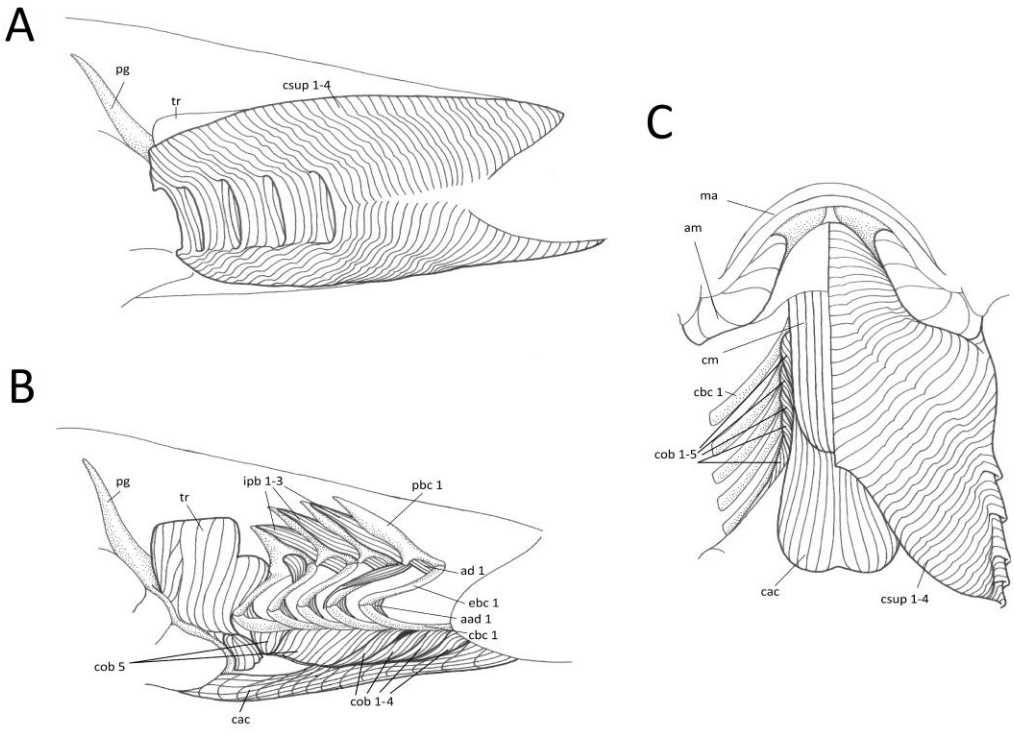

FIGURE 5. *Eusphyra blochii* (USNM 205342, 641mm). Lateral superficial (A) and deep (B) views. (C) Ventral superficial (right) and deep (left) views.

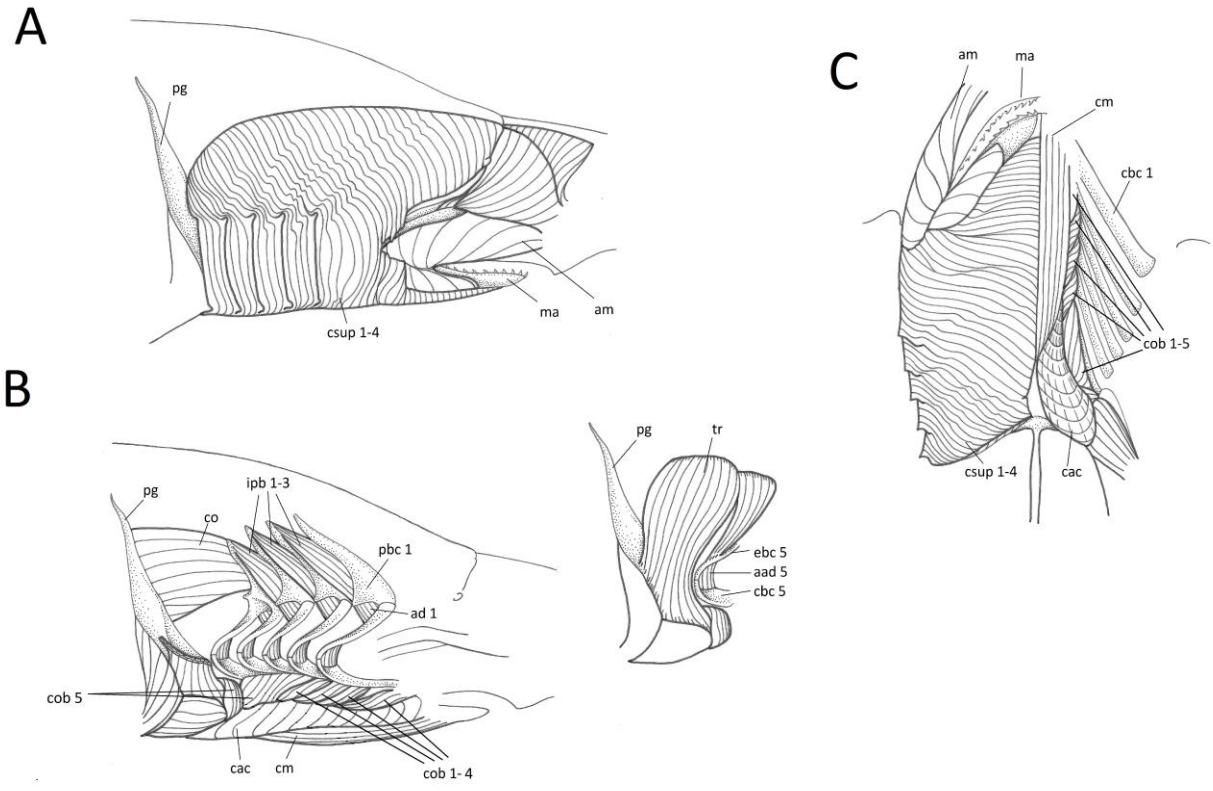

FIGURE 6. *Sphyrna tiburo* (MZUSP 37347, 371mm). Lateral superficial (A) and deep (B) views, with a detail on the *m. trapezius*. (C) Ventral superficial (right) and deep (left) views.

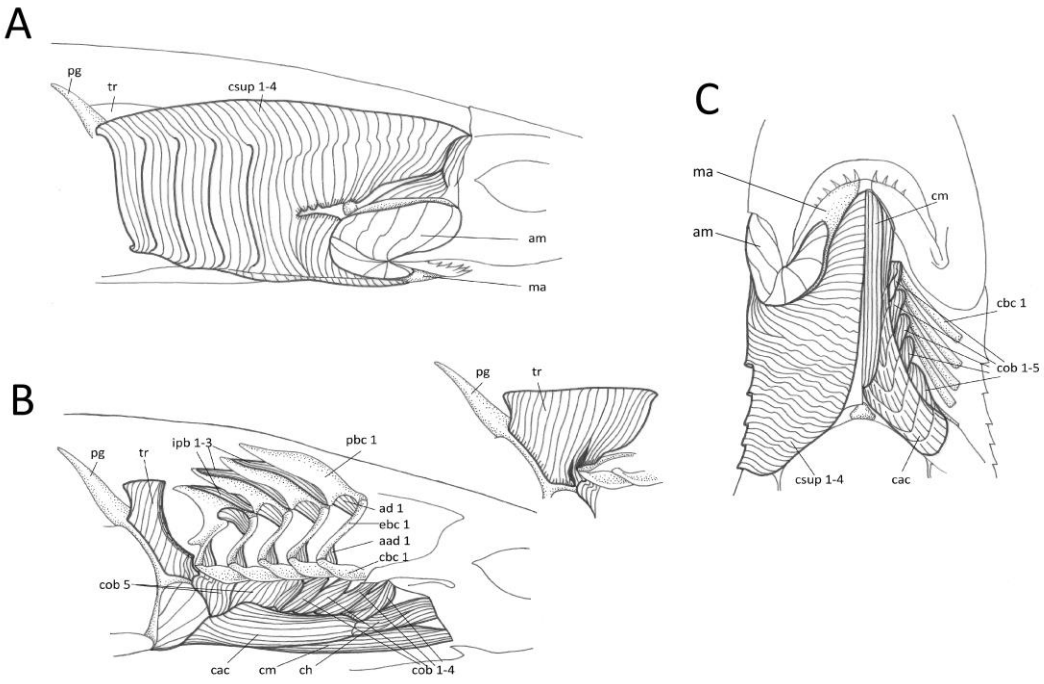

FIGURE 7. *Chaenogaleus macrostoma* (NMMBP 6414, 652mm). Lateral superficial (A) and deep (B) views, with a detail on the *m. trapezius*. (C) Ventral superficial (right) and deep (left) views.

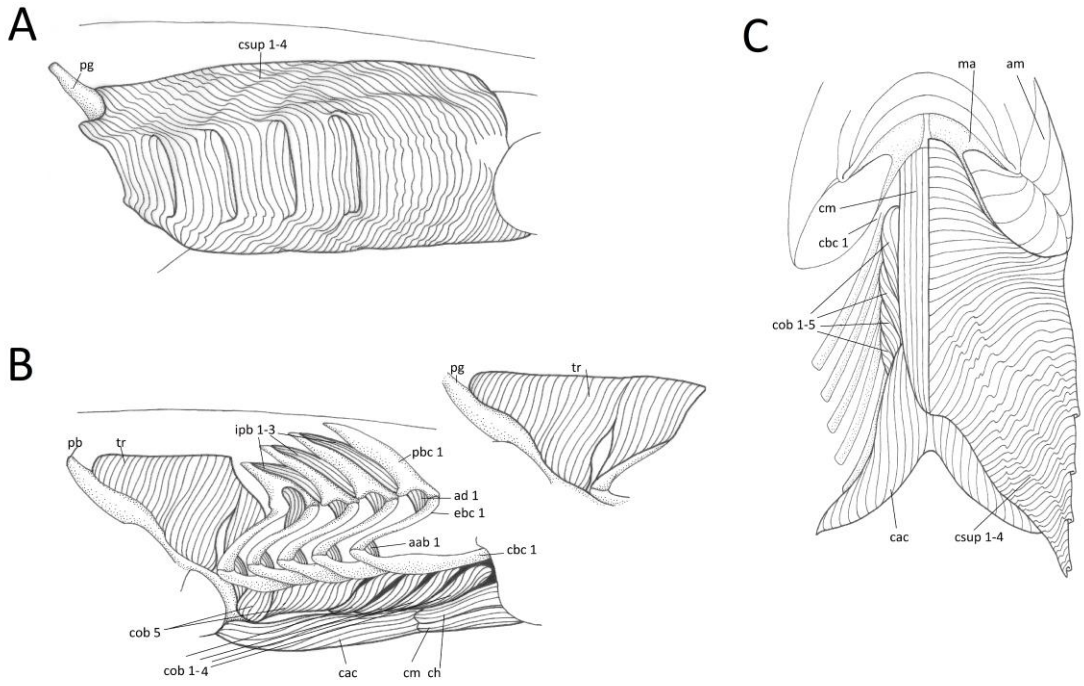

FIGURE 8. *Leptocharias smithii* (USNM 202677, 578mm). Lateral superficial (A) and deep (B) views, with a detail on the *m. trapezius*. (C) Ventral superficial (right) and deep (left) views.

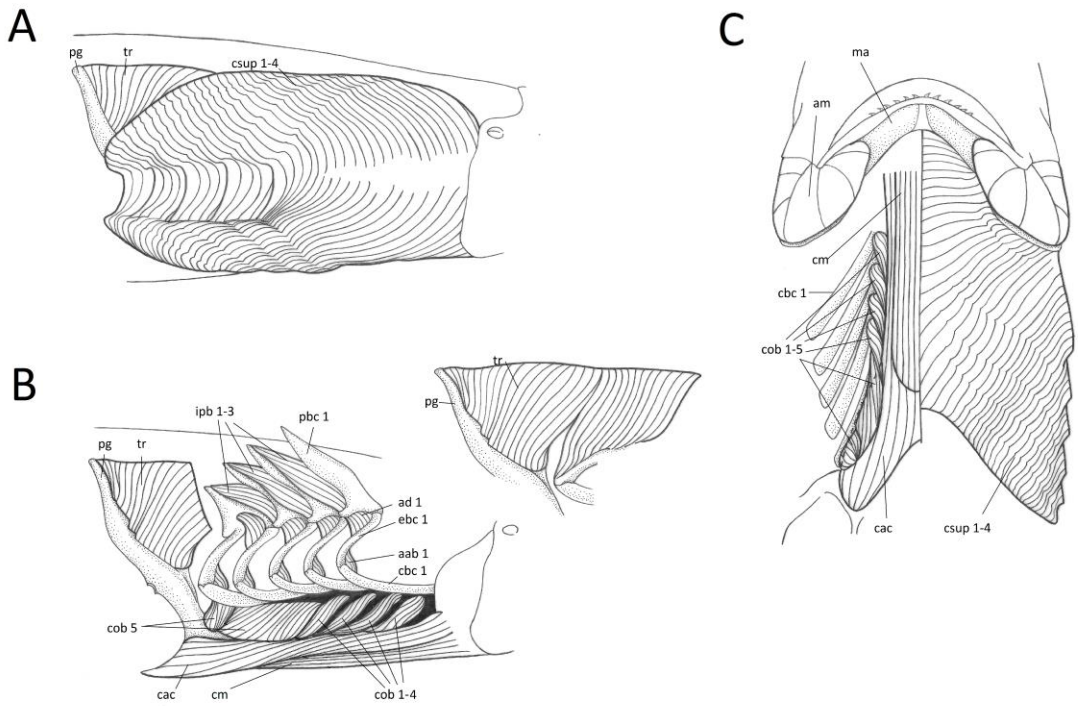

FIGURE 9. *Galeorhinus galeus* (CAS 21347, 352mm). Lateral superficial (A) and deep (B) views, with a detail on the *m. trapezius*. (C) Ventral superficial (right) and deep (left) views.

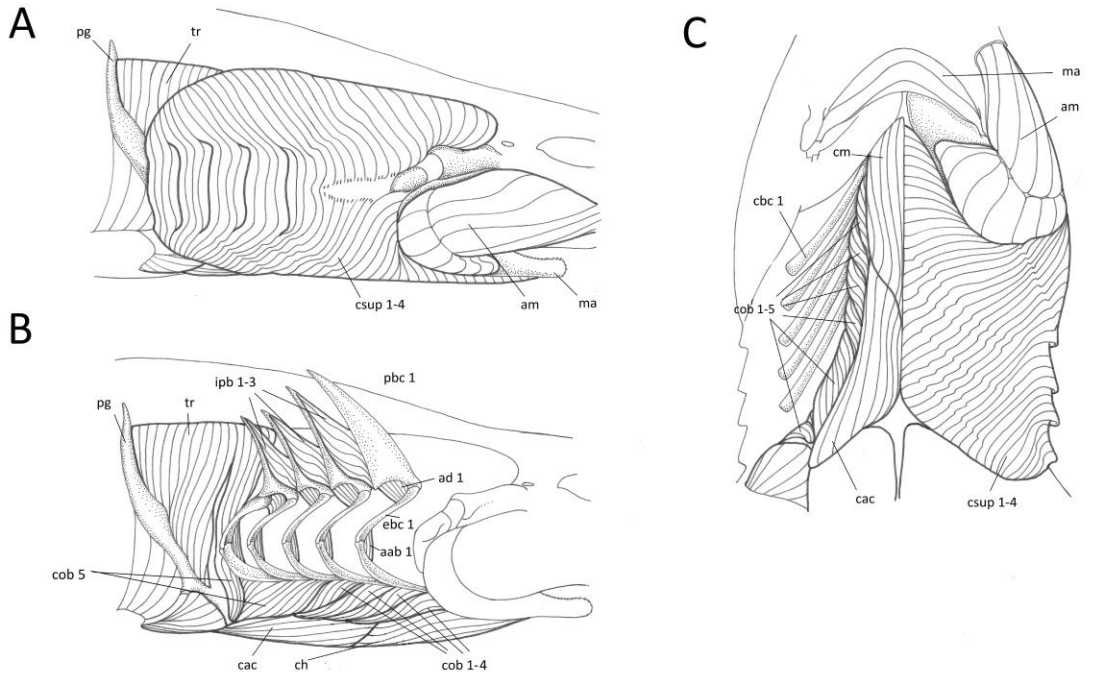

FIGURE 10. *Mustelus schmitti* (MZUSP 37327, 317mm). Lateral superficial (A) and deep (B) views. (C) Ventral superficial (right) and deep (left) views.

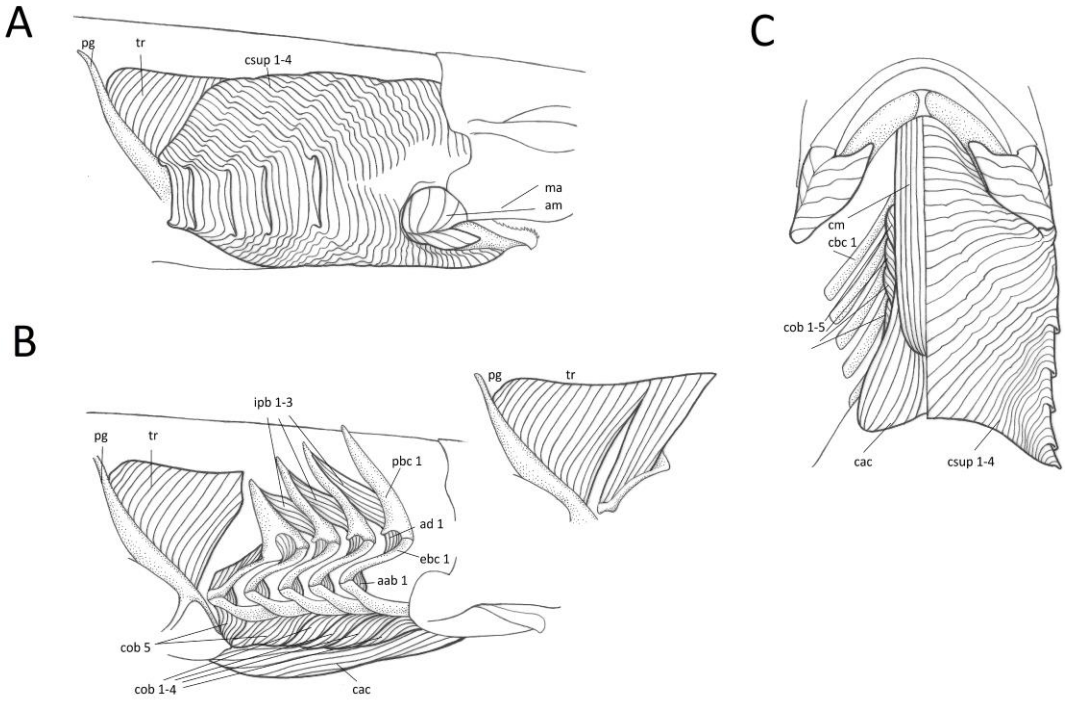

FIGURE 11. *Eridacnis radcliffei* (CAS 34140, 230mm). Lateral superficial (A) and deep (B) views, with a detail on the *m. trapezius*. (C) Ventral superficial (right) and deep (left) views.

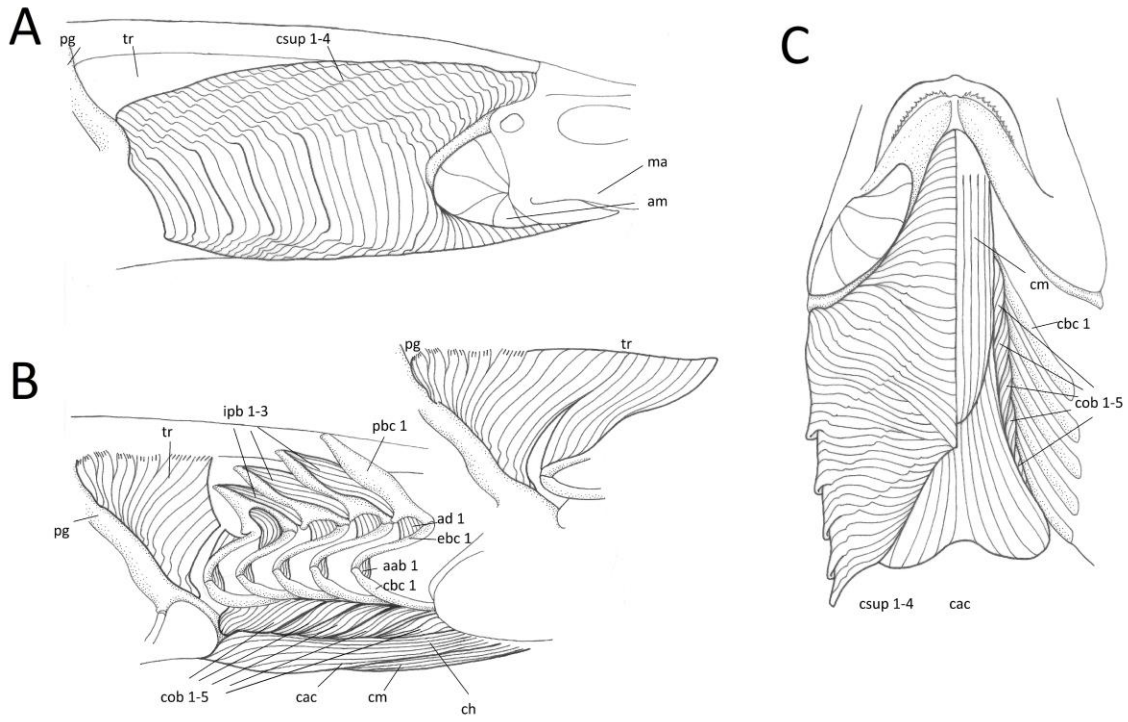

FIGURE 12. *Apristurus brunneus* (CAS 57475, 649mm). Lateral superficial (A) and deep (B) views, with a detail on the *m. trapezius*. (C) Ventral superficial (right) and deep (left) views.

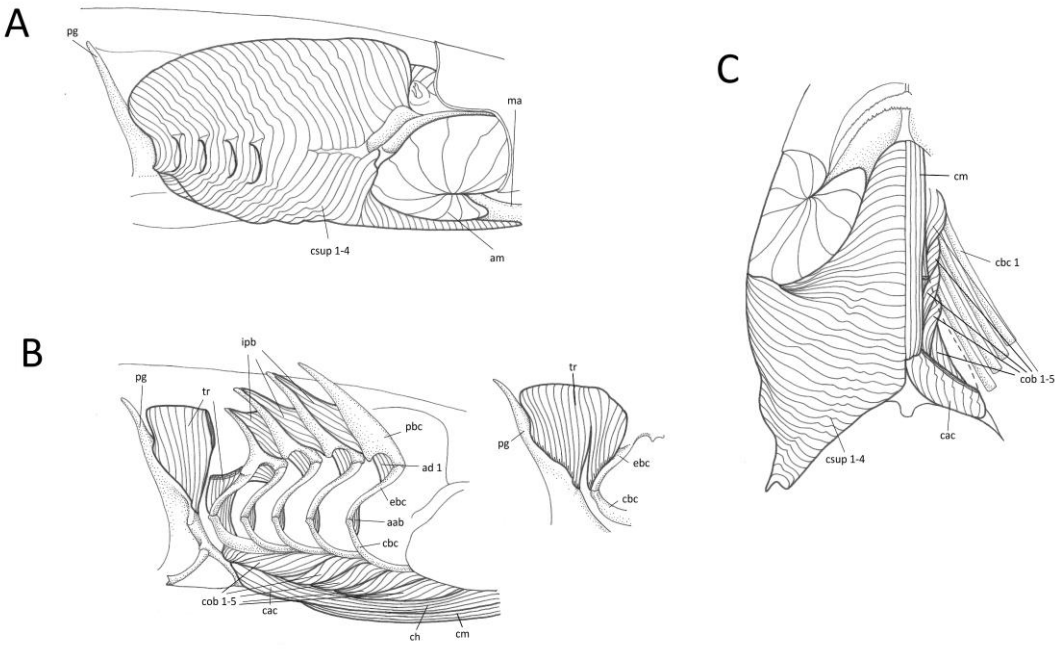

FIGURE 13. *Scyliorhinus haeckelli* (MZUSP uncat., 168mm). Lateral superficial (A) and deep (B) views, with a detail on the *m. trapezius*. (C) Ventral superficial (right) and deep (left) views.

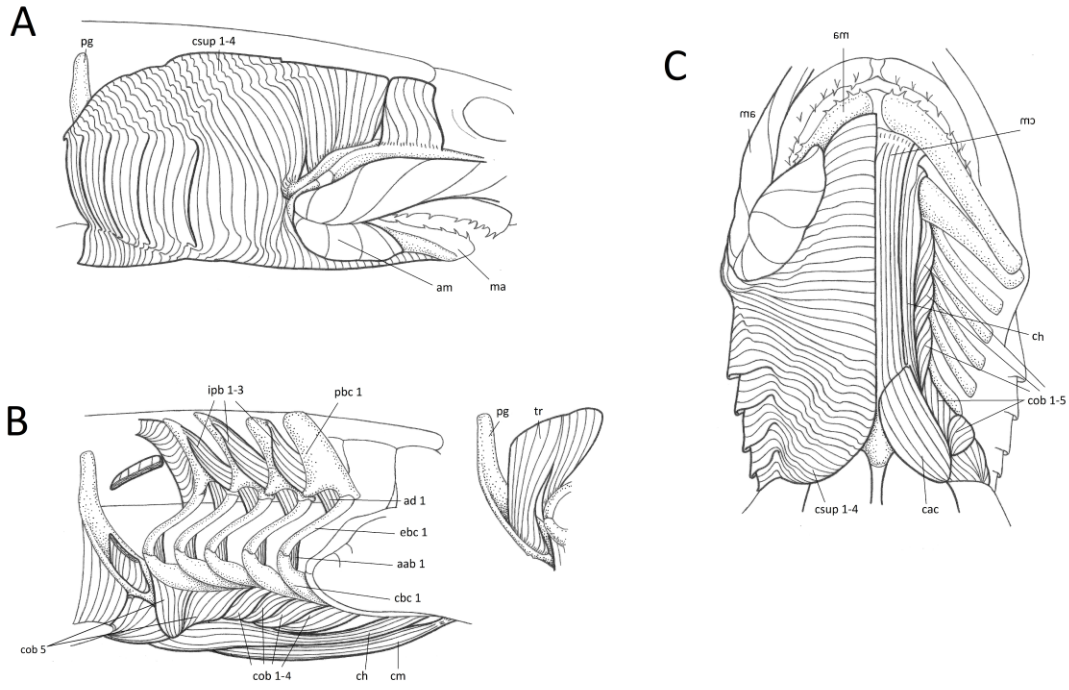

FIGURE 14. *Carcharias taurus* (MZUSP 37281, 335mm). Lateral superficial (A) and deep (B) views, with a detail on the *m. trapezius*. (C) Ventral superficial (right) and deep (left) views.

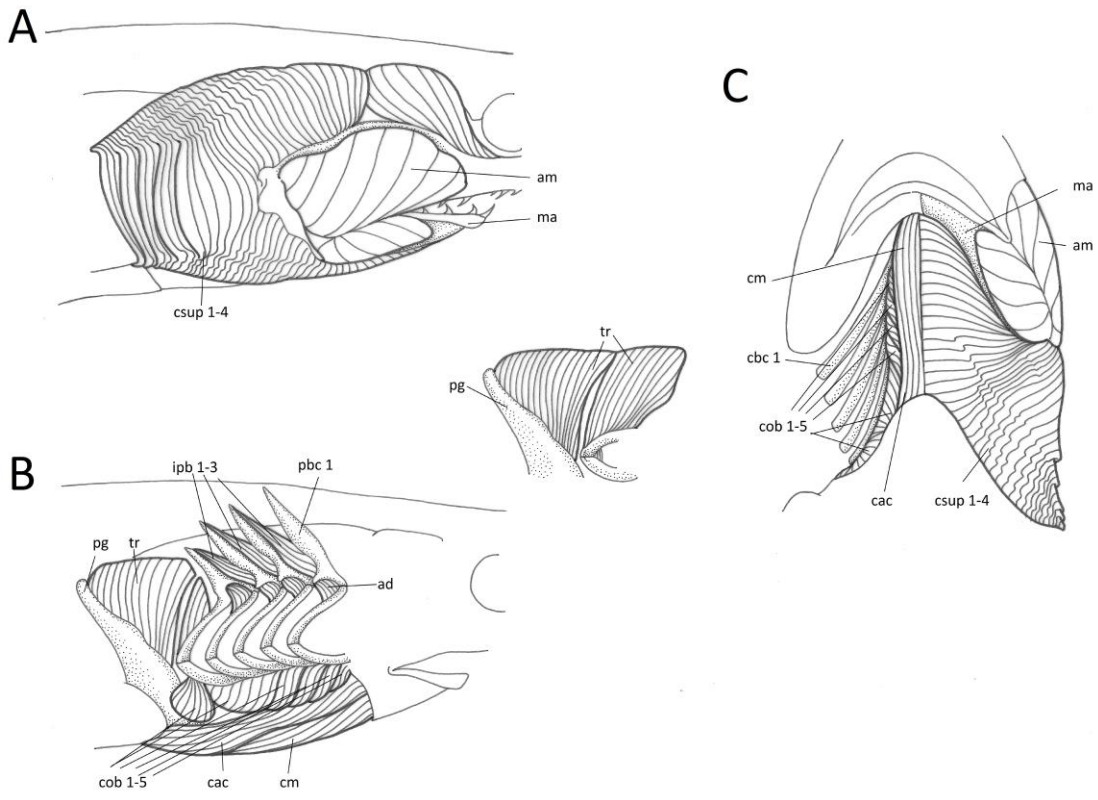

FIGURE 15. *Isurus oxyrinchus* (USNM 201733, 756mm). Lateral superficial (A) and deep (B) views, with a detail on the *m. trapezius*. (C) Ventral superficial (right) and deep (left) views.

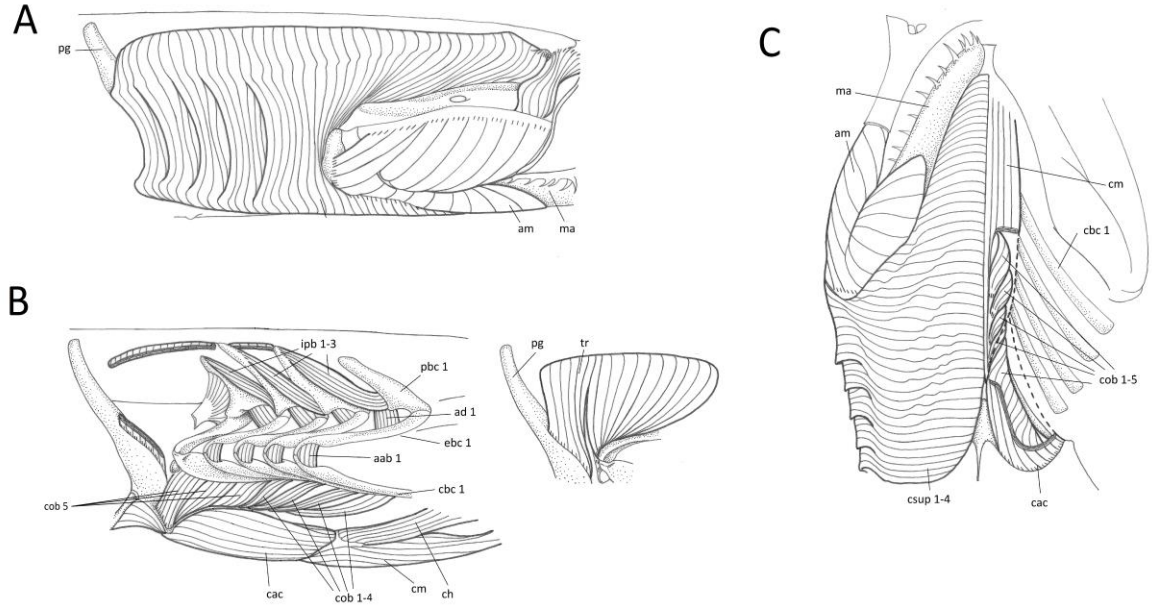

FIGURE 16. *Mitsukurina owstoni* (NMBP 15952, 1155mm). Lateral superficial (A) and deep (B) views, with a detail on the *m. trapezius*. (C) Ventral superficial (right) and deep (left) views. On the illustration, the divisions on the *m. coracobranchialis 5* correspond to artifacts due to its loose fibers.

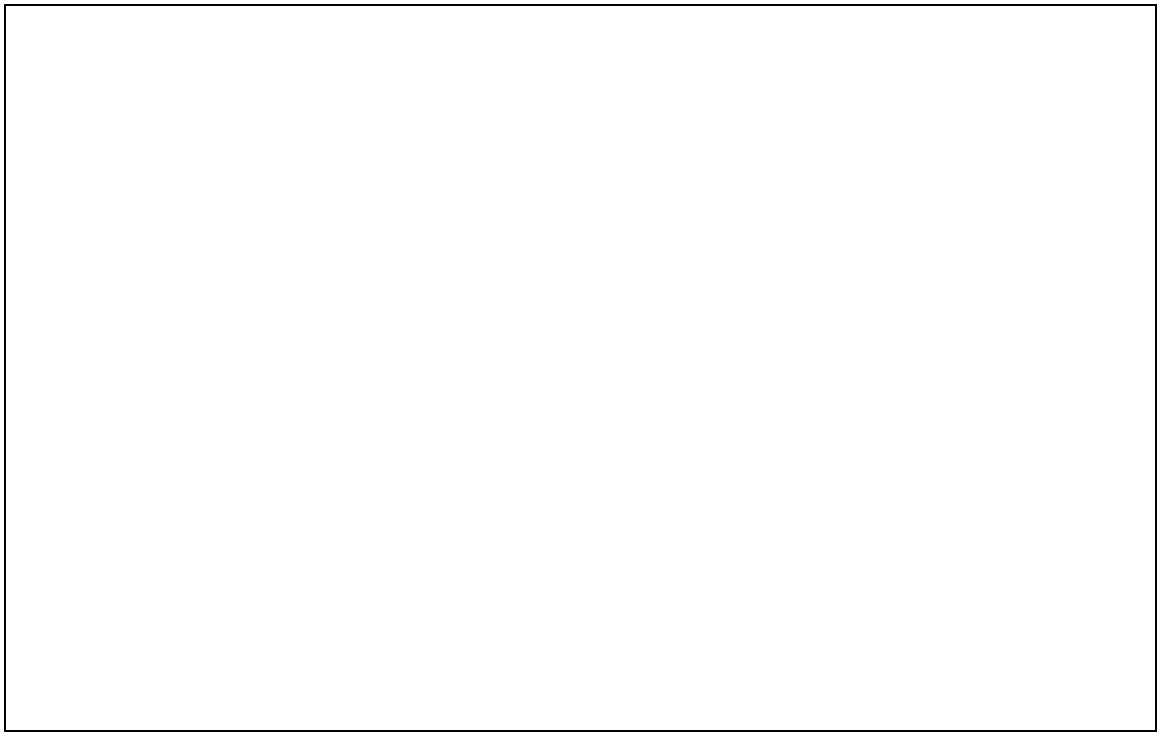

FIGURE 17. *Pseudocarcharias kamoharai* (MZUSP uncat., 269mm). Lateral superficial (A) and deep (B) views, with a detail on the *m. trapezius*. Ventral superficial (right) and deep (left) views.

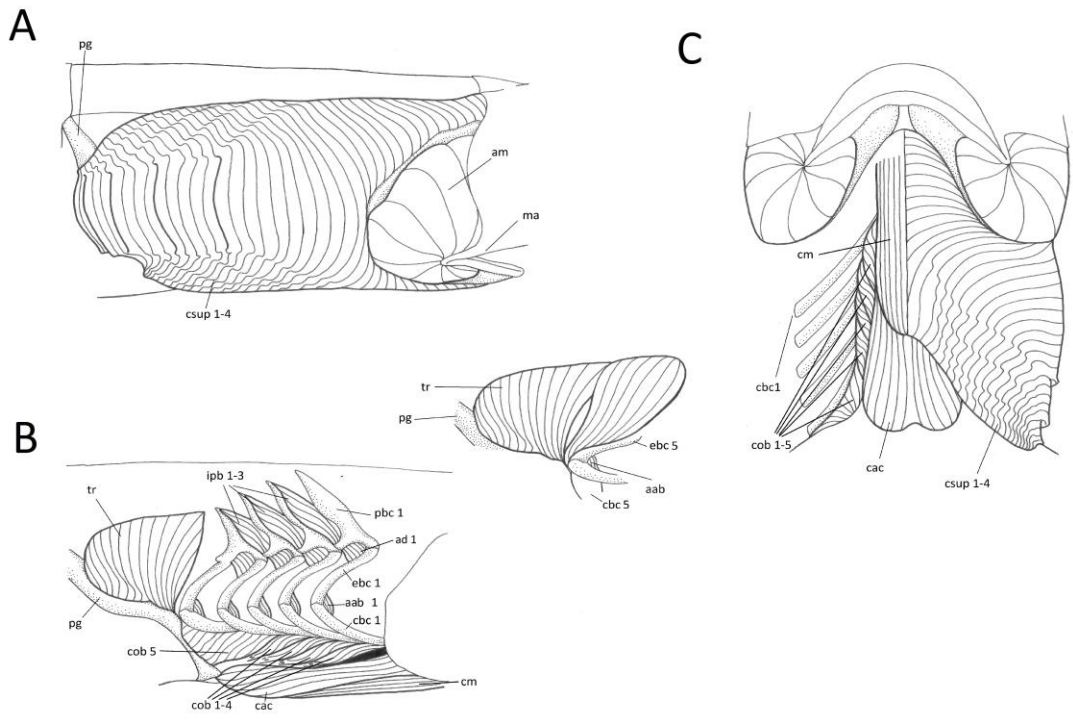

FIGURE 18. *Alopias pelagicus* (USNM 202675, 751mm). Lateral superficial (A) and deep (B) views, with a detail on the *m. trapezius*. (C) Ventral superficial (right) and deep (left) views.

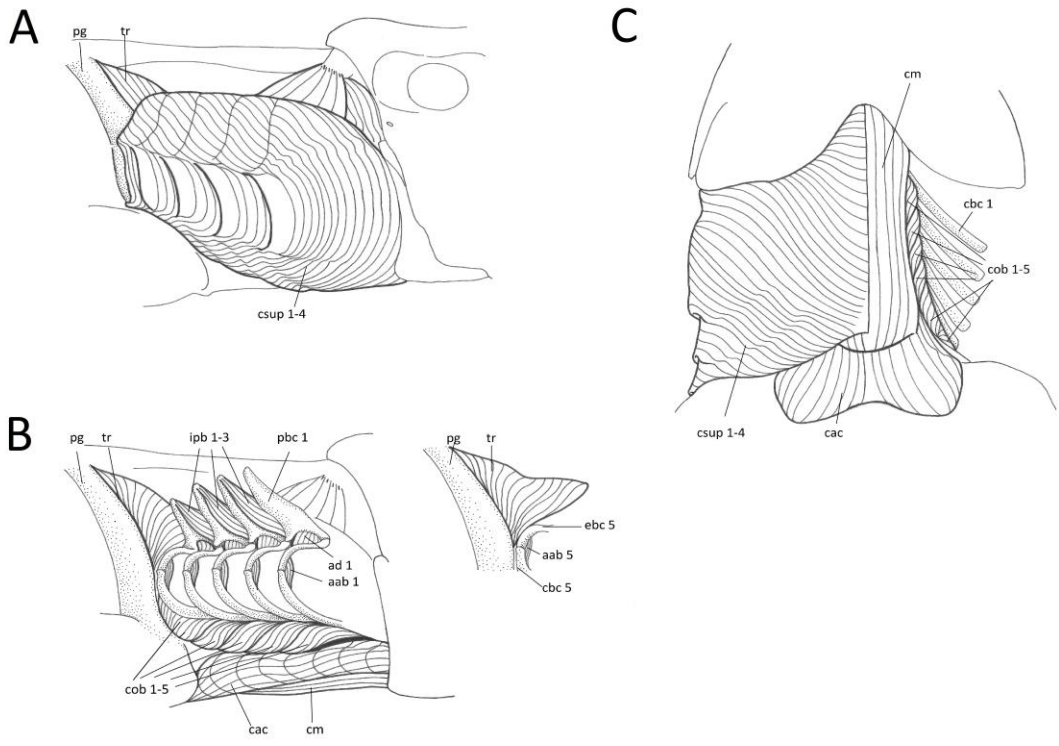

FIGURE 19. *Heterodontus francisci* (CAS 19176, 307mm). Lateral superficial (A) and deep (B) views, with a detail on the *m. trapezius*. (C) Ventral superficial (right) and deep (left) views.

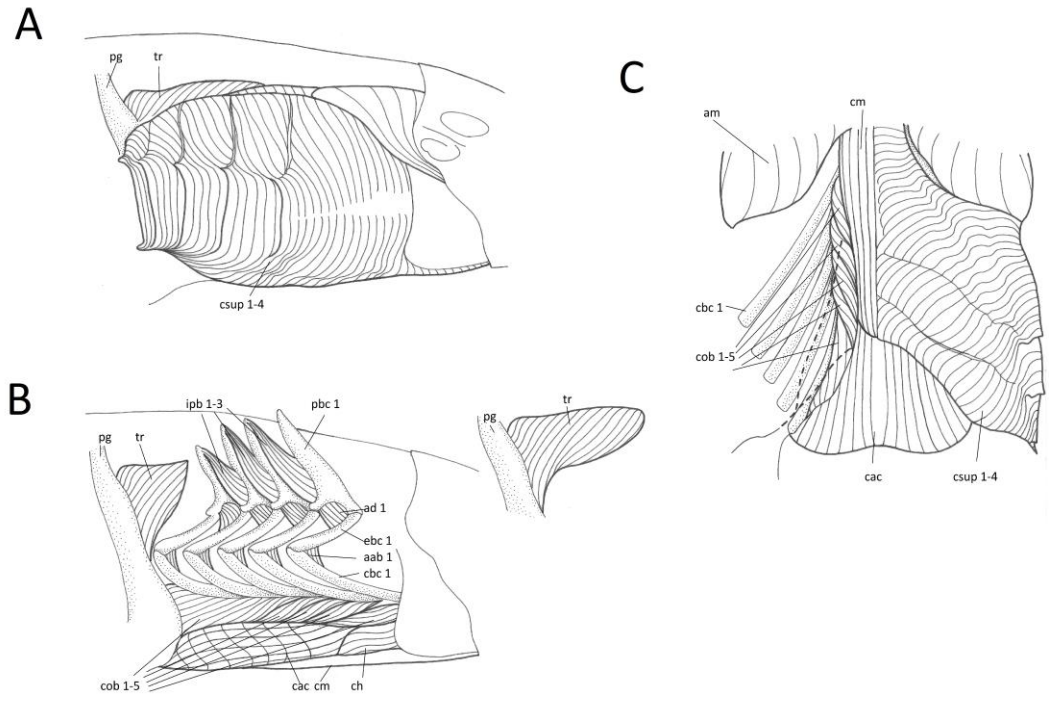

FIGURE 20. *Chilloscyllium punctatum* (USNM 176709, 729mm). Lateral superficial (A) and deep (B) views, with a detail on the *m. trapezius*. (C) Ventral superficial (right) and deep (left) views.

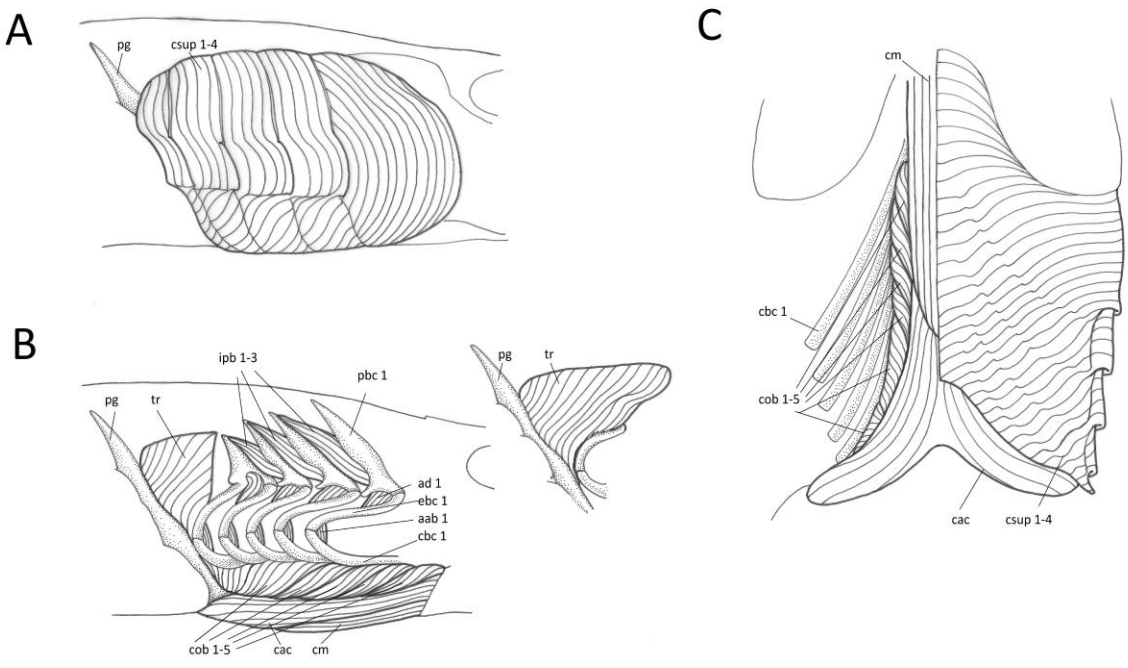

FIGURE 21. *Cirrhoscyllium formosanum* (USNM 395036, 226mm). Lateral superficial (A) and deep (B) views, with a detail on the *m. trapezius*. (C) Ventral superficial (right) and deep (left) views.

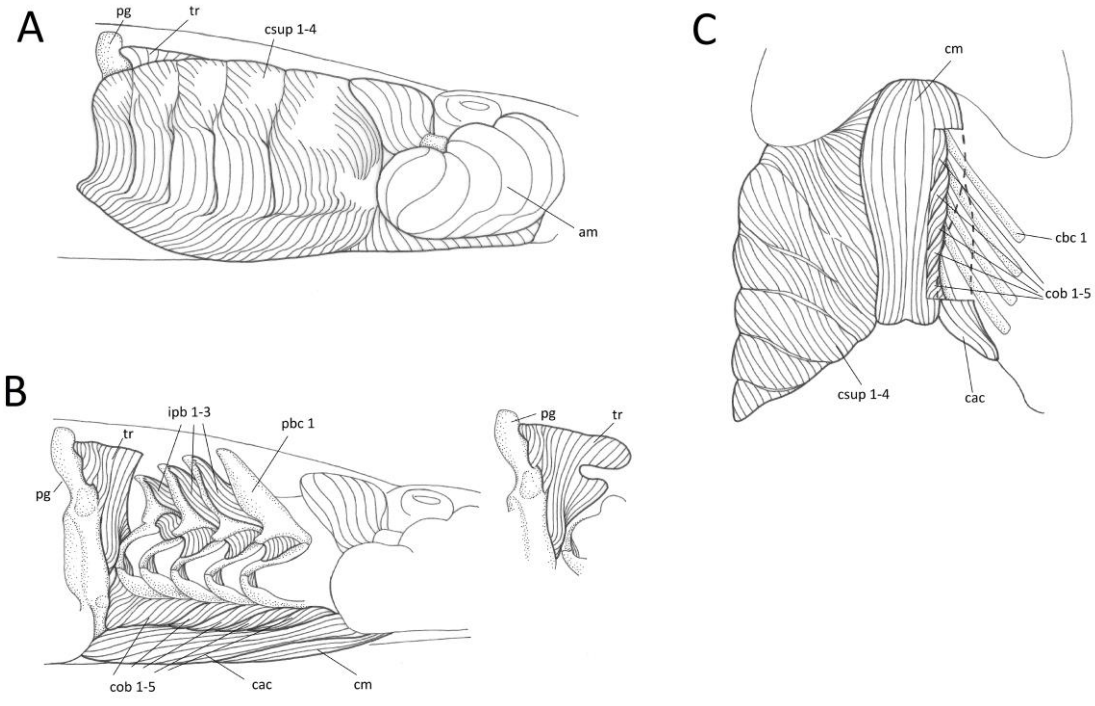

FIGURE 22. *Ginglymostoma cirratum* (SU 8116, 271mm). Lateral superficial (A) and deep views (B), with a detail on the *m. trapezius*. (C) Ventral superficial (right) and deep (left) views.

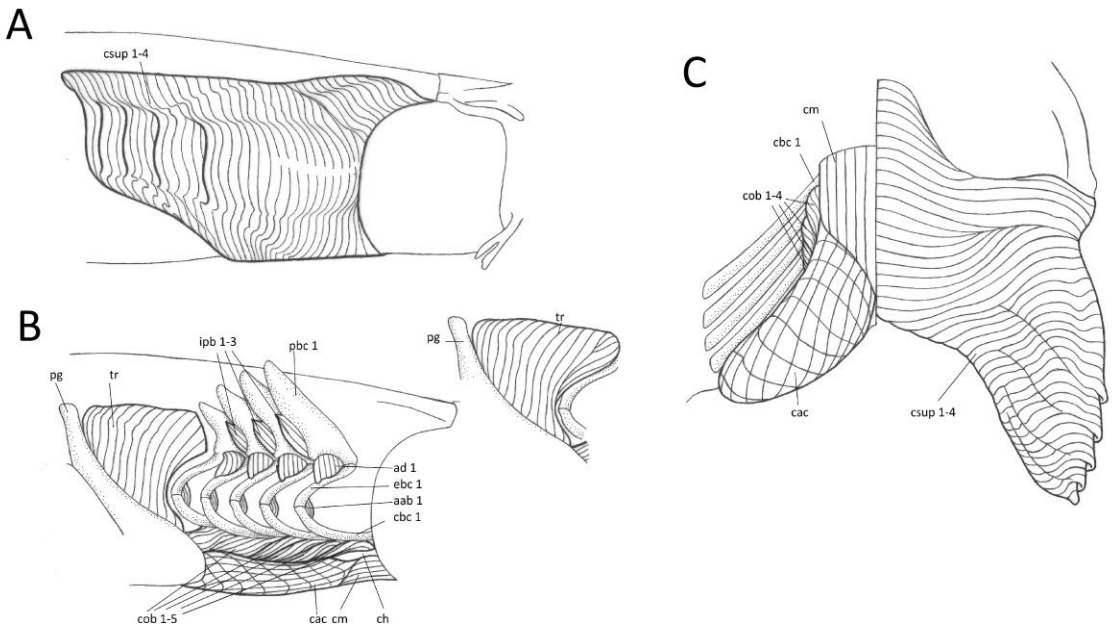

FIGURE 23. *Orectolobus maculatus* (USNM 39999, 615mm). Lateral superficial (A) and deep (B) views, with a detail on the *m. trapezius*. (C) Ventral superficial (right) and deep (left) views.

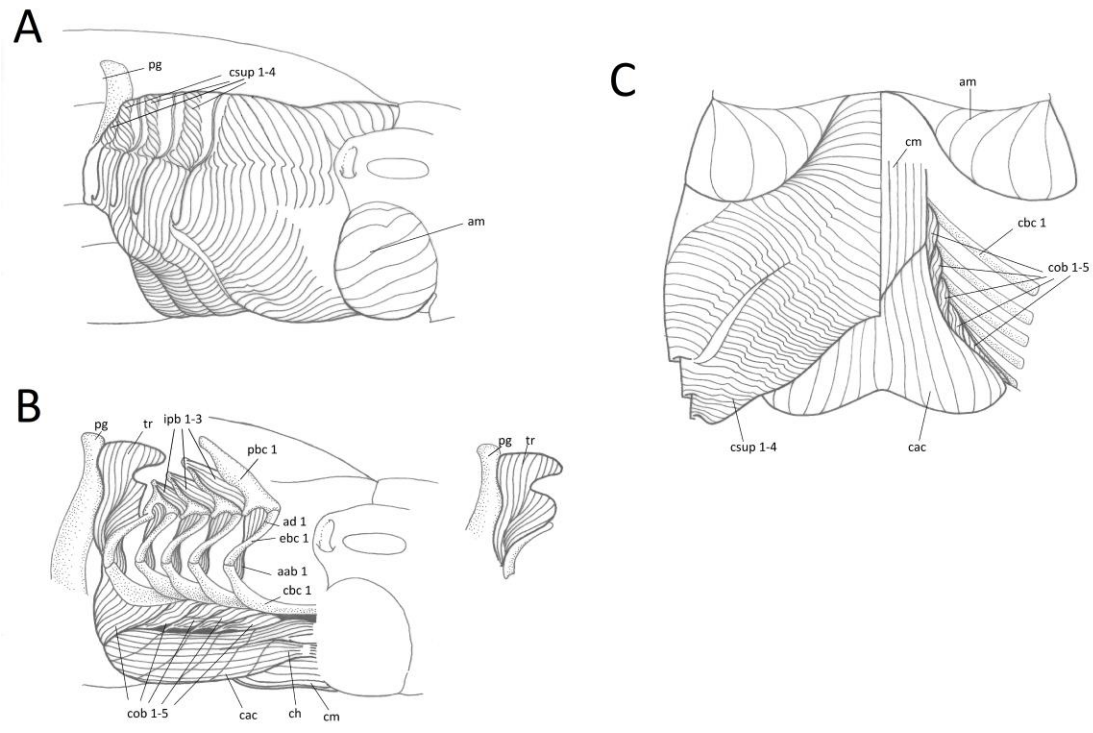

FIGURE 24. *Stegostoma fasciatum* (USNM 138548, 294mm). Lateral superficial (A) and deep (B) views, with a detail on the *m. trapezius*. (C) Ventral superficial (right) and deep (left) views.

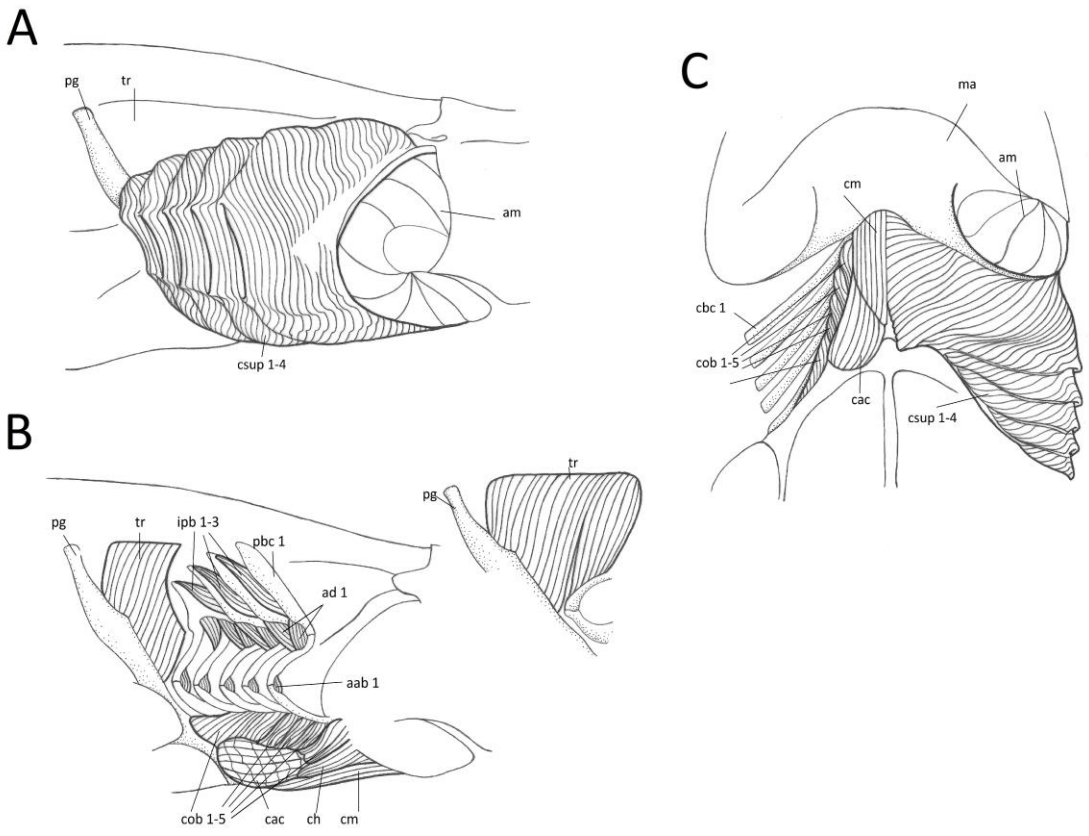

FIGURE 25. *Centrophorus squamosus* (SU 8582, 390mm). Lateral superficial (A) and deep (B) views, with a detail on the *m. trapezius*. (C) Ventral superficial (right) and deep (left) views.

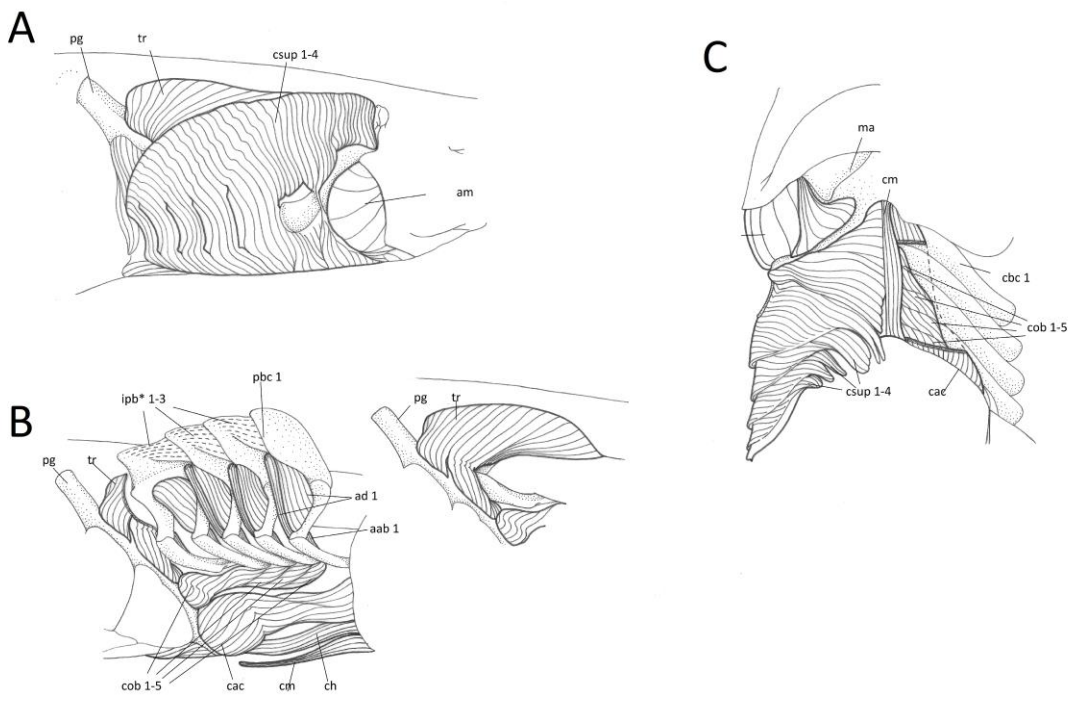

FIGURE 26. *Dalatias licha* (MZUSP uncat., 323mm). Lateral superficial (A) and deep (B) views, with a detail on the *m. trapezius*. (C) Ventral superficial (right) and deep (left) views.

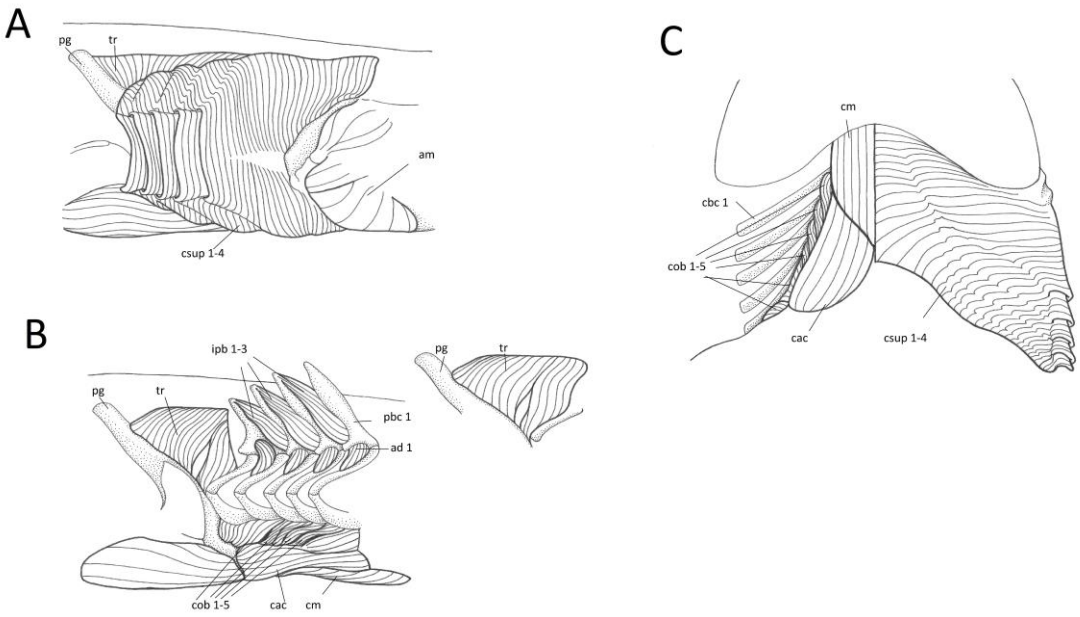

FIGURE 27. *Centroscyllium nigrum* (USNM 220270, 367mm). Lateral superficial (A) and deep (B) views, with a detail on the *m. trapezius*. (C) Ventral superficial (right) and deep (left) views.

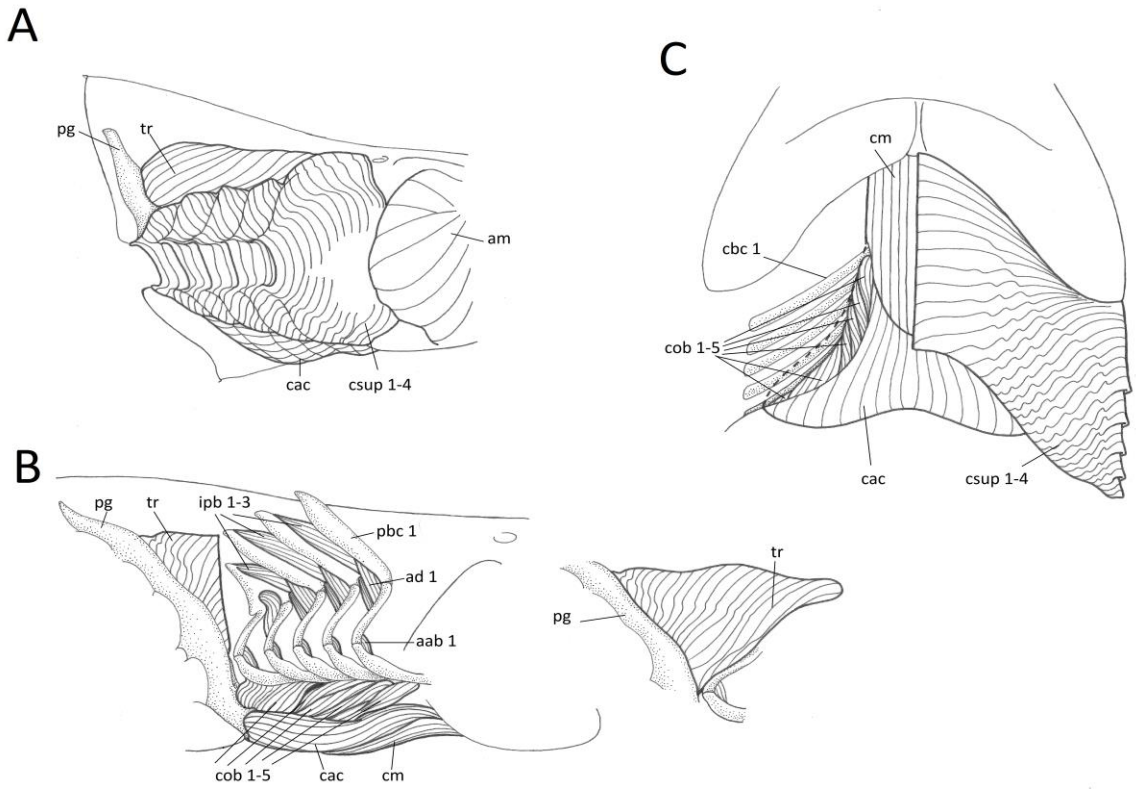

FIGURE 28. *Scymnodon obscurus* (USNM 220509, 361mm). Lateral superficial (*Centroscymnus coelolepis*) (A) and deep (B) views, with a detail on the *m. trapezius*. (C) Ventral superficial (right) and deep (left) views.

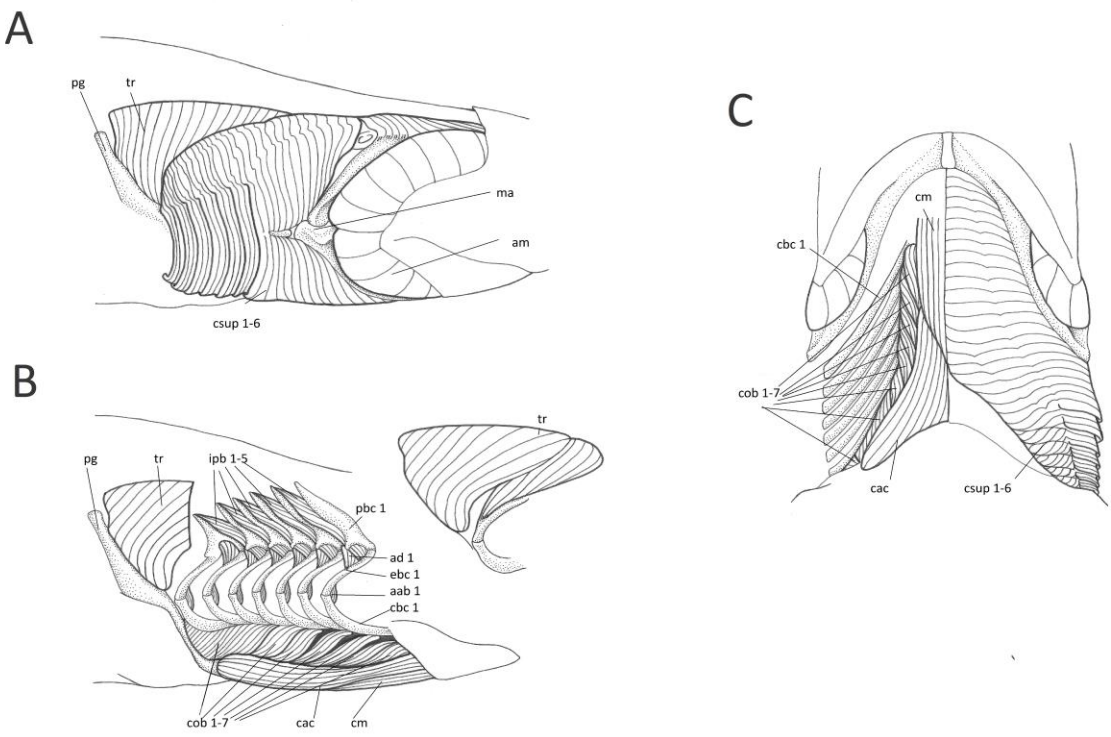

FIGURE 29. *Notorynchus cepedianus* (CAS 39612, 565mm). Lateral superficial (A) and deep (B) views, with a detail on the *m. trapezius*. (C) Ventral superficial (right) and deep (left) views.

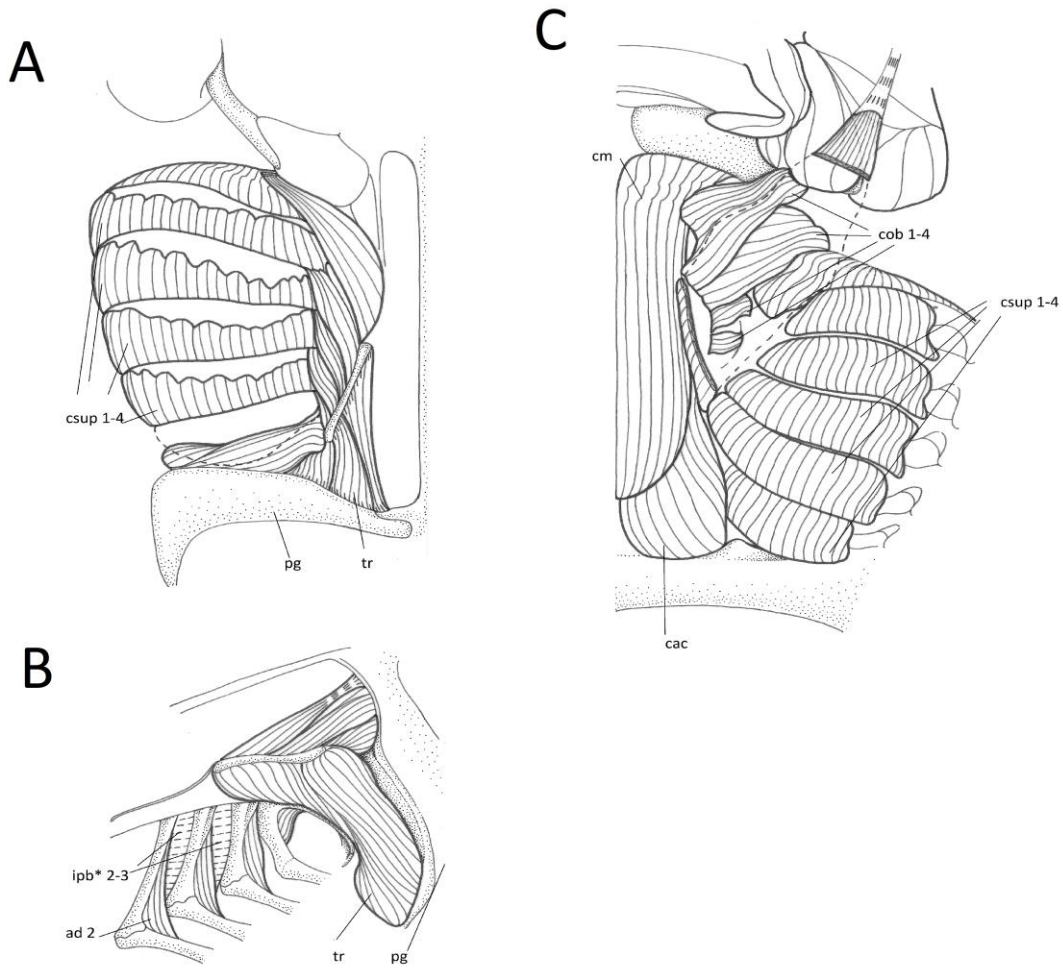

FIGURE 30. *Zapteryx brevirostris* (MZUSP uncat., 476mm). Dorsal superficial (A) and deep (B) views, with a detail on the *m. trapezius*. (C) Ventral view.

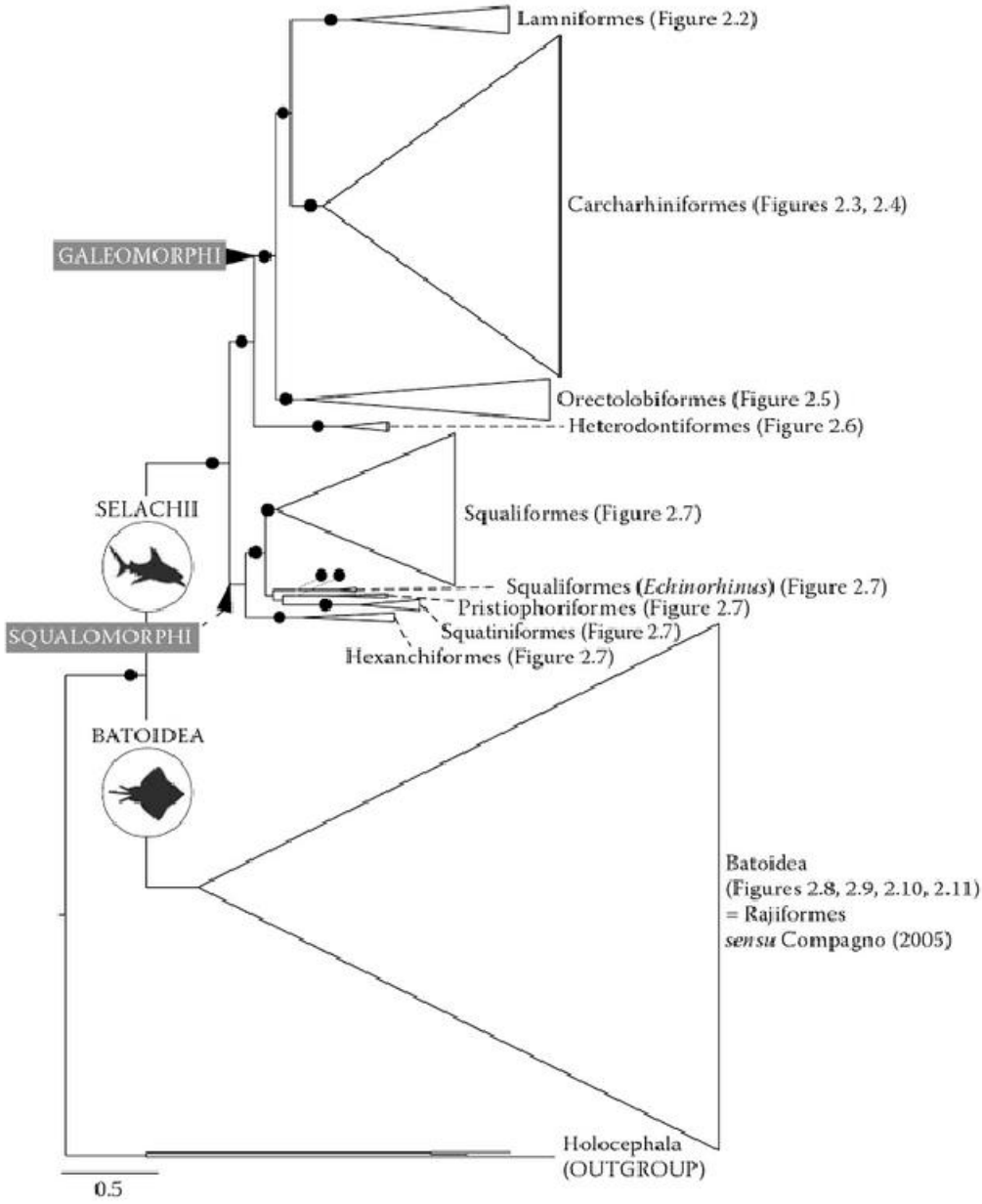

FIGURE 31. Cladogram extracted from Naylor et al. (2012), showing the interrelationships of the orders.

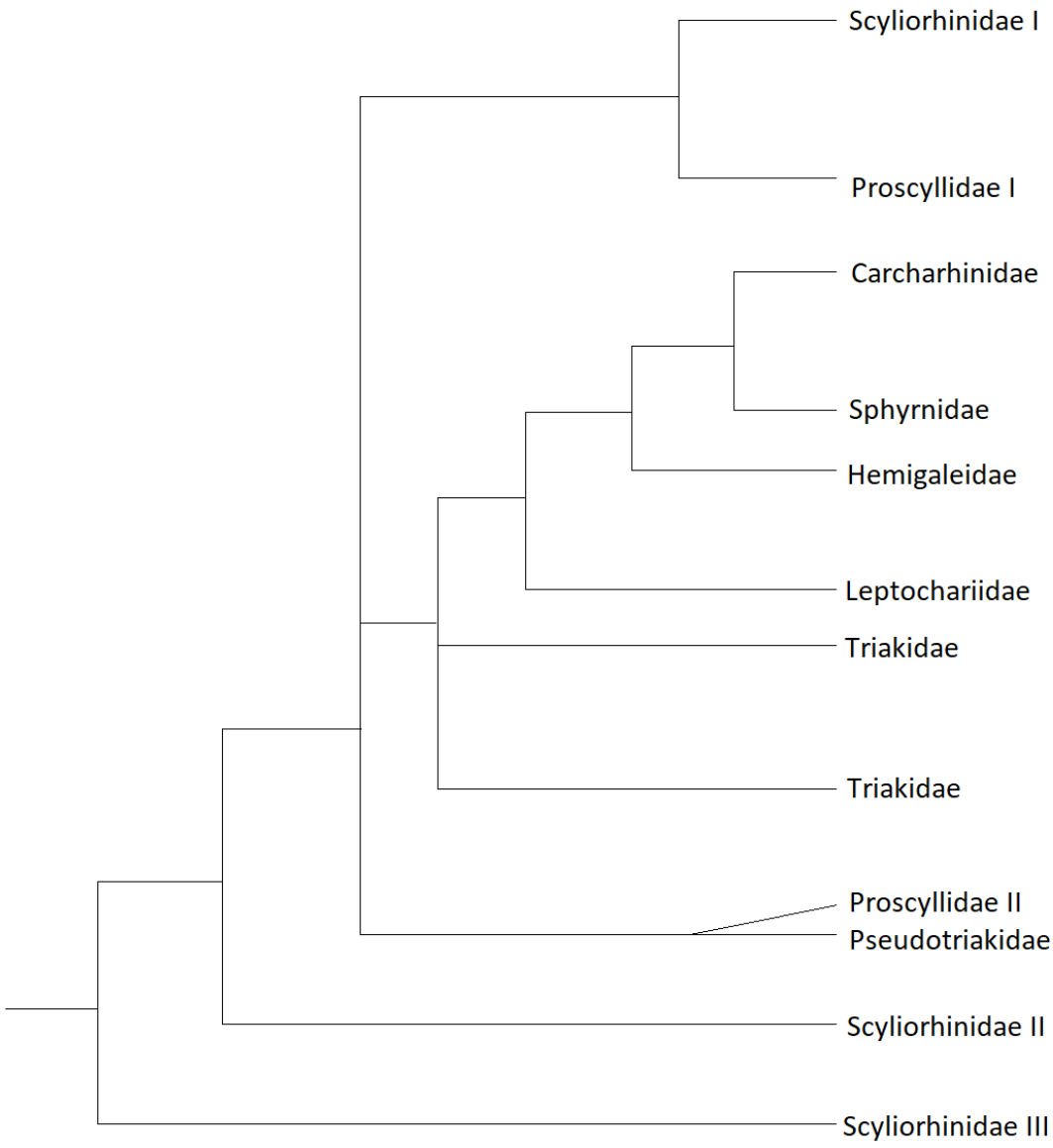

FIGURE 32. Cladogram of Carcharhiniformes according to Naylor et al. (2012), adapted.

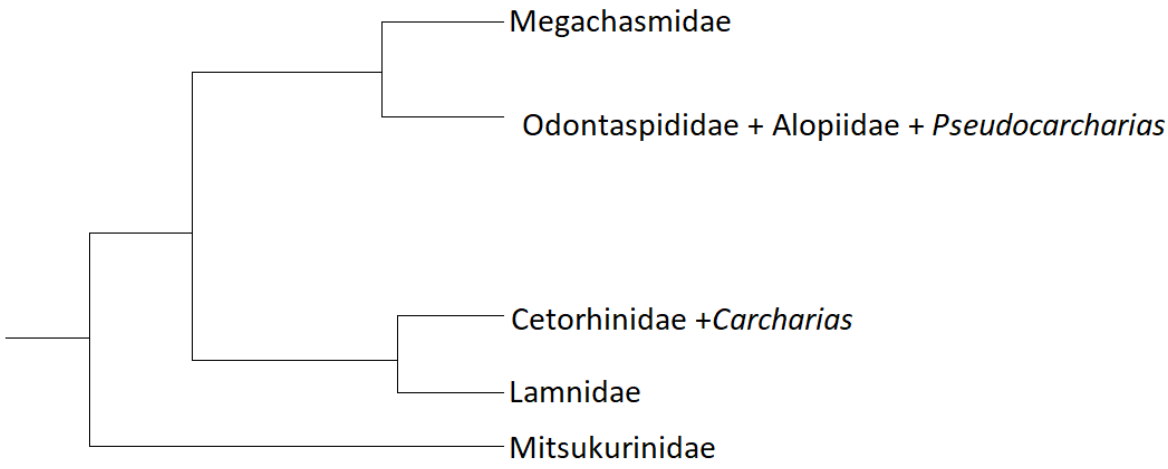

FIGURE 33. Cladogram of Lamniformes according to Naylor et al. (2012), adapted.

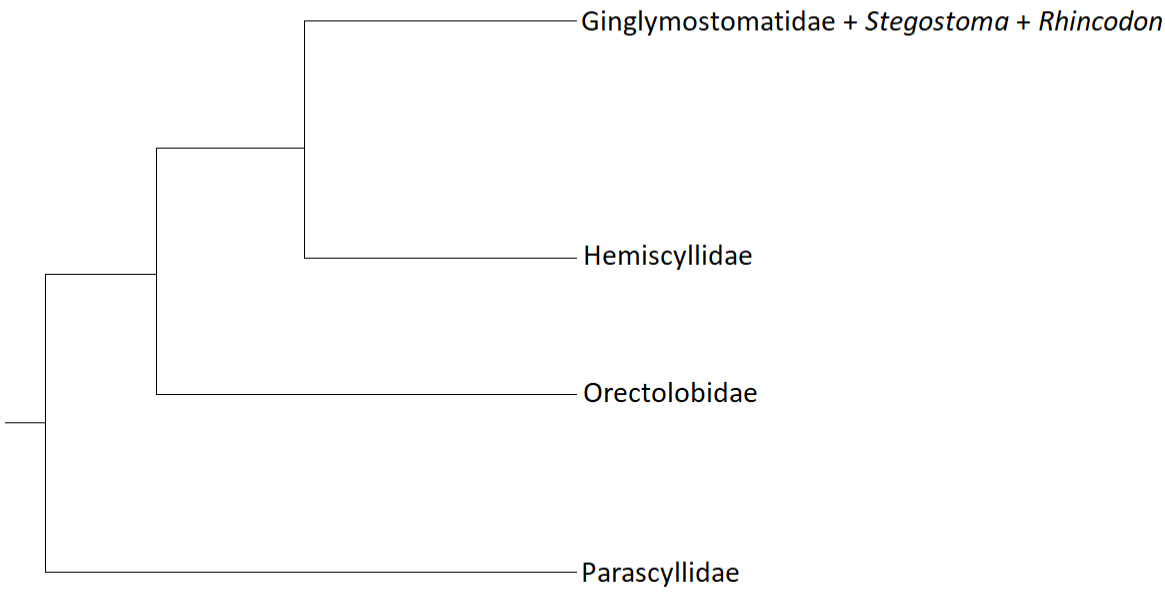

FIGURE 34. Cladogram of Orectolobiformes according to Goto (2001), adapted.

4. Characters recovered in this study

Muscle (Character)	State 1 (present in)	State 2 (present in)
m. constrictores branchiales superficiales	raphe not present between the two antimeres (Squalomorphi, Orectolobiformes, Heterodontiformes and *Zapteryx*)	raphe present between the two antimeres (Lamniformes and Carcahrhiniformes)
m. trapezius	divided in two, slender rami with both insertions (Hexanchiformes, Lamniformes, Carcharhiniformes and *Zapteryx*)	one single ramus with two insertions (Squaliformes)
m. adductores arcuum branchialium	triangular shaped muscle (Squalomorphi, Orectolobiformes, Heterodontiformes, Scyliorhinidae, Pentanchidae, Proscyllidae, Pseudocarchariidae, Alopiidae, Mitsukurinidae and *Zapteryx*)	crescent shaped muscle (Scyliorhinidae, Leptochariidae, Hemigaeidae, Sphyrnidae except *Eusphyra*, Carcharhinidae except *Galeocerdo*, *Loxodon* and *Triaenodon*, Lamnidae and Odontaspididae)
m. interpharyngobranchiales	all three elements muscular (Carcharhiniformes, Lamniformes, Heterodontiformes, Hexanchiformes, Squalidae, Ginglymostomatidae, *Stegostoma*, *Chilloscyllium* and *Zapteryx*)	the third element is composed of connetive tissue (Orectolobidae, Parascyllidae, Somniosidae and Etmopteridae
m. arcuales dorsales	single slip (Galeomorphi and *Zapteryx*)	double slips (Squalomorphi sharks)
m. coracobranchiales 1-4	compressed dorsoventrally (Squaliformes, Orectolobiformes, Heterodontiformes, Carcharhiinformes except Carcharhinidae, Alopiidae, Mitsukurinidae and *Zapteryx*)	compressed laterally (Lamnidae, Odontaspididae, Pseudocarchariidae and Carcharhinidae except *Nasolamia*)
m. coracobranchialis 5	not divided (Squalomorphi, Heterodontiformes, Orectolobiformes, Scyliorhinidae, Alopiidae, Mitsukurinidae and *Zapteryx*)	partially divided (Proscyllidae and Pentanchidae)
m. constrictor oesophagi	not reduced (every species dissected except *Mitsukurina*)	reduced (only present in *Mitsukurina*)

Muscle (Character)	State 3 (present in)
m. constrictores branchiales superficiales	raphe not present and reduced antimeres, with the presence of connective tissue (Ginglymostomatidae and *Stegostoma*)
m. trapezius	one single ramus with one insertion (Orectolobiformes and Heterodontiformes)
m. adductores arcuum branchialium	-
m. interpharyngobranchiales	all three elements connective (Dalatiidae and *Hemiscyllium*)
m. arcuales dorsales	-
m. coracobranchiales 1-4	cyllindrical (*Nasolamia*)
m. coracobranchialis 5	completely divided (Triakidae, Leptochariidae, Hemigaleidae, Carcharhinidae, Pseudocarchariidae,
m. constrictor oesophagi	-

Biography

Lucas Romero de Oliveira was born in 1992 and entered the University of São Paulo (USP) at age 17, in 2010, to study Biological Sciences. He was a monitor in the exhibition of the Museu de Zoologia – USP (MZUSP) on his first year as an undergraduate student and was a student in the Polychaeta lab for one semester during the second year, on the Departamento de Zoologia. Later, on his fourth year (late 2013), he entered the Laboratório de Ictiologia of the same department and got his bachelor´s degree presenting a morphological analysis of the tail musculature in sharks, with focus in the family Carcharhinidae among the order Carcharhiniformes. On September 2015, entered the graduate program in Zoology at Instituto de Biociências – USP (IBUSP) as a master's student.