

Nerves of the Mandibular Musculature of the Sand Tiger Shark *Carcharias taurus* (Rafinesque, 1810) (Chondrichthyes: Odontaspidae)

Nervios de la Musculatura Mandibular del Tiburón Toro *Carcharias taurus*
(Rafinesque, 1810) (Chondrichthyes: Odontaspidae)

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SUMMARY: During this study, fifteen shark heads of sand tiger shark *Carcharias taurus* (Rafinesque, 1810) were analyzed. The studied material was obtained in the Santos Fishing Terminal, São Paulo, Brazil. The heads dissection was focused on the characterization of the mandibular muscles and on the description of the mandibular branch of the trigeminal nerve. The *C. taurus* mandibular muscles are represented by: *m. preorbitalis*, *m. levator palatoquadrati*, *m. quadratomandibularis* and *m. intermandibularis*. The origin of the trigeminal nerve of *C. taurus* is located in a lateral portion of the medulla oblongata. In the orbita, the trigeminal nerve branches off to originate the mandibular branch that innervates the muscles which are derived from the mandibular arch. The proximal branches of the trigeminal nerve mandibular branch innervate the *m. levator palatoquadrati*. The muscles *preorbitalis* and *quadratomandibularis* receive fibers from the intermediate branches of the trigeminal nerve mandibular branch and the distal ramification of the mandibular branch can be visualized in the *m. intermandibularis*.

KEY WORDS: Shark; Anatomy; Trigeminal nerve; Mandibular musculature.

INTRODUCTION

Sharks and their relatives have been used as anatomic models of vertebrates ancestors for a long time by the researchers. However, few studies furnish information about the central and peripheral nervous system. These cranial nerves are a problematic subject, as well as in other vertebrates, especially in relation to the trigeminal, facial and auditory nerves origin and their ramification.

The trigeminal nerve has three main divisions: ophthalmic nerve, maxillary nerve and mandibular nerve in sharks and other vertebrates (Hildebrand, 1995, Romer & Parsons, 1985). The trigeminal nerve innervates structures derived from the mandibular arch in elasmobranchs and the mandibular nerve sends its branches to the mandibular muscles (Harder, 1975). Other authors have also described the mandibular musculature

as the effector of the mandibular nerve in some sharks and rays species like *Notorynchus cepedianus* (Daniel, 1934), *Squalus sp* (Gilbert, 1986, Whitehouse & Grove, 1947), *Squalus acanthias* (Gans & Parsons, 1964), *Mustelus canis* and *Raja eglanteria* (Song & Boords, 1993).

Recent studies described the mandibular musculature of *Negaprion brevirostris* and *Ginglymostoma cirratum* as *m. levator palatoquadrati*, *m. preorbitalis*, *m. quadratomandibularis* and *m. intermandibularis* (Motta & Wilga, 1995, 1999). These muscles are effectors of the mandibular nerve. Their ramifications were described as: proximal branches that innervates the *m. levator palatoquadrati*; intermediate branches that innervates the muscles *preorbitalis* and *quadratomandibularis* and the distal braches that reaches the *m. intermandibularis* (Song & Boord).

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The innervation of the muscles that derived from the mandibular arch and the location of the motoneurons (located in the mandibular nerve) reflect their segmental origins and are reliable criteria for homologizing mandibular muscles among the craniates (Song & Boord).

Only a very few studies have dealt with the Neuroanatomy of elasmobranches. The present study has been undertaken to describe the *C. taurus* mandibular musculature nerves and to provide more detailed information concerning the anatomical features of the trigeminal nerve of this species, as well as its precisely origin on the *encephalon*. This data will be very important to future comparative studies with others members of the Lamniformes Order.

MATERIAL AND METHOD

For the purpose of this investigation, fifteen specimens of *C. taurus* were used. The exemplars derived from the fishery discard, sited at the Terminal de Pesca de Santos, São Paulo, Brazil. Only the heads were collected and the species was confirmed by the Compagno (1984) and Figueiredo (1977) identification keys. The material was fixed in a 20% formaline solution by filling the space between the *canalis vertebralis* and the surface of the *medulla*. This procedure allowed reaching the cranial cavity, what promoted the nervous tissues fixation. The material was stored in the same solution for one year at the Núcleo de Pesquisa e Estudos em Chondrichthyes (NUPEC). Before the dissection, the heads were decalcified following the Behmer *et al.* (1976) decalcified technique, modified by Intelizano (1999) for bonny fishes. This procedure makes the sharks skin, cartilage and connective tissue softer, as well as produces a soft yellowish coloration in the muscular tissue that permitted a differentiation between muscles and nerves, allowing a better dissection approach. Before all the dissection session, the specimens were immersed in water. These procedures were performed from the superficial layers to the deep ones. With the naked eye, we handled the nerve branches with great care as not to injure them, no matter how great they were, so then we could keep them intact for subsequent analyses. The procedures were photographed and illustrated. The dissected material was stored in alcohol 700GL and pure Glycerin solution, contributing to keep the tissues flexible. All the dissections occurred with the naked eye. The muscles nomenclature was adopted following Motta & Wilga (1995, 1999) works and modified, when necessary, by the *Nomina anatomica veterinaria* norms (Schaller, 1999). For the nervous system nomenclature, Gilbert, Song & Boord and Schaller were adopted.

RESULTS

The mandibular muscles in *C. taurus* were:

1. *M. levator palatoquadrati*. Located caudally to the postorbital process. This muscle possesses a portion that could be found in the orbita, dorsally to the palatoquadrate cartilage. In the orbital portion of the *m. levator palatoquadrati*, it was possible to visualize the imprint of the mandibular branch of the trigeminal nerve. Dorsally to this muscle, we could find the *m. epaxialis* and ventrally, the *quadratmandibularis* one (Fig. 1).

2. *M. preobitalis*. Located laterally to the palatoquadrate cartilage. This muscle presents its cranial origin in the nasal capsule and ends caudally in the *m. quadratomandibularis* median *raphe*. The muscle fibers are parallelly placed and the muscle presents ventral and dorsal divisions (Fig.1).

3. *M. quadratomandibularis*. The greatest muscle that derives from the mandibular arch. This muscle presents two main divisions: dorsal (*m. quadrotomandibularis dorsalis*) (Fig.1) and ventral (*m. quadratomandibularis ventralis*) (Fig.2). The *m. quadratomandibularis dorsalis* also presents two proper divisions: *m. quadratomandibularis dorsalis lateralis* and *m. quadratomandibularis dorsalis medialis* (Fig.1). The *m. quadratomandibularis ventralis* does not present any subdivisions. The *m. quadratomandibularis* is a *digastricus* muscle. Dorso-laterally to the *m. quadratomandibularis*, we could verify a great ramification of the facial nerve and some branches lay over the *m. quadratomandibularis dorsalis*. This innervation does not send muscular branches to the *m. quadratomandibularis dorsalis* and during its dissection, we verified the presence of connective tissue, adipose tissue and a jelly substance from the Lorenzini *ampulla* channels surrounding the facial nerve branches.

The *m. quadratomandibularis* is located in the last third of both the palatoquadrate and the mandibular cartilage and jointly with the *m. preorbitalis*; it forms the *adductor mandibulae* complex. This complex is responsible for the mouth closure.

4. *M. intermandibularis*. Located in the ventral portion of the head. It extends caudally from the limit of the commercial incision up to the mandibular *symphysis*, cranially. It is a superficial constrictor muscle (Fig.2).

The trigeminal nerve and its ramifications in *C. taurus*. The trigeminal nerve has three divisions: mandibular, maxillary and ophthalmic branches (Fig. 8). Its origin is related to a lateral portion of the *medulla oblongata*, ventrally to the auricle of *cerebellum*. Three roots could be clearly distinguished, two of

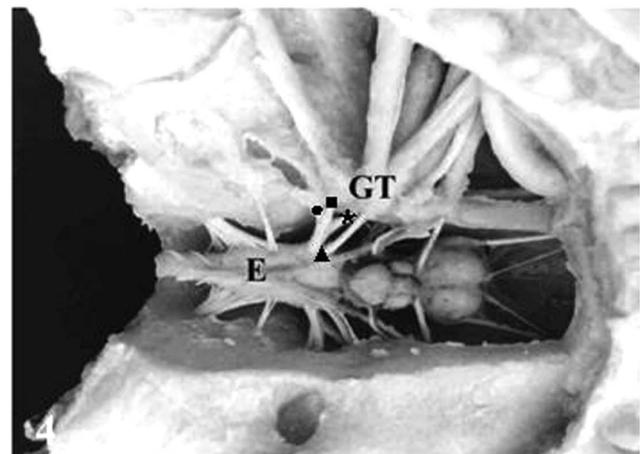
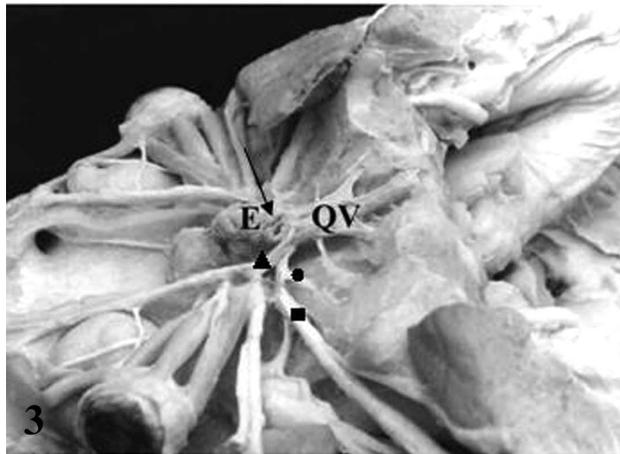
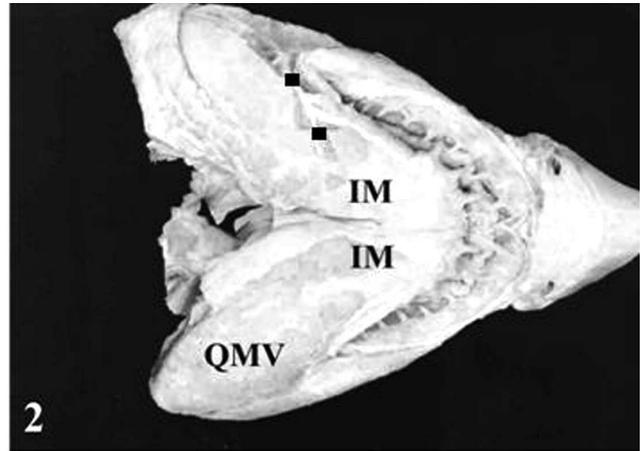
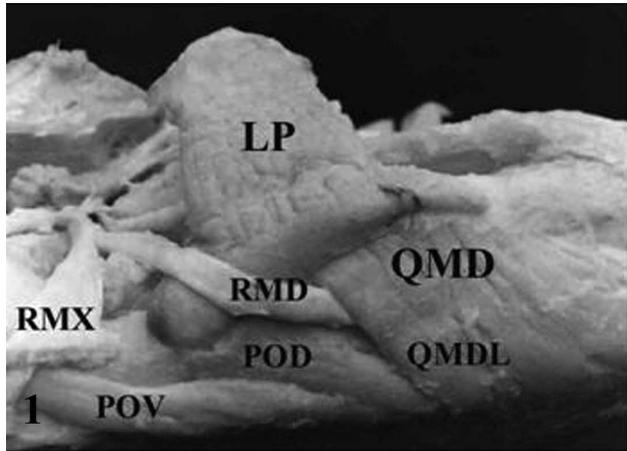


Fig. 1. Left lateral view. QMD. *M. quadratomandibularis dorsalis*; QMDL. *M. quadratomandibularis dorsalis lateralis*; LP. *M. levator palatoquadrati*; POD. *M. preorbitalis dorsalis*; POV. *M. preorbitalis ventralis*.

Fig. 2. Ventral view. IM. *M. intermandibularis*; QMV. *M. quadratomandibularis ventralis*; n. Distal branches of the trigeminal nerve.

Fig. 3. Left dorso-lateral view. E. *Encephalon*; QV. *Ventriculus quartus*; black arrow. Auricle of *cerebellum*; s. Proximal branches of trigeminal nerve; l. Auditory nerve; n. Facial nerve.

Fig. 4. Ventral view. E. *Encephalon*; GT. Trigeminal ganglion; s. Distal branches of trigeminal nerve; * Proximal branches of trigeminal nerve); l. Auditory nerve; n. Facial nerve.

then proximal to the auricle of *cerebellum* (Fig. 3) and another one located, in ventral view, cranio-medially in relation to the first ones (Fig. 4).

Two branches are proximal to the auricle of *cerebellum* and they leave the *encephalon* very close to the facial and auditory nerves, which could be visualized, in ventral view, caudo-laterally to them. The facial nerve origin, in relation to the origin of the proximal branches of the trigeminal nerve, is located in ventral position and both the proximal branches and facial nerve origins are very close. The origin of the auditory nerve is caudal to the facial nerve. The trigeminal proximal branches close to the auricle of *cerebellum*; the facial nerve and the auditory nerve get separated in the cranial cavity. The first ones run cranially and join the distal branch of the trigeminal nerve distantly to the auricle of *cerebellum*, forming the trigeminal ganglion located in the *orbita* medial wall. The auditory nerve runs caudally, ranging the optic capsule region and the facial nerve presents ramifications in the orbital region (Fig. 4).

Following the trigeminal ganglion, the trigeminal nerve presents the follow divisions:

1. The ophthalmic branch. It runs in the orbita in cranial direction laterally to the *orbita* medial wall. This nerve leaves the orbita through the infraorbital foramen and then reaches the *ampulla*'s channels widely distributed in the animal rostral region.

2. The maxillary branch (Fig. 5). Proximal to the trigeminal ganglion, the maxillary branch is joined to the mandibular one; nevertheless, we could clearly verify a division between both of them. The maxillary branch is cranio-ventrally located in relation to the mandibular branch and it runs in a lateral direction in the orbita. Great extension of its pathway is located ventrally to the extra-ocular musculature and the ocular bulb. Close to the *M. preorbitalis*, there is an enlargement of the maxillary branch, before it reaches the palatoquadrate cartilage.

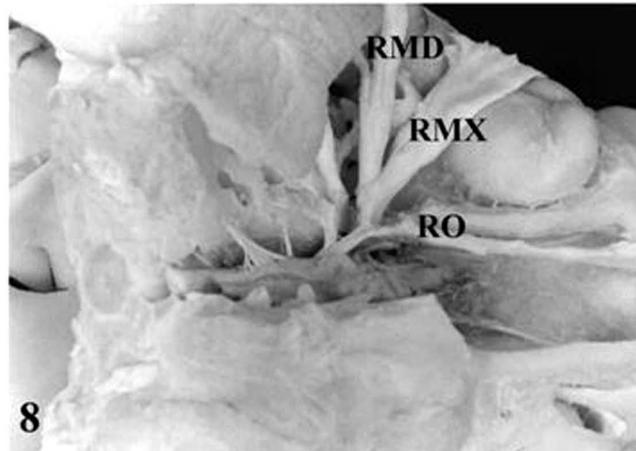
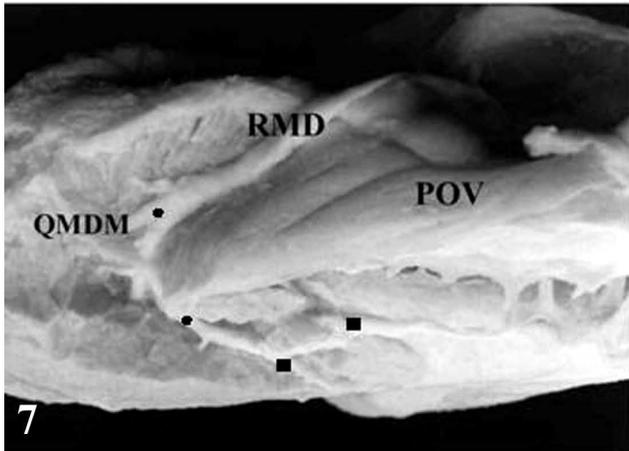
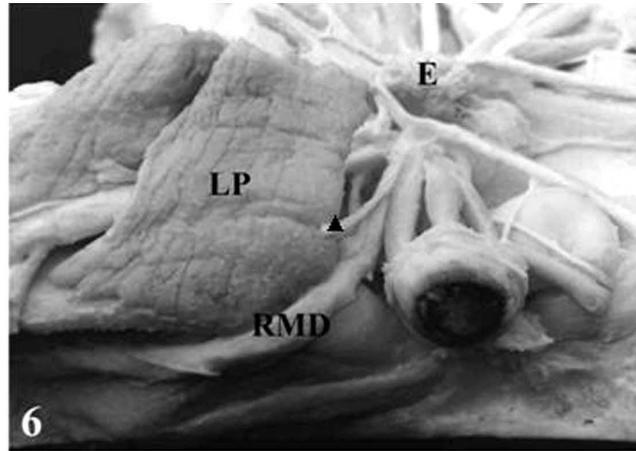
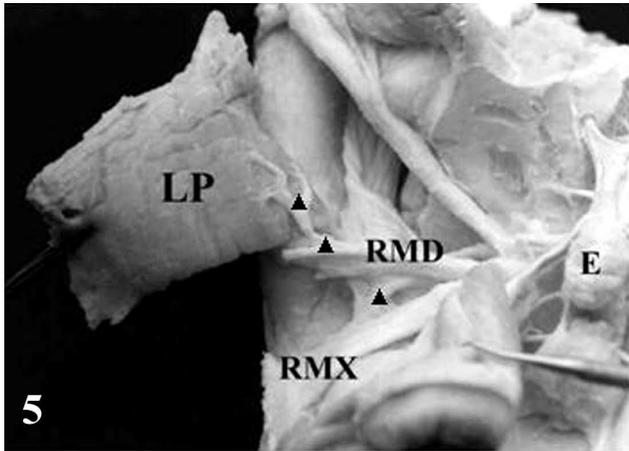


Fig.5- Dorsal view. RMD (mandibular branch); RMX (maxillary branch); LP (*M. levator palatoquadrati*); E (encephalon) and s (proximal branches of mandibular branch).

Fig.6- Right dorso-lateral view. E (encephalon); RMD (mandibular branch); LP (*M. levator palatoquadrati*) and s (proximal branches of mandibular branch).

Fig.7- Right lateral view. RMD (mandibular branch); QMDM (*M. quadratomandibularis dorsalis medialis*), PO (*M. preorbitalis*); l (intermediate branches of mandibular branch) and n (distal branches of the mandibular branch).

Fig. 8- Dorsal view. RMD (mandibular branch); RMX (maxillary branch) and RO (ophthalmic branch).

3. The mandibular branch. During its pathway in the orbita, a division of the branch takes place and sends a branch to both dorsal and ventral faces of the *M. levator palatoquadrati* (Figs. 5 and 6) The branches of this ramification are called proximal branches of the trigeminal nerve mandibular branch. Following the mandibular branch track over the orbital portion of the *M. levator palatoquadrati*, we observed that this nerve sends branches to the *Mm. preorbitalis* and *quadratomandibularis* (Figs. 6 and 7). The lateral and medial portions of the *M. quadratomandibularis dorsalis* receive muscular branches from the trigeminal nerve mandibular branch (Fig.7) and this nerve is also responsible for the innervations of the *M. quadratomandibularis ventralis* (Fig. 2). This ramification of the mandibular branches over the *Mm. preorbitalis* and *quadratomandibularis* receives the denomination of intermediate branches of the trigeminal nerve mandibular branch. In the final portion of its track, the mandibular branch is divided once again, sending branches to the *M. intermandibularis* and to the mandibular cartilage, that are identified as distal branches of the trigeminal nerve mandibular branch (Fig. 2).

DISCUSSION

Our results are in agreement with the pattern found in other studies about the musculature derived from the mandibular arch in elasmobranchs (Daniel; Gans *et al.*; Harder; Lagler *et al.*, 1977; Romer *et al.*; Gilbert; Hildebrand; Motta *et al.*, 1995, 1999).

The *M. levator palatoquadrati*, *M. preorbitalis*, *M. quadratomandibularis* and *M. intermandibularis* are present in *C. taurus* and other sharks and rays species. Thus, despite the interspecific differences among the studied animals, a pattern of muscles derived from the mandibular arch could be established.

In contrast, we found some differences between the anatomy of *C. taurus* and *N. brevirostris* related to the muscles that form the adductor mandibulae complex.

In *N. brevirostris*, the *M. preorbitalis* is clearly divided in a dorsal head and a ventral head, being this last one originated in the medial wall of the orbita (Motta *et al.*, 1995). Our results indicate

a muscle that presents divisions in the dorsal and ventral heads, being most of the time, lateral to the palatoquadrate cartilage. The *M. quadratomandibularis* can also be divided in two distinct parts: the *M. quadratomandibularis dorsalis*, which can be divided in another four parts and the *M. quadratomandibularis ventralis* (Motta *et al.*, 1995). In *C. taurus*, the dorsal and ventral divisions of the *M. quadratomandibularis* could be distinguished. Furthermore, the *M. quadratomandibularis dorsalis* presented two subdivisions that were denominated *M. quadratomandibularis dorsalis lateralis* and *M. quadratomandibularis dorsalis medialis*, being the mandibular branch of the trigeminal nerve laterally to the last one.

We believe that the *M. quadratomandibularis dorsalis* of *C. taurus* may present some other subdivisions besides the two subdivisions described above (Motta *et al.*, 1995). However, since our studied material has not been obtained from fresh samples captured exclusively for the research, as in other studies, we can not assert that the *C. taurus M. quadratomandibularis dorsalis* is a poligastricus a muscle.

Motta *et al.* (1995) could work with different kinds of analyses due to the condition of the collected material, what permitted the use of proper histological and anatomical studies that collaborated to the definition of the muscle quadratomandibularis as a poligastricus muscle in *N. brevirostris*. Such procedures were not done in our samples, in which we decided to characterize and identify the mandibular musculature, trying to delimitate the muscular effectors of the trigeminal nerve mandibular branch, what has facilitated the comprehension of *C. taurus* mandibular nerves.

The mandibular innervation of *C. taurus* is in agreement with the general pattern established for all the vertebrates, in which the trigeminal nerve presents the ophthalmic, maxillary and mandibular divisions (Hildebrand, 1995, Romer *et al.*, 1985). However, many peculiarities could be observed in other studies that describe the innervation of other species of elasmobranchs.

In *C. taurus*, the trigeminal nerve division takes place close to the medial wall of the orbita, similarly to what happens in *N. cepedianus* (Daniel, 1934); however, it is not possible to assert that the apparent origins of the trigeminal and facial nerves, according to the results obtained in *C. taurus*, are similar, as described for *N. cepedianus* by the author above cited.

Nevertheless, Daniel asserts that the origin of the trigeminal nerve is slightly cranio-facial to the facial nerve. Such assertive invalidates the first one: the apparent origins of the trigeminal and the facial nerves are similar. Comparing the results obtained in *C. taurus* it is possible to visualize, in ventral view, the apparent origin of the facial nerve located caudally to the trigeminal nerve, agreeing, this way, with the author in his second assertive.

C. taurus presented the ramification of the trigeminal nerve proximal to its own origin in the encephalon, what differs from

Witehouse *et al.* finds for *Squalus sp.* For this species, the branching of the trigeminal nerve takes place distally both to the medial wall of the orbita and the trigeminal ganglion.

To Witehouse *et al.* the trigeminal, the facial and the auditory nerves originate all together in lateral portions of the medulla oblongata. This assertive is not in agreement with the results found in *C. taurus*, once through carefully dissections on the naked eye; it was possible to evidence apparent origins for the nerves trigeminal, facial and auditory.

Our findings, that the apparent origin of the trigeminal, facial and auditory nerves in *C. taurus* are not the same, are in accordance to squalid sharks and rajid rays that presented separated origins for the facial, trigeminal and auditory nerves (Harder).

On the other hand, our results contrast with those described by Gilbert (1986) who affirms that the trigeminal, facial and auditory nerves presented a common origin in the medulla oblongata, ventrally to the auricle of cerebellum for *Squalus sp.* In *C. taurus* the facial and the auditory nerves leave the medulla oblongata in continuation with the proximal branches of the trigeminal nerve that has originated from the auricle of cerebellum. The facial nerve branch is located slightly ventrally to the branches of the trigeminal nerve, close to the auricle of cerebellum. The auditory nerve branch originates caudally to the branch of the facial nerve.

The results obtained in *C. taurus* contradict the findings of Harder in relation to the ramifications of the mandibular branch. For the author above cited, the mandibular branch does not present dorsal divisions in elasmobranchs; however in *C. taurus* the mandibular nerve dorsally ramifies to innervate the dorsal face and ventral faces of the *M. levator palatoquadrati*. Song *et al.* corroborate this result while describing the branches of the mandibular branch of the trigeminal nerve in *Raja eglanteria* and in *Mustelus canis*. The proximal branch of the mandibular nerve, in the species previously cited, are responsible for the innervation of the *M. levator palatoquadrati*, being originated from a dorsal branch of the mandibular nerve.

A dorsal branch, proximal to the medial wall of the orbita, originates in the mandibular branch of *C. taurus* and it is responsible for the innervation of the *m. levator palatoquadrati*. This description agrees with the one from Song *et al.* for rays and sharks that denominates the branch as proximal branches of the trigeminal nerve mandibular branch. There are also the intermediate branches responsible for the innervation of the muscles: *Quadratomandibularis* and *Preorbitalis* and the distal branches of the trigeminal nerve mandibular branch that innervates the *m. intermandibularis*. The distal and intermediate branches of the trigeminal nerve mandibular branch are also recognized in *C. taurus*, and as suggested Song *et al.* they are, jointly with the proximal branches of the mandibular branch, the motor components of the trigeminal nerve responsible for the innervation of the mandibular musculature.

The musculature innervation of sharks heads mandibular segment and their localizations and segmental origins are important criteria for homology compared studies (Song *et al.*). We agree with such assertive, being sure that the results obtained in *C. taurus* can be of great value for future comparative and evolutive studies among other member of the lamnids group.

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RESUMEN: Fueron analizadas 15 cabezas de tiburón toro *Carcharias taurus* (Rafinesque, 1810), obtenidas en el Terminal Pesquero de Santos, São Paulo, Brasil. La disección permitió caracterizar los músculos mandibulares y describir la rama mandibular del nervio trigémino. Los músculos mandibulares de *C. taurus* son: *M. preorbitalis*, *M. levator palatoquadrati*, *M. quadratomandibularis* y *M. intermandibularis*. El origen aparente del nervio trigémino de *C. taurus* está localizado en la porción lateral de la médula oblonga. En la órbita, las ramas del nervio trigémino salen para dar origen a la ramificación mandibular, la cual inerva a los músculos derivados del arco mandibular. Las ramificaciones proximales de la rama mandibular del nervio trigémino inervan al *M. levator palatoquadrati*. Los *Mm. preorbitalis* y *quadratomandibularis* reciben fibras de las ramas intermedias de la ramificación mandibular del nervio trigémino, y el *M. intermandibularis* recibe la ramificación distal de la rama mandibular del nervio trigémino.

PALABRAS CLAVE: Tiburón; Anatomía; Nervio trigémino; Musculatura mandibular.

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