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ARTICLE

Anatomy of the neurocranium, encephalon, and main sensory organs of the roundel skate, *Rostroraja texana* (Rajiformes: Rajidae)

Anatomía del neurocráneo, encéfalo y principales órganos sensoriales de la raya *Rostroraja texana* (Rajiformes: Rajidae)

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Resumen.- La organización del neurocráneo, encéfalo y los principales órganos sensoriales de *Rostroraja texana* (Familia Rajidae) corresponde al patrón morfológico general de los elasmobranquios y en particular al de los batoideos. El neurocráneo presenta el rostro, que corresponde a cerca del 50% de la longitud craneal; asimismo, muestra las dos fontanelas dorsales de similar forma y tamaño. Las relaciones anatómicas del neurocráneo de *R. texana* son con: el encéfalo, los principales órganos sensoriales, cartílagos antorbitales, espiraculares y sinarcual; así como con la musculatura mandibular, hioidea y extra-ocular. El encéfalo es relativamente angosto; el cerebelo es simétrico y muestra una división parcial en porciones anterior y posterior. Del sistema olfatorio resaltan los siguientes caracteres: la pigmentación externa de los órganos olfatorios, el gran número de laminillas olfatorias y la asimetría de los bulbos olfatorios; en el sistema óptico es notable la presencia en cada ojo del opérculo pupilar y la división en dos secciones del músculo oblicuo superior; y en el sistema estato-acústico sobresale en cada oído el gran tamaño de la otoconia sacular.

Palabras clave: Cráneo, cerebro, sistema nervioso, órganos sensoriales

Abstract.- The organization of the neurocranium, the encephalon, and the main sensory organs of *Rostroraja texana* (Family Rajidae) corresponds to the general morphological pattern of the elasmobranchs and, in particular, of the batoids. The neurocranium presents the rostrum, which corresponds to about 50% of the cranial length; additionally, it shows two dorsal fontanelles of similar shape and size. The anatomical relations of the neurocranium of *R. texana* are with the encephalon, the main sensory organs, the antorbital, synarcual, and spiracular cartilages, and with the mandibular, hyoid, and extra-ocular musculature. The encephalon is relatively narrow. The cerebellum is symmetrical and shows a partial division in the anterior and posterior portions. In the olfactory system, the following characteristics stand out: the external pigmentation of the olfactory organs, the high number of olfactory lamellae, and the asymmetry of the olfactory bulbs. In the optical system, the presence of the pupillary operculum and the division into two sections of the superior oblique muscle is notable. And, in the statoacoustic system, the large size of the saccular otoconia stands out.

Key words: Cranium, brain, nervous system, sensory organs

Introduction

According to Nelson *et al.* (2016), the class Chondrichthyes or "cartilaginous fishes" is formed by Elasmobranchii (sharks and rays) and by Holocephali (chimaeras). In turn, elasmobranchs are divided into Selachii (sharks) and Batomorphi (rays). According to Last *et al*. (2016), the rays are grouped in four orders: Rajiformes, Torpediniformes, Rhinopristiformes, and Myliobatiformes, of which the Rajiformes is the richest in species.

According to Del Moral-Flores *et al.* (2015), the Mexican chondrichthyan fauna is one of the richest in the world, accounting for 17.3% or more of the known species. In Mexican territorial waters there are 214 species of Chondrichthyes, of which 111 are sharks and 95 are rays; in this area, the Rajidae are represented by 31 species, which corresponds to 18% of the species worldwide.Within the Mexican ichthyofauna the *Rostroraja texana* (Chandler, 1921) can be found, which is distributed in coastal waters from the southeast coast of Florida, USA, to the Gulf of Mexico (McEachran & Fechhelm 1998). Last *et al.* (2016) determined that this species is found at depths between 1 and 183 m, is an oviparous species and feeds mainly on crustaceans and fish.

The general anatomy of the neurocranium, encephalon, and main sensory organs of some batoids from the Mexican coasts is described by Ramírez-Díaz (2014). The most extensive anatomical study of the neurocranium of the *Rostroraja* genus is that of Hulley (1972), which includes 16 species. Anatomic studies on the encephalon of the Batoidei are those from Northcutt (1977), Myagkov (1986), Puzdrowski & Leonard (1992), Hofmann (1999), Walker & Sherman (2001), Ari (2011), Lisney *et al*. (2008), Yopak (2012), Montes *et al*. (2014), and Kobelkowsky (2017). The studies of Duméril (1865) and Smeets *et al*. (1983) focus particularly on *Rostroraja clavata*.

General descriptions of the main sensory organs of the chondrichthyans are made by Belckmann & Hofmann (1999). Studies on the morphology and the physiology of olfactory organs of the Batoidea are those of Schluessel *et al*. (2008); Meredith & Kajiura (2010); on the optical system are those of Lisney & Collin (2007), and Cunha *et al*. (2016); on the acoustical system is that of Myrberg (2001) and Evangelista *et al*. (2010); and on the lateral line system those of Maruska & Tricas (1998), Maruska (2001), and particularly on Rajidae that of Sáez *et al*. (2014).

Considering its structural and functional significance, the objective of this study was the anatomical description of the neurocranium, encephalon, and main sensory organs of the roundel skate *Rostroraja texana*.

Materials and methods

The anatomical analysis was performed on five female and five male adult preserved specimens of both sexes of *R. texana*, captured in the coastal lagoons of Pueblo Viejo, Tamiahua, Tampamachoco, and Alvarado in the State of Veracruz and the littoral of the Gulf of Mexico, Mexico. The specimen collection capture was done by means of a shrimp trawl test net; they were fixed with 10% formaldehyde and stored in 70% ethyl alcohol.

The skin was removed from the dorsal and ventral surface of the anterior region of the disc of the rays, in order to expose the axial and visceral musculature (Fig. 1). The exposition of the neurocranium in its ventral aspect was done by removing the musculature associated with the visceral arches; and then, the jaws, the hyoid arch, and the branchial apparatus were removed. The dorsal aspect of the encephalon was exposed, by removing sections of the roof of the neurocranium. Similarly, the ventral aspect of the encephalon was exposed by removing sections of the floor of the neurocranium. The trajectory of the cranial nerves was followed, recognizing in each case the foramina through which they cross the neurocranium wall.

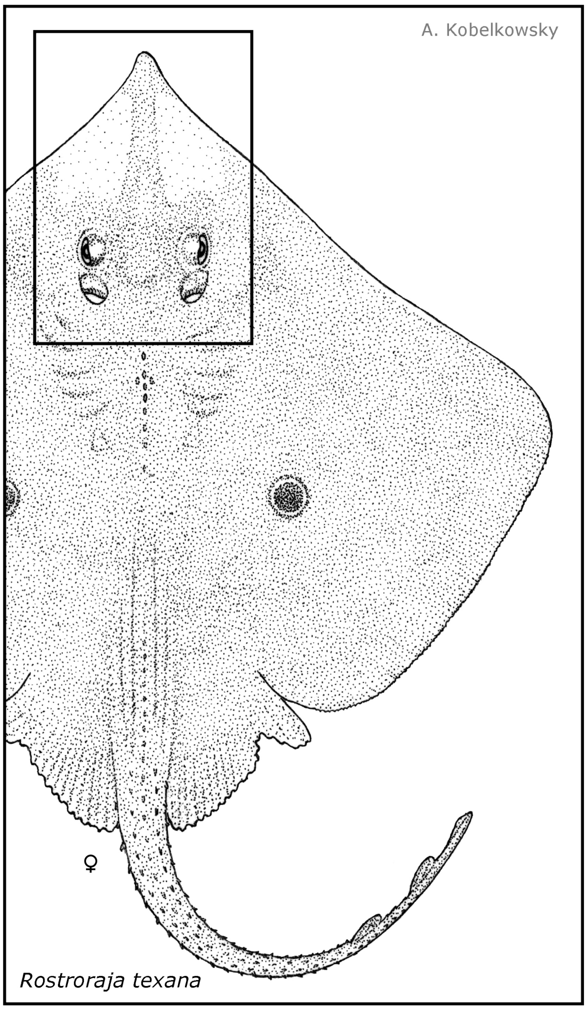

Figure 1. Adult female specimen of *Rostroraja texana*. The box delimits the dissection area of the neurocranium, encephalon, and sensory systems / Ejemplar adulto hembra de *Rostroraja texana*. El recuadro delimita el área de disección del neurocráneo, encéfalo y sistemas sensoriales

By means of dissection, the nasal flap cartilage was exposed and which, when removed, allowed the observation of the set of olfactory lamellae within the olfactory capsules. The olfactory capsules were removed in sections, in order to expose the olfactory bulbs. In the ocular orbit, the six extra-ocular muscles, the optic nerves (II), and the optic pedicle were identified. The inner ear was exposed in its dorsal and lateral aspects by breaking the cartilage from the otic capsules into small pieces. In its ventral aspect, after the anatomical analysis, the auditory (VIII) and glossopharyngeal (IX) nerves were identified.

The length of the neurocranium was considered from the tip of the rostrum to the level of the occipital condyles. The maximum width of the neurocranium was defined as the distance between the lateral ends of the olfactory capsules. Measurements of length and width were compared between the two fontanelles, and the thickness of the epiphyseal bar was described.

The terminology for the neurocranium followed Compagno (1999), that of the encephalon followed Gilbert (1973), and that of the sensory organs followed Bleckmann & Hofmann (1999). The illustrations were made by means of a *camera lucida* or drawing tube, coupled to a stereoscopic microscope Leica® Wild M3Z.

Results

Neurocranium

The neurocranium (Fig. 2) of *R. texana* is depressed; its length is about 40% of the total length of the disc. The most notable characters are: the great length of the rostrum, the presence of two fontanelles, and the reduction of preorbital and postorbital processes.

The length of the rostrum is about half of the total length of the neurocranium (46%), and is made up of a narrow axis, ending in the so-called rostral appendix, which is short, circular, and depressed (Fig. 2b, c); the base of the rostrum is broad and shows the foramen of the anterior ophthalmic canal. This base is continued with both the olfactory capsules and the cranial floor. The maximum width of the neurocranium is equivalent to the length of the rostrum.

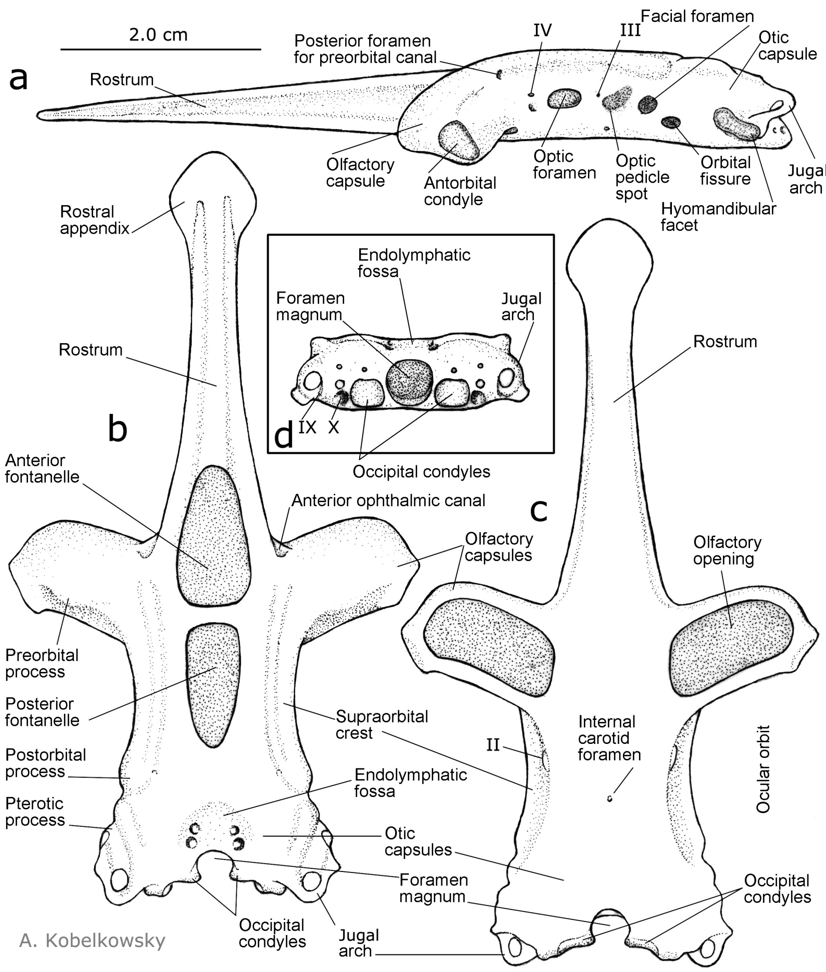

Figure 2. Neurocranium of *Rostroraja texana*. a) left lateral view, b) dorsal view, c) ventral view, d) posterior view / Neurocráneo de *Rostroraja texana*. a) vista lateral izquierda, b) vista dorsal, c) vista ventral, d) vista posterior

On the roof of the neurocranium (Fig. 2b), the anterior and posterior fontanelles can be found. They are triangular in shape and of equivalent length to each other, and are separated by the relatively thin epiphysial bar. The anterior fontanelle is slightly wider than the posterior fontanelle. Parallel to the supraorbital crests, the canals of the supraorbital branches of the lateral line sensory system can be observed.

The basal plate of the neurocranium (Fig. 2a, c) represents the palate; it continues from the rostrum, and in its middle portion the foramen of the internal carotid artery is located. In its posterior portion a notch is defined, which is part of the foramen magnum.

The olfactory capsules are in the same plane as the cranial box and have a diagonal orientation. Each olfactory capsule has, ventrally, a wide ovoid olfactory opening (Figs. 2c, 8c), with which corresponds the position of the nostril. Small nasal cartilages subdivide each nostril. At the lateral end of each capsule is the antorbital condyle (Fig. 2a, b, c), which receives the corresponding antorbital cartilage shaped like a hook.

The otic capsules are relatively small (Fig. 2). They have a slightly convex dorsal surface and a flat ventral surface. On the back, and between both otic capsules, the endolymphatic fossa is located (Fig. 3a, b) with the two endolymphatic and the two perilymphatic openings.

The ocular orbits are defined by the posterior walls of the olfactory capsules, the walls of the neurocranium, which have a slight concavity, the supraorbital crests, and the posterior processes (Fig. 2b, c); they have a row of thorns that protrude from the skin (Fig. 4a). The postorbital processes are represented by small prominences. Between the two fontanelles and the supraorbital crests, there is a superficially marked path of the two supraorbital branches of the lateral line (Figs. 2b, 3a). The jugal arch protrudes from each postero-lateral angle of the neurocranium (Figs. 2b, c).

The foramen magnum is located on the posterior wall of the neurocranium. It is flanked by the two occipital condyles, which have a square aspect (Fig. 2d). On the sides of the occipital condyles the foramina for the vagus (X) and glossopharyngeal nerves (IX) are present and, on the lateral ends, the jugal arches are observed.

In the wall of each ocular orbit (Fig. 2a) the foramina for the optic (II), oculomotor (III), trochlear (IV), trigeminal (V), abducens (VI) and facial (VII) nerves are located; additionally, the insertion area of the optic pedicle is marked. In the area posterior to each ocular orbit the hyomandibular facet is defined, diagonally oriented and, posterior to it, the jugal arch is located; this facet is articulated with the hyomandibular cartilage.

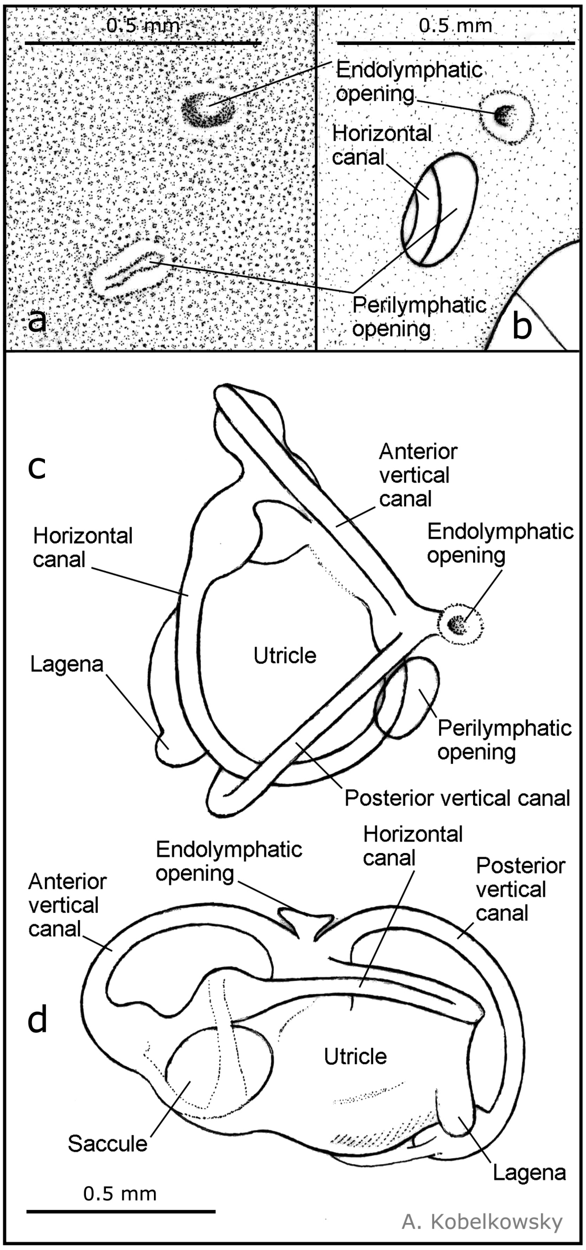

Figure 3. Statoacoustic system of *Rostroraja texana*. a) dorsal view of the left side of the endolymphatic fossa, b) dorsal view of the left endolymphatic and perilymphatic foramina, c) dorsal view of the left inner ear, d) lateral view of the left inner ear / Sistema estatoacústico de *Rostroraja texana*. a) vista dorsal del lado izquierdo de la fosa endolinfática, b) vista dorsal de los orificios endolinfático y perilinfático izquierdos, c) vista dorsal del oído interno izquierdo, d) vista lateral del oído interno izquierdo

Skeletal relations of the neurocranium

The neurocranium is indirectly related to the propterygium cartilages of the scapular girdle, by the antorbital cartilages (Fig. 5a, b). From its lateral border, each olfactory capsule supports two nasal cartilages (Fig. 8c), which give structure to the nostril; on the opposite edge a cartilage gives structure to the nasal flap. The neurocranium supports the lower jaw by means of the hyomandibular cartilage, which is articulated to the facet of the hyomandibular, located on the lateral surface of each otic capsule (Fig. 5a). Posterior to the optic foramen, the optic pedicle is fixed (Fig. 2a), which has a curved and ribbon-like appearance and supports the eye (Fig. 4b). Posterior to each ocular orbit, the spiracular cartilage is located (Fig. 5a), which is in direct contact with the spiracular muscle (Fig. 5b). By means of the occipital condyles, the neurocranium is articulated with the synarcual cartilage (Fig. 5a), which is formed by the fusion of the first vertebrae. The supraorbital row of spines, surrounding the eye and the spiracle, is implanted directly into the cartilage at the posterior border of the olfactory capsule and part of the border of the supraorbital crest (Fig. 5a).

Several sections of the lateral line sensory system make direct contact with the neurocranium. Two sections, the supraorbital 1, run parallel to the supraorbital crests (Fig. 5a); the prenasal sections run on the sides of the rostrum and continue backwards as orbital, suborbital, nasal, rostral, and subrostral sections.

Muscular relations of the neurocranium

The *levator palatoquadrati* muscle originates from the wall of each ocular orbit; it is inserted on the palatoquadrate cartilage or upper jaw (Fig. 5b). On the wall of each otic capsule and the jugal arch the *levator hyomandibulae* muscle originates, which inserts into the hyomandibular cartilage (Fig. 5b). In the space between the hyomandibular cartilage, the otic capsule, and the eye, the spiracle is located on each side, which in turn is surrounded by the spiracular cartilage, the *spiracularis* muscle, and the *levator hyomandibulae* muscle (Fig. 5b). Some sections of the *adductor mandibulae* muscle are inserted in the posterodorsal portion of each olfactory capsule (Fig. 5b), while the six extra-ocular muscles originate from two areas of each ocular orbit. The four *recti* muscles (Fig. 4c, d) are originated on the wall of the ocular orbit, namely, anterior rectus, posterior rectus, superior rectus, and inferior rectus, whereas in the posterior wall of the olfactory capsule the two superior oblique and inferior oblique muscles originate (Fig. 4a, d).

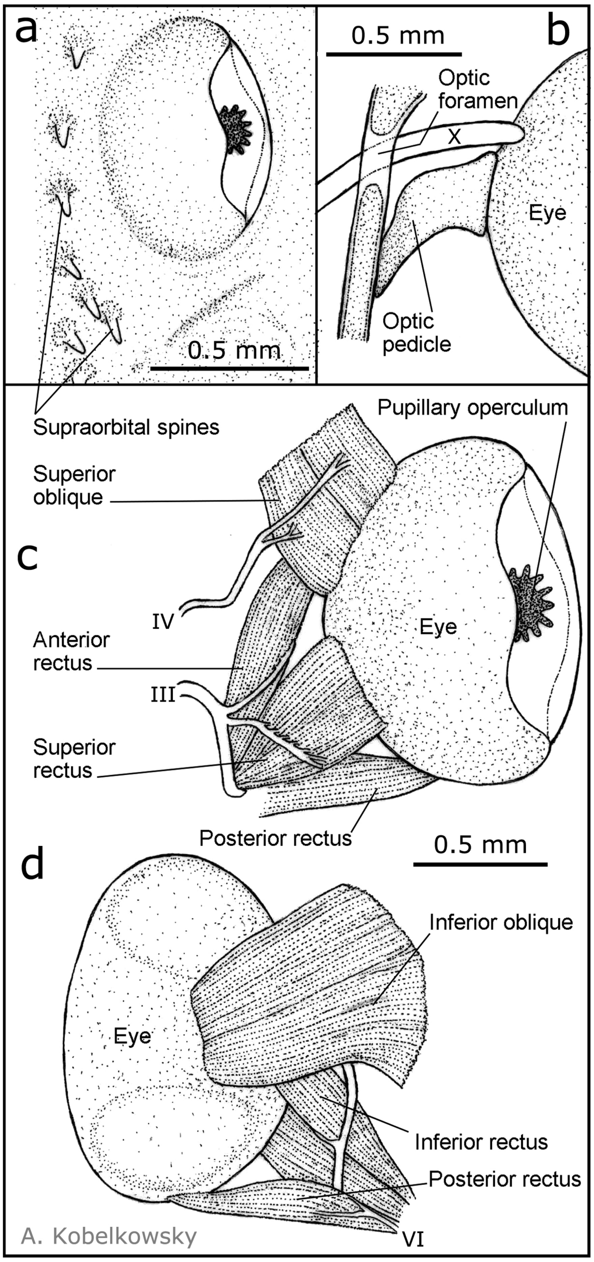

Figure 4. Optic system of *Rostroraja texana*. a) dorsal view of the right eye and supraorbital spines, b) cross section of the ocular orbit at the level of the optic foramen, c) dorsal view of the right eyeball and the extraocular muscles, d) ventral view of the right eyeball and the extraocular muscles / Sistema óptico de *Rostroraja texana*. a) vista dorsal del ojo derecho y las espinas supraorbitales, b) corte de la órbita ocular al nivel del foramen óptico, c) vista dorsal del globo ocular derecho y los músculos extra-oculares, d) vista ventral del globo ocular derecho y los músculos extra-oculares

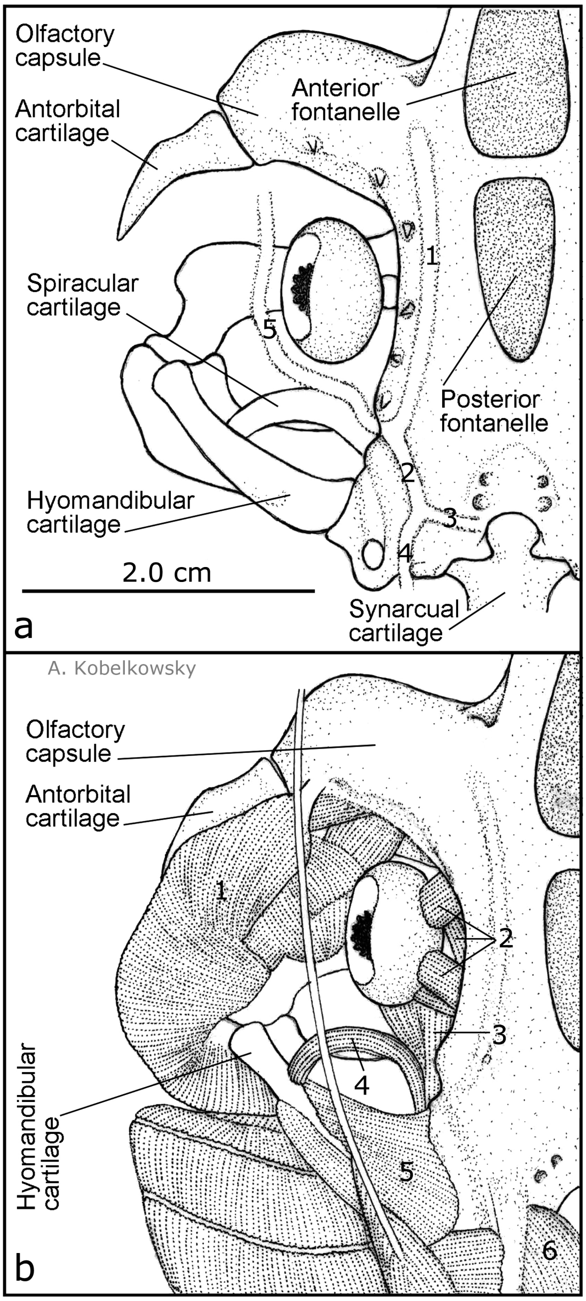

Figure 5. Main anatomical relations of the neurocranium of *Rostroraja texana*. a) Skeletal relations. 1. Supraorbital canal, 2. Postorbital canal, 3. Supratemporal canal, 4. Posterior canal, 5. Infraorbital canal. b) Muscle relations. 1. *Adductor mandibulae* muscle, 2. Extra-ocular muscles, 3. *Levator palatoquadrati* muscle, 4. *Spiracularis* muscle, 5. *Levator hyomandibulae* muscle, 6. *Epaxialis* musculature / Principales relaciones anatómicas del neurocráneo de *Rostroraja texana*. a) Relaciones esqueléticas. Canal supraorbital, 2. Canal postorbital, 3. Canal supratemporal, 4. Canal posterior, 5. Canal Infraorbitario. b) Relaciones musculares. 1. Músculo *adductor mandibulae*, 2. Músculos extra-oculares, 3. Músculo *levator palatoquadrati*, 4. Músculo *spiracularis,* 5. Músculo *levator hyomandibulae*, 6. Musculatura *epaxialis*

Encephalon

The *R. texana* encephalon is relatively elongated and slender (Figs. 6a, b; 7), however, the olfactory lobes and olfactory tracts protrude noticeably on both sides. The olfactory bulbs are elongated and narrow, and are located in direct contact with the dorsal surface of the olfactory organs (Fig. 6a). The olfactory tracts are relatively short and thick; their trajectory is oblique in relation to the sagittal plane (Figs. 6a, 7). The olfactory lobes are broad; however, they do not differentiate externally from the cerebral hemispheres.

Prosencephalon

The cerebral hemispheres (Fig. 6a) are relatively reduced and do not show a clear division between them, some protuberances rise discreetly from their dorsal portion, and the terminalis nerves (0) leave from their antero-dorsal surface (Fig. 6a). The terminal nerves are notably thin, and with a diagonal trajectory they join the olfactory bulbs near their inner end. The diencephalon (Fig. 6a, b) is short and narrow, and it shows, on its dorsal surface, the anterior *tela choroidea*; while from the ventral surface, the inferior lobes of the infundibulum, the vascular sacs, and the hypophysis protrude (Fig. 7).

Mesencephalon

The mesencephalon (Fig. 6a) is dorsally formed by the optic lobes, ovoid in appearance, and ventrally by the tegmentum.

Rhombencephalon

The metencephalon (Fig. 6a) is formed by the cerebellum, which develops the auricles towards the sides. The cerebellum has an elongated dorsal appearance, with a pair of short anterior lobes with a rounded anterior border, and another pair of long, convex, and triangular posterior lobes. The medulla oblongata (Fig. 6a) is elongated; its width decreases gradually towards the back.

Cranial nerves

The cranial nerves of *R. texana* (Figs. 6 and 7) are the following: terminalis (0), olfactory (I), optic (II), oculomotor (III), trochlear (IV), trigeminal (V), abducens (VI), facial (VII), auditory (VIII), glossopharyngeal (IX), and vagus (X).

Each terminalis nerve (0) is noticeably thin and extends from the anterior surface of the cerebral hemisphere to the base of the olfactory bulb. Each olfactory tract is relatively thick and follows an oblique path between the olfactory bulb and the olfactory lobe. Each oculomotor nerve (III) originates from the mesencephalon, near the vascular sac, it has an

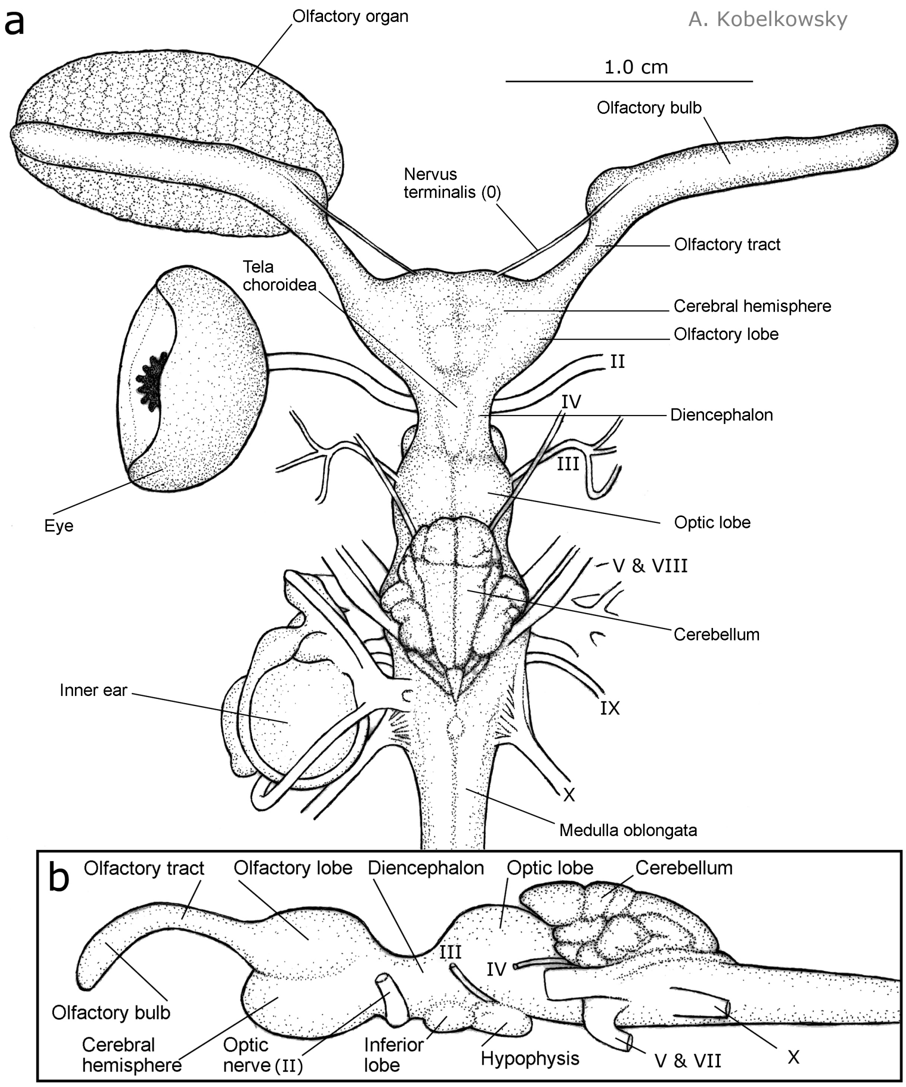

Figure 6. Encephalon and main sensory organs of *Rostroraja texana*. a) dorsal view, b) left lateral view / Encéfalo y principales órganos sensoriales. a) vista dorsal, b) vista lateral izquierda

oblique path and passes through the wall of the ocular orbit through the oculomotor foramen. Near the origin of the *recti* muscles of the eye, this nerve is divided into three branches; the most anterior branch innervates the anterior rectus muscle (Fig. 4c), the middle branch innervates the superior rectus muscle, while the posterior branch is subdivided into two other branches that innervate the inferior rectus and the inferior oblique (Fig. 4c). Each trochlear (IV) nerve is noticeably thin, it detaches from the roof of the mesencephalon between the optic lobe and the cerebellum (Fig. 6a, b); it passes through the trochlear foramen, distally divides into two branches and innervates the two sections of the superior oblique muscle of the eye (Fig. 4b). Each abducens nerve (VI) leaves the ventral part of the medulla oblongata (Fig. 7), crosses the wall of the neurocranium and innervates the posterior rectus muscle of the eye (Fig. 4d). The trigeminal (V), facial (VII), and auditory (VIII) nerves on each side emerge from a common trunk in the anterolateral part of the medulla oblongata (Figs. 6 and 7). Each glossopharyngeal nerve (IX) (Fig. 7) emerges from the lateral surface of the medulla oblongata, ventrally passes to the inner ear (Fig. 7) and goes through the posterior wall of the neurocranium through the glossopharyngeal foramen (Fig. 2d). Each vagus or pneumogastric nerve (X) is thick and emerges from the side of the medulla oblongata (Fig. 6a, b), it is oriented backwards and passes through the vagus foramen (Fig. 2d).

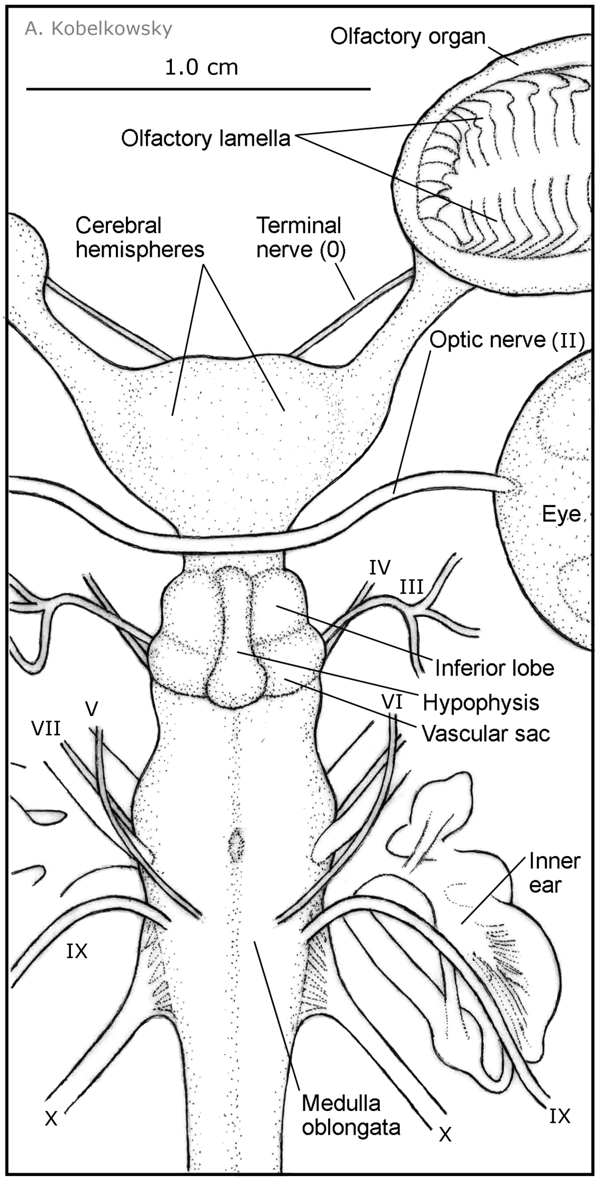

Figure 7. Encephalon and main sensory organs of *Rostroraja texana* in ventral view / Vista ventral del encéfalo y principales órganos sensoriales de *Rostroraja texana*

Olfactory system

The olfactory system (Fig. 8) is composed of the nostrils, olfactory capsules, olfactory organs, olfactory bulbs, olfactory tracts, and olfactory lobes. Each nostril is broad and oval-shaped, and is delimited by a set of skin folds, which are partly supported by some cartilages (Fig. 8b, c). Each olfactory organ has an ovoid appearance, and its external surface is rough and noticeably pigmented (Fig. 6a). On the inside, the olfactory lamellae are arranged in a series along the organ (Figs. 7, 8c). Each olfactory lamella (Fig. 8d) is partially divided into an anterior and a posterior portion by means of a septum, which in turn originates from the olfactory bulb. Both the anterior and posterior ends of each lamella end up in several tips. On both sides of the lamella, the secondary lamellae are observed with the appearance of several fine grooves.

Optical system

The optical system (Fig. 4) is formed by the eyes eyelids, optic pedicles, optic nerves, six pairs of extraocular muscles, and the three pairs of corresponding cranial nerves. Each eye is approximately semi-spherical, with the upper eyelid fused to the eyeball; the sclera shows two ovoid areas of porous tissue, and is supported by the optic pedicle which is flattened and has a curved appearance. The pupillary operculum is shown in the upper part of the iris. The superior oblique and inferior oblique muscles are remarkably broad, while the four *recti* muscles are narrow. The anterior rectus, posterior rectus, superior rectus, and inferior rectus muscles originate from the same area in the middle part of the ocular orbit, while the superior oblique and inferior oblique muscles originate in separate areas of the olfactory capsules. The character of the superior oblique muscle consisting in its division into two sections is remarkable (Fig. 4c). Each section is innervated by a branch of the trochlear nerve (IV). The inferior oblique muscle is bigger than the superior oblique, it originates at the lower edge of the ocular orbit, and it is innervated by a branch of the oculomotor nerve (III). Of the *recti* muscles, the widest is the superior rectus (Fig. 4c). The posterior rectus muscle is innervated by the abducens nerve (VI), while the remaining *recti* muscles are innervated by branches of the oculomotor nerve (III).

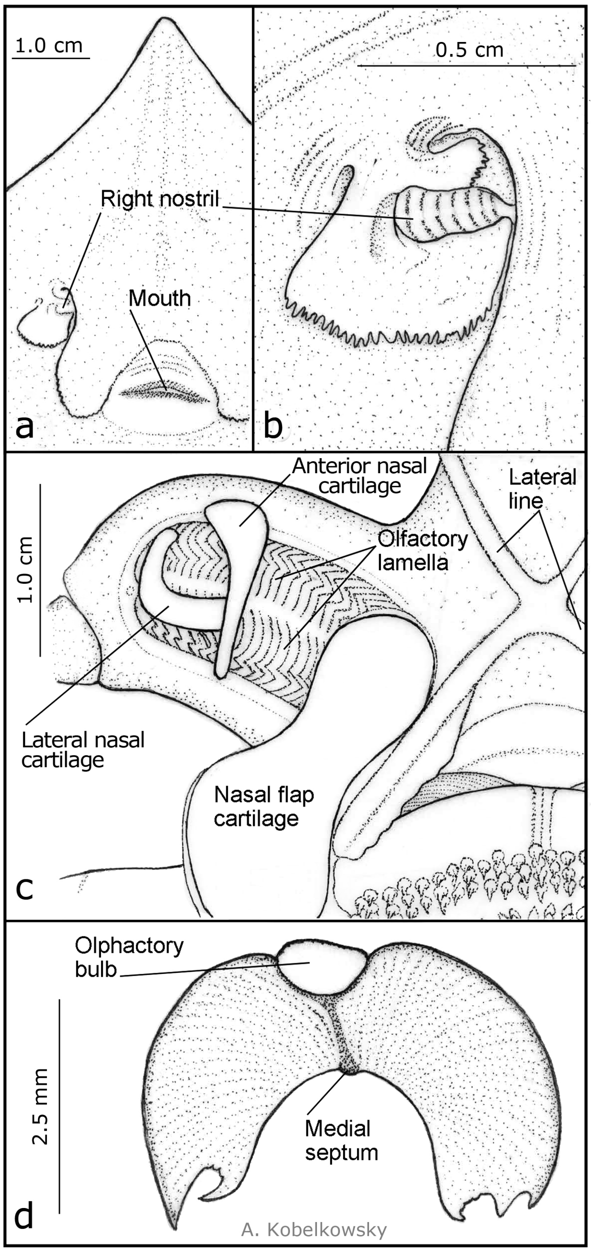

Figure 8. Olfactory system of *Rostroraja texana*. a) ventral view of the rostral region of the ray, b) right nostril, c) olfactory organ and nasal cartilages in ventral view, d) olfactory lamella in lateral view / Sistema olfatorio de *Rostroraja texana*. a) vista ventral de la región rostral de la raya, b) narina derecha, c) órgano del olfato y cartílagos nasales en vista ventral, d) laminilla olfatoria en vista lateral

Statoacoustic system

The statoacoustic system (Figs. 3a, b) consists of the endolymphatic fossa, the perilymphatic and endolymphatic orifices, and the inner ears. Each inner ear is constituted by the vesicles and the semicircular canals. The vesicles of each inner ear are the utriculus, the sacculus, and the lagena (Fig. 3c, d), the largest being the sacculus and the smaller one, the lagena. The sacculus is pear shaped and dorsally continued with the endolymphatic duct, which in turn opens into the endolymphatic fossa. The utriculus has a medium size and an approximately horizontal orientation. The lagena has the appearance of a downwards-oriented diverticulum. Within the vesicles, the otoconia are located. In each inner ear, the semicircular canals (Fig. 3c, d) are the anterior vertical, the posterior vertical, and the horizontal; each of which has an ampulla at one end. The ampullae of the vertical anterior and horizontal canals are close to each other, while that of the posterior vertical canal is located behind the sacculus and near the lagena.

Lateral line sensory system

The portion of the lateral line sensory system (Fig. 5a) that has direct contact on each side with the neurocranium is the supraorbital canal, which runs parallel to the supraorbital crest; and, secondly, the postorbital canal which is located at the same level of the posterior vertical semicircular canal; from this canal, the supratemporal is detached transversally over the endolymphatic fossa, and it joins the canals on the other side. From the junction of the supraorbital and postorbital branches, the infraorbital branch is detached forward and to the side of the eye, while the posterior branch is oriented to the back from the posterior end of the postorbital.

In the ventral portion of the neurocranium, between the nostrils a cross is recognized (Fig. 8c), formed by the union of the nasal and prenasal sections of the lateral line; the prenasals are oriented to the front, accompanied by the subrostral sections running along the rostrum of the neurocranium.

Discussion

The anatomical characteristics of the neurocranium and the encephalon of *R. texana* correspond to the general anatomical pattern of the Elasmobranchii and in particular of the Batoidei.

In general terms, the neurocranium of the rays differs from that of the sharks by presenting a greater dorso-ventral flattening, which is related to the dorsal-ventral flattening or general depression of the body. It also differs in the presence of the dorsal fontanelles and the reduced development of the preorbital and postorbital processes.

According to Kobelkowsky (2017), a greater similarity of the morphology of the neurocranium of *R. texana* with that of *Pseudobatos lentiginosus* (Rhinobatidae) is recognized, mainly due to the presence of the rostrum, the two fontanelles, and a greater separation between olfactory openings. This contrasts with the representatives of the Myliobatiformes (*Urotrygon chilensis*, *Hypanus sabinus*, and *Gymnura micrura*) which lack a rostrum and have a single fontanelle.

The topographic relations of the neurocranium of *R. texana* are the same as in other batoids. They can be classified into four categories: a) skeletal, b) muscular, c) encephalic, and d) sensorial.

a) As in other rays, *R. texana* has an indirect articular relation with the propterygium cartilage of the pectoral fin, by means of the antorbital cartilage, being a common character of the Batoidei, not recognized in the Selachii. The neurocranium of *R. texana*, as well as that of other species of Rajidae described in the literature, lack the anterior condyles, which Kobelkowsky (2017) describes in *G. micrura* (Gymnuridae), and which are articulated with the first pectoral radials. Likewise, the contact of the propterygium cartilages with the olfactory capsules is notable; the articulation of the hyomandibular cartilage with the neurocranium is characteristic of all elasmobranchs and represents the mandibular suspension, which is of euhyostylyc type in rays; and, the thickness and shape of the optic pedicle stand out. As in all batoids, the neurocranium of *R. texana* is articulated with the synarcual cartilage, which results from the fusion of the first vertebrae.

b) Muscular relations of the neurocranium involve the mandibular, hyoid, extra-ocular, and axial muscles. Similar to sharks, the olfactory capsules, otic capsules, and ocular orbits are recognized as muscle insertion areas.

c) In general terms, the encephalon of the skates and rays differs from that of the sharks by having a greater dorso-ventral flattening associated with the extreme flattening of the body. Similarly, the batoids also differ, in general terms, by presenting longer and more slender olfactory bulbs. According to authors such as Northcutt (1977), the encephalon/body ratio in some elasmobranchs is comparable to that of birds and mammals, and exceeds that of amphibians and reptiles. While, among sharks, the galeomorphs have an encephalon/body ratio two to six times bigger than those of the squalomorph sharks; among the Batoidei, those of the order Rajiformes have a low encephalon/body relation, however, the rays of the advanced order Myliobatiformes show the highest ratios within the elasmobranchs.

Yopak (2012) concludes that in the elasmobranchs, the encephalon is large, having a well-developed telencephalon, and a large and highly foliated cerebellum, which is observed in species that occupy reef or oceanic habitats; in contrast, benthic or benthopelagic species have a relatively small encephalon, and show a relative hypertrophy of the medulla oblongata. According to Ramírez-Díaz (2014), the encephalon of the batoids is classified into symmetrical and asymmetrical categories, depending on the shape of the cerebellum. Thus, *R. texana* corresponds to the first category, while *U. chilensis* and *H. sabinus*, due to the presence of more developed lobulations on one side of the cerebellum than on the other, correspond to the second category. A greater similarity of the morphology of the encephalon of *R. texana* with that of *P. lentiginosus* was recognized, however, the second one differs in the absence of the olfactory tracts and in presenting an asymmetric cerebellum.

d) It is interpreted that *R. texana* has a greater olfactory acuity compared to other rays, due to the high number of olfactory lamellae; however, a microscopic study is required to determine the density of olfactory cells in the olfactory lamellae. The greater size of the otoconias is probably related to a greater complexity of movements in *R. texana* compared to other species.

The morphology of the lateral line sensory system of *R. texana* follows the general pattern that Maruska (2001) describes in the Batoidei. It implies that the canals with orifices are distributed mainly on the dorsal surface, presenting complex branching, while the canals without orifices are mainly distributed on the ventral surface. This condition is observed in the cephalic region of *R. texana*, presenting, in addition, a greater topographic relation of the dorsal canals with the neurocranium.

Comparing the morphology of the neurocranium of *R. texana* with that described by Hulley (1972) in the rays of the south coast of Africa, a greater similarity with *R. alba* is recognized. The morphology of the encephalon of *R. texana* is similar to that of *R. clavata*, illustrated by Duméril (1865).

Literature cited

Ari C. 2011. Encephalization and brain organization of Mobulid rays (Myliobatiformes, Elasmobranchii) with ecological perspectives. The Open Anatomy Journal 3: 1-13.

Bleckmann H & MH Hofmann. 1999. Special senses. In: Hamlett WC (ed). Sharks, skates and rays. The biology of elasmobranch fishes, pp. 300-328. The Johns Hopkins University Press, Baltimore.

Compagno LJV. 1999. Endoskeleton. In: Hamlett WC (ed). Sharks, skates and rays. The biology of elasmobranch fishes, pp. 69-92. The Johns Hopkins University Press, Baltimore.

Cunha CM, LE Oliveira & JR Kfoury. 2016. Comparative anatomy of the extraocular muscles in four Myliobatoidei rays (Batoidea, Myliobatiformes). Journal of Anatomy 228: 877-886.

Del Moral-Flores LF, JJ Morrone, J Alcocer-Durand, H Espinosa-Pérez & G Pérez-Ponce de León. 2015. Lista patrón de los tiburones, rayas y quimeras (Chondrichthyes, Elasmobranchii, Holocephali) de México. Arxius de Miscel-lània Zoològica 13: 47-163.

Duméril A. 1865. Histoire naturelle des poissons ou ichtyologie générale. Tome Première. Élasmobranches, plagiostomes et holocéphales, ou chimères. Première partie, 720 pp. Libraire encyclopédique de Roret, Paris.

Evangelista C, M Mills, UE Siebeck & SP Collin. 2010. A comparison of the membranous inner ear in Elasmobranchs. Journal of Morphology 271: 483-495.

Gilbert SG. 1973. Pictorial anatomy of the dogfish, 59 pp. University of Washington Press, Seattle and London.

Hofmann MH. 1999. Nervous system. In: Hamlett WC (ed). Sharks, skates and rays. The biology of elasmobranch fishes, pp. 273-299. The Johns Hopkins Press, Baltimore.

Hulley PA. 1972. The origin, interrelationship and distribution of southern African Rajidae (Chondrichthyes, Batoidei). Annals of the South African Museum 60: 1-103.

Kobelkowsky A. 2017. Anatomía comparada del neurocráneo y el encéfalo de la raya mariposa *Gymnura micrura* (Batoidea: Gymnuridae). International Journal of Morpholology 35: 644-650.

Last PR, WT White, MR de Carvalho, B Séret, FW Matthias, MFW Stehmann & GJP Naylor. 2016. Rays of the world, 790 pp. Cornell University Press, Ithaca and London.

Lisney TJ & SP Collin. 2007. Relative eye size in elasmobranchs. Brain, behavior and Evolution 69: 266-279.

Lisney TJ, KE Yopak, JC Montgomery & SP Collin. 2008. Variation in brain organization and cerebellar foliation in chondrichthyans: batoids. Brain, behavior and Evolution 72**:** 262-282.

Maruska KP. 2001. Morphology of the mechanosensory lateral line system in elasmobranch fishes: ecological and behavioral considerations. Environmental Biology of Fishes 60: 47-75.

Maruska KP & TC Tricas. 1998. Morphology of the mechanosensory lateral line system in the Atlantic stingray, *Dasyatis sabina*: The mechanotactile hypothesis. Journal of Morpholology 238: 1-22.

McEachran JD & JD Fechhelm. 1998. Fishes of the Gulf of Mexico. Vol. I. Myxiniformes to Gasterosteiformes, 1112 pp. University of Texas Press, Austin.

Meredith TL & SM Kajiura. 2010. Olfactory morphology and physiology of elasmobranchs. The Journal of Experimental Biology 213: 3449-3456.

Montes DHM, BR López & M González-Isais. 2014. Estudio morfológico del cerebro y pares craneales de *Diplobatis ommata* (Elasmobranchii: Narcinidae). International Journal of Morphology 32: 1152-1155.

Myagkov NA. 1986. Brain structure of skates in relation to their ecology. Neuroscience and Behavioral Physiology16: 356-362.

Myrberg AA Jr. 2001. The acoustical biology of elasmobranchs. Environmental Biology of Fishes 60: 31-45.

Nelson JS, TC Grande & MH Wilson. 2016. Fishes of the world, 707 pp. John Wiley & Sons, Hoboken.

Northcutt RG. 1977. Elasmobranch central nervous system organization and its possible evolutionary significance. American Zoologist 17: 411-429.

Puzdrowski RL & RB Leonard. 1992. Variations in cerebellar morphology of the Atlantic stingray, *Dasyatis sabina*. Neuroscience Letters 135: 196-200.

Ramírez-Díaz C. 2014. Morfología comparada de encéfalo y órganos de los sentidos de las rayas (Chondrichthyes: Batoidea). Tesis de Maestría, Instituto de Ciencias del Mar y Limnología, Universidad Nacional Autónoma de México, Ciudad de México, 114 pp. <http://132.248.9.195/ptd2014/octubre/0720957/0720957.pdf>

Sáez S, J Lamilla & G Pequeño. 2014. Morfología del sistema mecanosensorial de la línea lateral de *Zearaja chilensis* (Batoidea: Rajidae). Revista de Biología Marina y Oceanografía 49: 55-59.

Schluessel V, MB Bennet, H Bleckmann, S Blomberg & SP Collin. 2008. Morphometric and ultrastructural comparison of the olfactory system in elasmobranchs: The significance of structure-function relationships based on phylogeny and ecology. Journal of Morphology 269(11): 1365-1386.

Smeets WJA, RN Nieuwenhuys & BL Roberts. 1983. The central nervous system of cartilaginous fishes. Structure and functional correlations, 267 pp. Springer-Verlag, Heidelberg.

Walker BK & RL Sherman. 2001. Gross brain morphology in the yellow stingray, *Urobatis jamaicensis*. Florida Scientist 64: 246-249.

Yopak KE. 2012. Neuroecology of cartilaginous fishes: The functional implications of brain scaling. Journal of Fish Biology 80: 1968-2023.

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