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External Brain Form and Cranial Nerves of the Megamouth Shark, *Megachasma pelagios*

HIRONOBU ITO, MASAMI YOSHIMOTO, AND HIROAKI SOMIYA

The external brain form and cranial nerves of the megamouth shark, *Megachasma pelagios*, were studied morphologically. The brain of a mature female specimen, 5.44 m long and 1040 kg in weight, was examined. The brain is small, weighing 19.8 gm, and is positioned caudally in an extremely large cranial cavity. The length between the rostral end of the telencephalon and the caudal end of the medulla oblongata is 97 mm. The olfactory bulbs and the telencephalon are well developed, and the inferior lobe is rather small. The optic tectum is medium in size. The corpus cerebelli is proportionally small, whereas the auricle is large. The medulla oblongata is so widely everted that the visceral afferent, visceral efferent, and somatic efferent columns, as well as the sulci between them, are clearly visible in the rhomboid fossa. Terminal nerves were not found. The olfactory tracts and cranial nerves course for long distances within the expanded cranial cavity. Allometry of the brain size and the functional importance of the crainal nerves in this rare species are discussed in comparison with those of other cartilaginous fishes.

A megamouth shark *Megachasma pelagios* was captured 12 miles offshore south of Mikizaki, Owase City (33°44′N, 136°16′E), by purse seining, at 2340 h on 30 April 1997. The purse seine net was knotless, 255 m in height, and 1200 m in circumference. This represents the 10th recorded specimen of megamouth shark. The central nervous system of many cartilaginous fishes has been studied (e.g., Daniel, 1928; Smeets et al., 1983; Nieuwenhuys et al., 1998); however, there is no information from *M. pelagios* because of the very few number of specimens and the newness of the species to science. We therefore present this description of the external morphology and cranial nerves of the megamouth shark.

MATERIALS AND METHODS

The specimen of *M. pelagios* was a mature female, 5.44 m long, weighing 1040 kg. The specimen was weighed on a commercial cargo scale, as the difference between the weights of a forklift loaded and unloaded with the specimen. The body was kept frozen (−35 C) for one month, and transferred to a refrigerator at +5 C to thaw gradually. After 11 days, a part of the cranium was opened and the brain with a few upper segments of the spinal cord was removed together with the cranial and spinal nerves. The brain was immediately immersed in 10% formalin and fixed for one week.

The connective tissue and blood vessels around the brain were carefully removed. The disk-shaped distal ends of each cranial nerve [from the optic nerve (II) to the vagal nerve (X)] of the left side were transected and weighed. The weight of each cranial nerve was calculated by multiplying the weight of the disk by the length of the remaining nerve in both sides. The total weight of the cranial nerves (Cw) was calculated by summing the weights of the cranial nerves. The caudal end of the upper spinal cord was transversely cut and weighed to calculate the weight of the spinal cord (Sw) below the occipitospinal nerve. Finally, the remainder of the whole brain was weighed (WBw). Actual brain weight (Bw) was estimated by the following equation: Bw = WBw − (Cw + Sw).

Photographs of the brain were taken from dorsal, ventral, and lateral aspects, and drawings were made by tracing the photographs (Fig. 1). Histological preparation of the brain was not possible, because it was frozen and thawed gradually. Ice crystals damaged the fine structure, and the preservation was not good enough to make meaningful interpretations.

RESULTS AND DISCUSSION

The brain was 19.8 gm in weight. Northcutt (1977) measured brain-body weight ratios in 16 species of chondrichthyans and showed a minimum convex polygon, in which the interspecific coefficient of allometry is 0.67 with a coefficient of determination of 0.86. The megamouth shark is not included within that polygon because of its extremely large body. However, the megamouth shark is at the boundary of a similar convex polygon shown in the most recently published book of the comparative neuroanat-

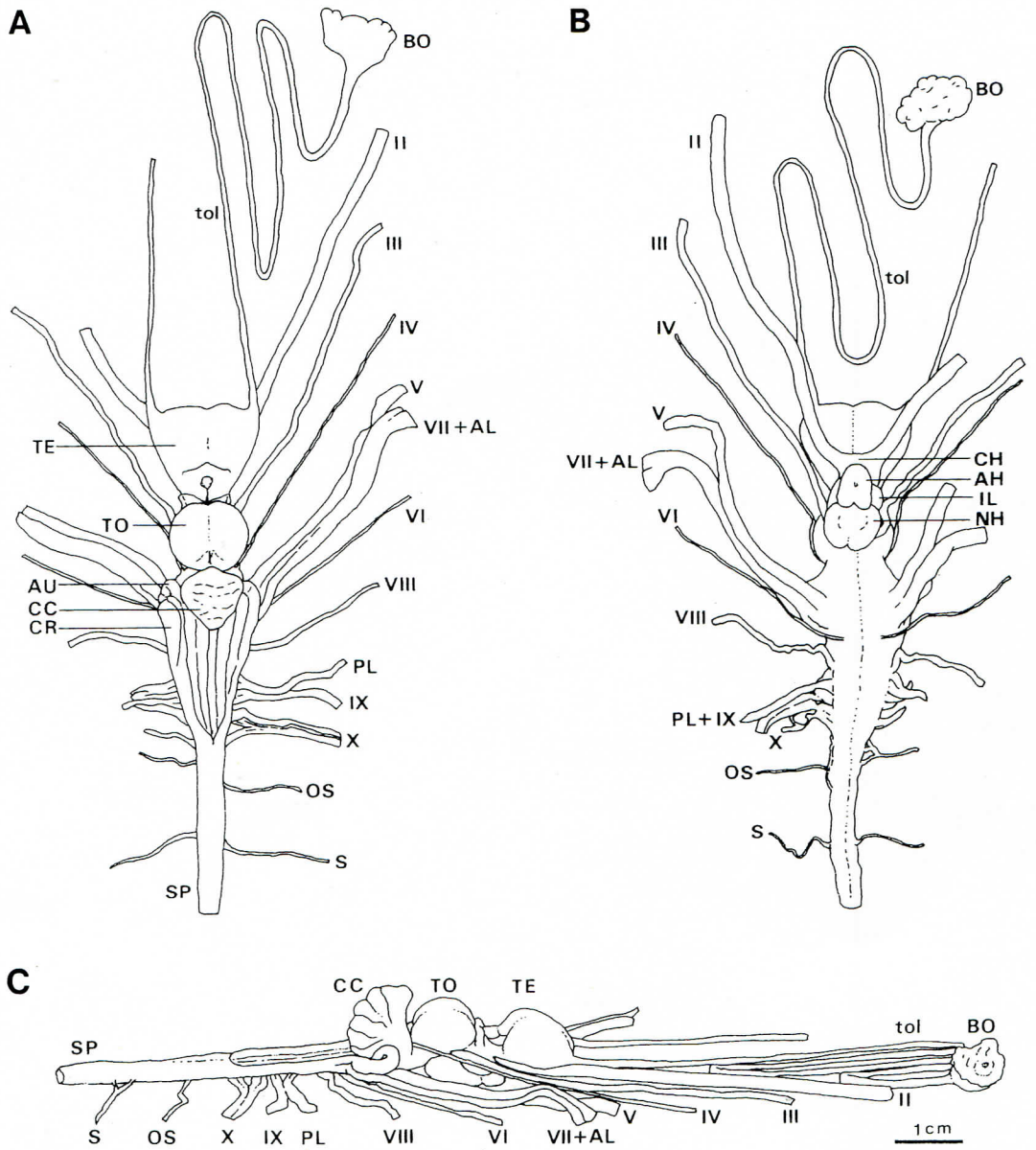

Fig. 1. Drawing of dorsal (A), ventral (B), and lateral (C) views of the brain. AH = adenohypophysis, AL = anterior lateral line nerve, AU = auricle, BO = olfactory bulb, CC = corpus cerebelli, CH = optic chiasm, CR = crista cerebelli, IL = inferior lobe, NH = neurohypophysis, OS = occipitospinal nerve, PL = posterior lateral line nerve, S = spinal nerve, SP = spinal cord, TE = telencephalon, TO = optic tectum, tol = olfactory tract, II = optic nerve, III = oculomotor nerve, IV = trochlear nerve, V = trigeminal nerve, VI = abducens nerve, VII = facial nerve, VIII = octaval nerve, IX = glossopharyngeal nerve, X = vagal nerve. Scale bar = 1 cm.

omy (Nieuwenhuys et al., 1998, fig. 23.6). The brain of the megamouth shark is proportionally very small compared with those of other species. This might suggest that the brain approaches its maximum size at early developmental stages, whereas the body size, especially the head size, continues to increase. The quite large cranial cavity relative to the brain, as described below, may also be explained by the different rates of growth.

The brain was positioned at the base of the caudal portion of the large cranial cavity. The

horizontal shape of the cavity was roughly an isosceles triangle with the base directed rostrally and the apex caudally. Width of the rostral part of the cavity was about 35 cm, and the rostrocaudal length was about 37 cm. The maximum height of the rostral part of the cavity was about 10 cm. Because the boundary of the medulla oblongata and the spinal cord coincides with the boundary of the cranial cavity and the vertebral canal, the brain occupies the most caudoventral position of the cranial cavity. Except for the ventral surface of the brain, the space between the brain and the inner surface of the cranium was filled with a large amount of connective tissue.

The external form of the brain is shown in Figure 1. The olfactory bulbs are located just behind the nasal sacs. The rostrocaudal length, width, and thickness of the right olfactory bulb were 11 mm, 18 mm, and 6 mm, respectively. Extremely long (about 32 cm) olfactory tracts connect the bulbs to the rostral end of the telencephalon.

The length between the rostral end of the telencephalon and the caudal end of the medulla oblongata is 97 mm. The maximum width of the brain is 28 mm at the telencephalon, and maximum height is 22 mm at the cerebellum. The olfactory bulbs and the telencephalon are well developed, as in other sharks and rays. The inferior lobe is relatively small. The pituitary gland is large, and the adenohypophysis and neurohypophysis are clearly demarcated rostrocaudally. The optic tectum is medium-sized. The general shape of the brain is similar to those of *Chlamydoselachus anguineus* (Masai, 1961) and *Notorynchus maculatus* (Northcutt, 1977) in terms of the proportionally small corpus cerebelli and the large auricle. The latter two species are regarded as members of primitive groups (Shirai, 1996), and *Megachasma* may also retain these primitive features. However, the surface of the corpus cerebelli of this species is not smooth, unlike those of *C. anguineus* and *N. maculatus*, but shows six transverse convolutions in spite of its small size. This may suggest an independent evolution of the corpus (Northcutt, 1977) in the species. *Megachasma* is known to be a filter-feeding elasmobranch (Morrissey et al., 1997; Martin and Naylor, 1997). Therefore, another possibility is that the small corpus cerebelli and the large auricle reflect a relatively inactive feeding behavior.

The chorioid plexus of the dorsal roof of the medulla oblongata is extensive. The medulla oblongata is so widely everted that the visceral afferent, visceral efferent, and somatic efferent columns, as well as the sulci between them, were clearly visible in the rhomboid fossa when the chorioid plexus was removed.

Terminal nerves were not found. Because the cranial cavity was filled with a large amount of connective tissue intermingled with numerous ice crystals, it is not clear whether these nerves were destroyed by ice crystals or whether the nerves do not exist outside the brain. If so, it would differ from other species of elasmobranchs (Wu et al., 1992) and more closely resemble teleost species (Stell et al., 1987; Uchiyama, 1989).

Other cranial nerves (Fig. 1) course for long distances in the wide cranial cavity. The optic nerves (II) are also long and course for about 10 cm within the cranial cavity. Their thickness is about 3 mm in diameter. The oculomotor (III), trochlear (IV), and abducens nerves (VI), which innervate eye muscles in the orbital cavity, are also long and more than 10 cm in length. The thin trochlear nerves (IV) emerge from the dorsal surface of the isthmic region. The abducens nerves (VI), however, arise from the most ventromedial zone in the medulla oblongata.

The trigeminal (V), facial (VII), and anterior lateral line nerves arise from an area ventrolateral to the auricles. These nerves are very thick. Sensory fibers of the trigeminal nerves (V) supply the skin of the huge head and the mucous membrane of the large oral cavity, and the motor fibers innervate movements of the large mouth (megamouth). The facial nerves (VII) and the anterior lateral line nerves, respectively, supply taste buds and lateral line neuromasts distributed over the huge head.

The octaval nerves (VIII) emerge from a ventral area of the crista cerebelli. The nerves are rather thick, suggesting the functional importance of equilibrium. The posterior lateral line, glossopharyngeal (IX), and vagal (X) nerves appear consecutively from the ventrolateral wall of the caudal rhomboid fossa. We could not find accessory nerves (XI), which have been reported in some sharks (Masai, 1961, 1963). It is generally believed that the accessory nerve (XI) in amniotes is included in the vagal nerve (X) and that the shark occipitospinal nerve is homologous to the hypoglossal nerve (XII; see Ariëns-Kappers et al., 1936; Romer and Parsons, 1977; Nieuwenhuys et al., 1998).

This is the first report on the external form and the cranial nerves of the megamouth brain. The systematic or evolutionary significance of the recorded observations needs further study. Histological analyses remain to be performed.

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