The Rete Mirabile Cranica in the Genus Mobula: A Comparative Study

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ABSTRACT  Devil rays (Mobulidae) have large brains that rest in a voluminous chondrocranium almost completely filled by a rete mirabile cranica (RMC). The RMC is a massive arterial network grossly divisible into a "caudal RMC" supplying blood to the brain, and an expanded, more complex "precerebral RMC" nested within the large cranial cavity rostral to the telencephalon.

Both the caudal and precerebral retia originate from the posterior portion of the profundae cerebri arteries, which lie ventral to the brain and form the sides of a vascular triangle, the base of which is anterior and formed by the joining of the internal carotids; the vertex is posterior and median, corresponding to the anterior extreme of the spinalis impar artery. Vessels of the caudal RMC branch posteriorly from the profundae cerebri and course over and into the brain. Vessels branching more anteriorly course rostrally to form the precerebral RMC, which takes the shape of the cranial cavity and completely envelops the olfactory peduncles. Large retia arteries (1-mm diameter) branch and taper to about 50–150 µm, forming a system of small arteries or arterioles. Many give rise to a mesh of tertiary vessels (precapillary arterioles or capillaries, ca. 20–50 µm in diameter), which, along with arterioles, are embedded in the adventitia of these arteries, with which they communicate by numerous anastomoses. Although the function of the RMC remains enigmatic, its complexity and fine structure are suggestive, and hypotheses of its role are discussed.

Anatomical investigations of the elasmobranch vascular system have spanned two centuries, and cranial blood supply has been described in diverse species of batoids and sharks (Monroe, 1785; Hyrtl, 1858; Garazzi, '05). Yet despite the considerable effort to study brain vascularization, the rete mirabile cranica (RMC) in the highly specialized devil rays (Mobulidae; genera Manta and Mobula) has received little attention. The RMC, a mass of convoluted blood vessels overlying the brain and filling the cranial cavity, was discovered in Cephaloptera giorna (= Mobula mobular) and described in an account of disparate anatomical peculiarities of this species (Panceri and De Sanctis, 1869). That description remains the sole treatment of the RMC, with the exception of that by Gohar and Bayoumi ('59) who mistakenly identified the structure in Manta as "innumerable fine strands of connective tissue."

The purpose of this study is to describe in detail the morphology of the RMC employing histological, electron microscopic, and plastic corrosion cast techniques, and to highlight interspecific differences in RMC morphology within the genus Mobula.

MATERIALS AND METHODS

The classification of Mobula species adopted here is derived from a recent overview of mobulid taxonomy (Notarbartolo-di-Sciara, '85). For a comprehensive list of synonyms of the genus Mobula, see Notarbartolo-di-Sciara, '85; Bigelow and Schroeder, '53). The four species studied (M. thurstoni, M. japanica, M. tarapacana, and a species previously undescribed) were obtained from

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local fishermen at the Cooperativa Pesquera of Punta Arena de la Ventana, Baja California, Mexico, and were caught with gillnet or harpoon. One specimen of *M. japonica* was captured in a drifting gill net 30 km west of San Diego.

**Preparation of corrosion casts**

Intracardial perfusions were performed on anesthetized rays in which the heart was vigorously beating. Preceding each perfusion, heparin and papaverin solutions, each diluted to 1%, were injected directly into the ventricle. Elasmobranch Ringer's solution was introduced into the conus arteriosus by means of a hand-held peristaltic pump (Black and Decker Jackrabbit), and blood was drained though a cut in the sinus venosus.

Subsequent to perfusion, the RMC was cast with Batson's #17 Anatomical Corrosion Compound (Polysciences, Inc.) mixed in the following proportions: 200 ml base solution, 40 ml catalyst, 24 drops promoter, and 5% (total volume) of Batson’s red dye. So made, the mixture solidified within 1 hour at ambient temperatures ranging from 26°C to just over 38°C. The plastic was injected by means of a 10-ml syringe, refilled to need, connected to a small catheter placed in an appropriate blood vessel. In small rays, the catheter was inserted into the dorsal aorta, exposed by severing the spinal column well caudal to the head and flexing the animal at the level of the cut. In larger rays, plastic was introduced into the spinalis impar artery, revealed by excising the head. This latter method, although more difficult to implement, was necessary in large animals in order to avoid filling the voluminous gills. An injection through the dorsal aorta was considered complete when plastic was seen to exit the spinalis impar artery at the level of the dorsal cut. Injections into the spinalis impar were more problematic and were considered complete when the pressure in the syringe made further injection difficult. In some cases the injection was monitored by removing a small portion of the chondrocranium overlying the RMC in order to visualize movement of the dyed plastic through the vessels.

Following solidification of the plastic, injected specimens were placed in a solution of 1% formalin in seawater filling a large pit. The pit was dug into the beach above high tide level and was lined and covered with a double layer of heavy-duty plastic sheets. This method of preservation was necessary owing to the large size of the animals. At the end of the collecting expedition, the pit was drained with a hand-held peristaltic pump, thoroughly flushed, and refilled with sand. The formalin solution was stored in metal containers and delivered to a local marine biological station.

To isolate corrosion casts, the carcasses were digested by submersion in KOH (20% by weight), which was renewed every third day for up to 9 days, depending upon the animal’s size. Recovered casts were rinsed thoroughly in deionized water and stored dry.

**Morphology**

The fine structure of the RMC was examined by scanning electron microscopy (SEM) with a Cambridge Scanning Electron Microscope at the Scripps Institution of Oceanography. For this purpose, portions of the cast were isolated and coated with gold-palladium with a Technics Hummer Sputter Coater at 5 mamp for 6 min. SEM photomicrographs were taken at 20 kV.

For each *Mobula* species studied, at least one complete RMC-brain complex was preserved for histological examination so that the relationship between the rete and brain could be examined. The material was fixed in 10% formalin and preserved in 50% isopropanol. Small sections of the preserved retia were isolated, dehydrated through increasing concentrations of ethanol, transferred to xylene, and embedded in paraffin. Samples then were sectioned at 7 and 12 μm, mounted on glass slides, and stained with Masson trichrome.

**RESULTS**

At the Punta Arena de la Ventana fisheries, *M. thurstoni* was caught most frequently and, consequently, was most thoroughly studied. Thus, the RMC of *M. thurstoni* is the standard against which the retia of less abundant species are compared. Noticeable morphological differences between the retia of *M. thurstoni* and the other species are emphasized, while similarities are only noted briefly. We follow the terminology adopted by Hyrtl (1858) and Panceri and De Sanctis (1869). In both works, mammalian terms were borrowed to name elasmobranch vessels, implicitly implying homology where none has been proved. However, we adopt this terminology for the sake of continuity, without endorsing the implied phylogenetic relationships.
The rete mirabile cranica of Mobulathurstoni

Precerebral RMC

Accessed dorsally, the brain case of *M. thurstoni* appears as a triangular chamber with the base anterior and parallel to the rostral body margin, and the vertex posterior and median underlying the caudal extreme of the medulla. Within this chamber lies the rete mirabile cranica, divisible into a caudal RMC, which envelopes and enters the brain, and a more complex expanded precerebral RMC (Fig. 1). The latter structure constitutes about 40% of the total RMC–brain volume and completely fills the cranial cavity rostral to the telencephalon. The precerebral RMC is encased in a thick gelatinous matrix, previously hypothesized to be an anterior hypertrophy of the arachnoid (Panceri and De Sanctis, 1869), and within the matrix the rete is bilaterally symmetrical (Fig. 1). The two sides are contiguous throughout their length but do not communicate across the midline, except by means of a transverse vessel at the rostral margin of the RMC. The precerebral RMC completely envelopes the olfactory peduncles, and is in intimate contact with the olfactory bulbs at its anterolateral extreme, where retial vessels become markedly smaller in diameter.

The primary vessels of the precerebral RMC are identified unambiguously as arteries by their large size (ca. 1-mm diameters) and thick, muscular tunicae mediae. Secondary vessels, derived from arteries that branch and taper to reduced diameters (ca. 50 to 150 μm, Fig. 2A,B), appear to be small arteries or arterioles. Interestingly, the tunicae mediae of the secondary vessels appear to be
free of muscle (Fig. 3). Many of these secondary vessels course along the large arteries and give rise to a mesh of even finer (20–50 μm) tertiary vessels that ensheath those same arteries (Fig. 2C,D). Both secondary and tertiary vessels are embedded in the arterial adventitia (Fig. 3A,B) and communicate with the arteries by numerous anastomoses (Fig. 3C–F). The tertiary vessels most likely represent small arterial sinuses, precapillary arterioles, or capillaries. Although the tertiary vessels are relatively large, it is important to note that capillaries can attain several times the erythrocyte diameter (cf. Andrew, '59).

Although more detailed histology from well preserved tissue is necessary to label the secondary and tertiary vessels unambiguously, they will be referred to tentatively herein as arterioles and capillaries, respectively. Some of these vessels may form a vasa vasorum serving to nourish the largest arteries.

Venous blood does not communicate with the precerebral RMC. Veins draining blood from the chondrocranium are distinct from and lie on the dorsal surface of the RMC, and are easily dissected away from that struc-
Fig. 3. Photomicrographs of transverse sections (12 \( \mu \)m) through the RMC of *M.thurstoni*. A, B. The arterioles and capillaries (arrows) are embedded in the adventitia of the arteries, which have thick, muscular tunicae mediae. C–F. Arteries communicate with capillaries and arterioles through numerous anastomoses (arrows), the diameters of which are close to that of the erythrocytes. D is C at higher magnification. Calibration bars: A, 100 \( \mu \)m; B, C, 125 \( \mu \)m; D, 50 \( \mu \)m; E, F, 75 \( \mu \)m.

...structure. This organization was similar in all mobulids examined, and is evident in the dissection shown in Figure 6.

**Caudal RMC**

Unlike its precerebral counterpart, the caudal RMC envelops and supplies the brain. In addition, the gelatinous matrix and network of arterioles, prominent features of the precerebral RMC, are absent in the caudal portion.

**Organization of cranial arteries**

The major cranial arteries form a vascular...
triangle that lies ventral to the brain and rests on the floor of the chondrocranium. The sides of the triangle are formed by the profundae cerebri arteries, which run rostrocaudally along the ventrolateral edge of the brain and merge at the vertex of the triangle. The vertex is posterior and median, corresponding to the anterior extreme of the spinalis impar artery. The base of the triangle, the anterior communicating artery, is just rostral to the telencephalon and is formed by the joining of the paired internal carotids, which enter the chondrocranium laterally. The anterior communicating artery is about half the length of the profundae cerebri. All cranial nerves depart from the brain dorsal to the triangle, with the exception of nIII, which crosses the profunda cerebri ventrally.

The precerebral and caudal retia originate together from the caudal half of the profundae cerebri in a branching region extending along 45% of the total length of each vessel. The caudal portion of each of the profundae cerebri is mediolaterally compressed, and a wide ridge is formed dorsomedially along its length. All vessels destined to form the RMC depart from this ridge. Near the point of origin, arteries communicate by numerous large collaterals, even as they arise from the profundae cerebri; two or three arteries converge into large chambers from which many more depart, forming a vascular net. A few arteries turn rostrally to wrap around the profunda cerebri. The rostral portion of the latter vessel has no branching and contributes nothing to the RMC. The anterior communicating artery contributes only a few small vessels.

Within the branching region along the profundae cerebri, an anterior section is distinguished from the posterior three quarters. From the anterior portion arise the arteries that project to the telencephalon and form the precerebral RMC. Vessels supplying the forebrain branch off dorsally, and those destined to form the precerebral RMC remain lateral and ventral before fanning out rostral to the telencephalon. Additionally, a dense vascular bundle arises bilaterally from the most anterior region of branching, just rostral to the hypophysis, and extends ventromedially for a short distance before turning rostrally to merge into the precerebral RMC. These dense prehypophyseal arterial bundles on either side communicate by a small transverse artery that is rostrally curved and posterior to the optic chiasma. Branching from this small transverse artery are two bilaterally symmetrical vessels that join at the midline to form a small triangle whose apex is just caudal to the optic chiasma. Other small vessels arise from the sides of this triangle to join the precerebral RMC.

Arteries arising from the caudal three quarters of the branching region of the profundae cerebri project dorsomedially to wrap around and penetrate the brain, supplying the brain with blood. A large number of vessels enter the third sulcus (cf. Panceri and De Sanctis, 1869) between the cerebellum and forebrain to supply the optic tectum. In addition, a small number of fine vessels of the caudal RMC rest at the midline on the dorsal surface of the cerebellum and telencephalon. These vessels coalesce at a midline node rostral to the forebrain and from there spread out bilaterally to become part of the precerebral RMC.

Embryonic RMC

The embryonic condition is significantly different from that in the adult. In a term embryo the cranial cavity is nearly completely filled by the brain, with the exception of a small space just rostral to the telencephalon. This space is filled with a gelatinous matrix similar to that embedding the precerebral RMC in adult rays. Interestingly, a few large coiled vessels are embedded in the matrix along the anterior margin of the telencephalon.

The rete mirabile cranica of Mobula japonica

Retia of the various mobulids are superficially similar, but variability is evident between species in size, shape, and position relative to the brain (Fig. 4). Although brain morphology also exhibits interspecific variability, all mobulid brains are characterized by a huge telencephalon and large convoluted cerebellum (Fig. 5), so that landmarks to compare RMC position are easily identified between species. The retia of *M. japonica* differ from those of *M. thurstoni* as follows:

1) The precerebral RMC only partially fills the rostral portion of the cranial cavity owing to a pronounced rostral concavity, which conforms to the RMC the shape of a crescent. Accordingly, the precerebral RMC constitutes only 20% of the total RMC-brain volume.

2) The ventral arterial triangle differs from that in *M. thurstoni* in position and proportions (Fig. 4). The anterior communicating
artery traverses the brain caudal to the anterior margin of the telencephalon and is about three quarters the length of either profunda cerebri.

3) The region of the profundae cerebri from which the RMC originates is two thirds the length of that vessel, extends back to the origin of the spinalis impar, and exhibits a greatly expanded lumen. Most arterial branches arise directly from the dorsomedial wall of the profundae cerebri, rather than originating from a dorsomedial crest. The RMC in proximity of the branching region is much less complex than in *M. thurstoni*, and shows a reduced pattern of convergence and divergence in the anterior portion.

4) Although the appearance of the caudal RMC does not differ substantially from that in *M. thurstoni*, the bundle of arteries that enters the third sulcus to supply the optic tectum is much more developed in *M. japonica*.

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**The rete mirabile cranica of Mobula tarapacana**

The RMC of *M. tarapacana* shares with *M. japonica* a pronounced rostral concavity, but in the following respects differs most dramatically from those in other mobulid rays:

1) The precerebral RMC makes up over 45% of the total RMC-brain volume and is the largest found in any species studied. The vessels of the precerebral RMC are larger than others in the species, typically about 1.5 mm in diameter.

2) The ventral arterial triangle found in other mobulids takes the shape of a rectangle in *M. tarapacana* (Fig. 4). The profundae cerebri diverge abruptly from the spinalis impar and course rostrally in parallel. Consequently these vessels run ventral to the brain rather than along its ventrolateral edge as in other species (Fig. 4). The anterior communicating artery forms the rostral short
Fig. 5. Dorsal (left), ventral (right), and lateral (bottom) views of a brain of *M. japonica* (95 kg, 2.1-m disc width). Note the huge telencephalon and the large, convoluted cerebellum overlying the optic tectum. The morphology of this brain is superficially similar to that found in all *Mobula* species. C, cerebellum; OT, optic tectum; OP, olfactory peduncle; T, telencephalon. Calibration bar: 1 cm.
Fig. 6. Dorsal view of the exposed brain of *Mobula* sp. (8.8 kg, 0.86-m disc width). This species is the smallest of those studied, as is the precerbral RMC. The caudal RMC is greatly simplified. In this dissection (performed by Dr. Hans Duncker), the position of the RMC relative to the chondrocranium and brain is clearly visible, as is the venous drain from the cranial cavity. All venous blood from the brain apparently exits the brain case at the level of the olfactory bulbs and just caudal to the otic capsules. Some retial blood exits the chondrocranium at the rostrolateral extreme of the RMC; the destination of this blood remains unknown. C, cerebellum; OB, olfactory bulb; OC, otic capsule; R, rostral exit of retial blood; S, spinal cord; T, telencephalon; V, exits of venous blood from cranial cavity. Calibration bar at top left: 1 cm.
side of the rectangle, traverses the brain caudal to the anterior margin of the telencephalon, and is about 2.5 times shorter than the profundae cerebri. At the junction of the profundae cerebri and anterior communicating, the arterial lumen widens markedly. The orbital (stapedial) artery branches from the internal carotid within the brain case (Fig. 4) instead of well outside as in other moleoids.

3) The RMC originates from the caudal portion of the profundae cerebri, extends over 80% of its total length, and includes the anterior portion of the spinalis impar. The wall of the profundae cerebri at the branching region is at least twice as thick as in the rostral portion. The thickening is asymmetrical, with the thicker portion being ventral. In the caudal portion of the branching region a large number of small transverse arteries ventral to the brain course parallel to the short sides of the rectangle and connect the two profundae cerebri between the level of the spinalis impar and hypophysis. Other vessels from the caudal portion of the branching region form a complex network of converging and diverging arteries that supply the cerebellum and enter the third sulcus as a thick bundle, as in M. japonica. Vessels of the anterior branching region originate from short dorsal ridges that coalesce rostrally into a single ridge similar to that found in M. thurstoni. The arteries branching from these ridges, including a large artery whose lumen is comparable to that of the profundae cerebri, course rostrally along the lateral edge of the brain to supply the telencephalon and form the precerebral RMC.

The anterior communicating contributes to the RMC to a greater extent than in M. thurstoni. At the junction of the profundae cerebri and anterior communicating a large artery extends toward the center of the vascular rectangle where it branches into smaller vessels to contribute to the RMC. In addition, vessels that originate from the anterior margin of the anterior communicating also contribute to the RMC.

The rete mirabile cranica of Mobula sp.

Mobula sp. is the smallest of the species studied, reaching a maximum disc width of only 1.1 m (Notarbartolo-di-Sciara, 1985). The precerebral RMC is less elaborate than in other species (Figs. 4, 6) and constitutes about 20% of the total RMC-brain volume. The typical diameter of the precerebral arteries is comparable to that in M. thurstoni, and as in that species, the anterior margin of the pre-cerebral RMC is only slightly concave (Fig. 4). Retial characteristics worthy of note are as follows:

1) The caudal RMC is simplified to the point where it can not be readily distinguished from the vascularization found in other batoids.

2) The relative dimensions of the ventral arterial triangle are similar to those of M. thurstoni, but the position of the anterior communicating artery is more caudal, lying tangent to the rostral margin of the telencephalon (Fig. 4).

3) Although the RMC of this species is smaller than that in M. thurstoni, the anterior communicating contributes to the RMC as it does in M. tarapacana, and the branching region in Mobula sp. extends over 60% of the length of the profundae cerebri.

4) The pre-cerebral RMC originates from a doral medial ridge of the profundae cerebri located in the anterior portion of the branching region. The prehypophyseal bundles are less well developed than in M. thurstoni, and no midline triangle is formed around the optic chiasm. The two small arteries that form the triangle’s sides in M. thurstoni do not meet at the midline, but instead course rostrally along the optic nerves. A third small artery runs along the ventral midline of the telencephalon. In the posterior branching region the dorso-medial ridge disappears, and vessels originate from the profundae cerebri over a wide arc. Arteries from this branching area course as relatively straight vessels both rostrally and dorsally to supply the brain.

The rete mirabile cranica of Manta birostris

An elaborate RMC is present in Manta, but the paucity of well preserved material prevents a description of the structure at this time.

Blood flow in the RMC

Blood enters the cranial cavity by means of the paired internal carotids and the spinalis impar. The latter vessel receives blood from the paired dorsal aorta through small communicating vessels; at the junction of these communicating vessels and the spinalis impar, blood diverges and flows caudally to supply the body, and rostrally to enter the chondrocranium.

Vascular anatomy suggests that arterial blood from the RMC that nourishes the brain


exists the chondrocranium through two paired venous outlets, one at the level of the otic capsules, the other just caudal to the olfactory bulbs. Two large veins that are clearly separate from, and which course dorsally over the precerbral RMC (Fig. 6), drain venous blood from the rostral brain through the latter exit. Blood supplying the caudal brain exits at the level of the otic capsules. Arterial blood exits the precerbral RMC at the anterolateral extreme through vessels that penetrate the chondrocranium rostral to the olfactory bulbs (Fig. 6). The course of these arteries after exiting the cranial cavity is not known and deserves further attention.

**DISCUSSION**

The rete mirabile cranica is a familial character of the Mobulidae. This study has described and compared the gross morphology and fine structure of the RMC in four species of *Mobula* by using corrosion cast, histological, and scanning electron microscopic techniques.

**RMC morphology**

Details of the morphology of the retia can be used as a distinguishing taxonomic characteristic (Fig. 4). Of particular interest are the substantial differences between the rete mirabile cranica of *M. japonica* examined here and that of *M. mobular* as described by Panceri and De Santis (1869). These include most noticeably the branching region along the profundae cerebri and the contribution to the RMC from the anterior communicating artery. The classification of these mobulids has been controversial (Notarbartolo-di-Sciara, '85), but the morphological differences of the retia support a division into two species.

Interestingly, the morphology of the precerbral RMC reflects the presumed phylogeny of myliobatiform rays. In *Myliobatis* (Lower Cretaceous, Romer, '66) the precerbral RMC is simply a coiled pair of arteries that originate from the internal carotids inside the brain cavity and that lie rostral to the telencephalon. This is strikingly similar to the structure observed in embryonic *M. thurstoni*. In *Rhinoptera* (Upper Cretaceous, Romer, '66) the precerbral RMC is already recognizable as paired, clearly separated bundles of convoluted vessels anterior to the brain. Simply an increase in branching and total mass would transform this structure into the more complex and developed precerbral RMC of the Mobulidae (Eocene, Herman, '79).

**RMC function**

The RMC is clearly not a counter-current exchanger; no veins are present in the precerbral RMC, and hairpin loops are absent. The function of the RMC therefore remains problematic, but its morphology is suggestive. A structure as complex as the RMC may serve several important functions simultaneously. This is not without precedent, for evolutionary inertia often results in the repetitive use of a single organ for diverse purposes. Examples of this are abundant among vertebrates: the liver in elasmobranchs is vital for buoyancy (Bone and Roberts, '69); stomachs of several teleosts, such as the armored catfishes, are used in both digestion and air breathing (Graham and Baird, '82); lungs of some snakes are used to enlarge the body as a means of defense or to maintain body form (Duncker, '78). One function of the RMC may be to serve as a mechanical support and padding of the brain. This was first suggested by Gohar and Bayoumi ('59) for *Manta*. The adult brain rests in a voluminous cranial cavity, and therefore needs support; along with connective tissue, the RMC filling the chondrocranium may satisfy this requirement. If important mechanical support is derived from the RMC, similar structures may be found in other elasmobranchs with voluminous chondracrania, such as *Cetorhinus* (Scott, '80). The lack of reports of such retia may simply reflect the need for further examination. It is interesting to note that in mobulid embryos, in which the brain completely fills the cranial cavity, the RMC is rudimentary.

Although the RMC may serve to support the brain, its tremendous complexity and fine structure suggest other more specialized functions. For example, the secondary system of arterioles and capillaries, apparently a general feature of circulation in fishes (Vogel and Claviez, '81; cf. also review by Laurent, '84), may be involved in the monitoring of rheological, osmotic, or chemical properties of the blood in the primary arterial system (Vogel and Claviez, '81). The secondary system may also be involved in plasma skimming and the production of cerebrospinal fluid. This could be particularly important in mobulid rays in which the lateral ventricles and probably the choroid plexuses are greatly reduced.
The RMC, which is supplied by cold blood from the gills, may also serve to cool the brain. This could be advantageous to mobulids, which are known to bask at the surface, exposing to the tropical sun the dark dorsal surface of the head (Gill, '08; Notarbarto-
di-Sciara, '85). A large volume of cold blood within the chondrocranium may act as a heat sink to reduce intracranial temperature.

No experimental evidence is currently available to falsify any of the above hypotheses; to elucidate the role or roles of the RMC, greater access to these animals for prolonged periods of time is necessary. It is our hope that this preliminary study and our speculations on function will stimulate further research of this impressive vascular structure.

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