COMPARATIVE AND FUNCTIONAL ANATOMY OF CEREBRALLY RELATED RETIAL SYSTEMS IN THE FAMILY MONODONTIDAE (ORDER CETACEA)

by

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ABSTRACT

In this study, I consider the comparative and functional anatomy of cerebrally related retial systems in the two constituent species (Monodon monoceros and Delphinapterus leucas) of the family Monodontidae (order Cetacea).

The internal carotid arteries, the "classical" vessels of cerebral supply in vertebrates, are completely non-functional as cerebral supply vessels in the Monodontidae. Moreover, there are no other channels that contribute directly to intracranial supply. Rather, the brain, or more precisely, the entire central nervous system, is vascularized indirectly via an extensive arterial plexus or rete mirabile. This plexus is found in the thorax, lumbar region, neural canal and cranium. Vessels that contribute to retial formation are numerous and include those which in other mammals contribute directly to supply of the central nervous system and/or its membranes. Efferent retial vessels are few and include two pairs of subdural intracranial trunks that supply the brain, and numerous small segmental vessels that penetrate the spinal dura and vascularize the spinal cord.

Subdural arterial circulation in the Monodontidae is modified after the basic mammalian pattern. Within the cranium, it is characterized by:

(1) an incomplete circle of Willis (due to (a) independence of the anterior cerebral arteries and (b) the lack of anastomoses between the two pairs of
trunks which take origin from the rete),

(2) extensive cortical supply by the anterior choroid arteries, and

(3) absence of a vertebral basilar system.

Subdural arteries coursing to the spinal cord do so mainly between successive ventral spinal roots. An A. radicularis magna is not evident, nor are anterior or posterior spinal arteries. Hence, there are differences between the subdural circulatory patterns in the Monodontidae and those in other mammals, however the major site of vascular modification is epidural with formation of the rete mirabile.

Though gross retial anatomy is the same in Monodon monoceros and Delphinapterus leucas, and is generally similar to that described for other odontocetes, there are two related characteristics that appear species specific: thoracic retial size and the number of intercostal spaces supplied by the supreme intercostal arteries. Both are larger in Monodon monoceros, as are hematological values (hematocrit and hemoglobin concentration) which, in this study, are used as indices of diving ability. These data are consistent with the hypothesis that cerebral related retia in the Cetacea are related to the diving habit.

Microscopically, the rete generally consists of small muscular arteries embedded in fatty connective tissue interlaced with a few nerve trunks and veins. Arterial walls are characterized by a distinct internal elastic lamella, a tunica media of 12-14 layers of vascular smooth muscle, and an adventitia of alternating layers of collagen and elastin. Retal
arteries are at best poorly innervated.

The substructure of retial arteries resembles that of other mammalian arteries except for the presence of large deposits of glycogen (alpha particles) in vascular smooth muscle and endothelial cells. On the basis of this observation, and theoretical considerations, I generate the hypothesis that the rete may contribute to blood glucose levels during a dive.

This hypothesis could not be tested directly, hence I chose an indirect approach involving biochemical and ultrastructural analyses. I conclude that free glucose release is not a major function of the rete since: (1) G-6-phosphatase activities are low, (2) LDH electrophoretic profiles suggest that most stored glycogen is used intrinsically, and (3) I could not demonstrate glycogen deposits in retial vessels of other species.

All proposed retial functions are evaluated, and I conclude that the system probably functions in a mechanical way (pressure reservoir) and that it does so passively.
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GENERAL INTRODUCTION

In the Cetacea (whales, dolphins, and porpoises) blood supply to the brain occurs via a massive arterial plexus located in the thorax, neck, neural canal and cranium. This pattern differs from the classical vertebrate plan in which internal carotid arteries are the major sources of cerebral circulation (Gillilan 1967) and from other mammalian patterns in which internal carotid supply is complemented or replaced by branches of the subclavian and/or external carotid arteries (Ask-Upmark 1935; du Boulay and Verity 1973; Bugge 1974, 1977). The functional significance of this plexus or rete mirabile is not known, though numerous hypotheses have been suggested. Retial function is the underlying theme of this thesis.

The term rete mirabile is used to describe plexiform arrangements of blood vessels. Ask-Upmark (1935) categorizes retia into two major groups: (1) unipolar (diffuse), and (2) bipolar (ambicentric). A unipolar plexus originates from a single trunk and constituent vessels do not reunite. Examples of this form are the brush retia of Dugong dugon (Elsner 1969). A rete having a distinct afferent and efferent vessel of the same type (artery or vein), such as a renal glomerulus, is ambicentric.¹ Cerebrally related retial systems in the Cetacea are of this type.

¹Some authorities (Field and Harrison 1968; Friel 1974) restrict use of the term rete mirabile to this form of plexus.
Retia of one form or another are widespread in the vertebrates; however they seldom occur along vessels leading to the central nervous system or its derivatives. Exceptions include the carotid labyrinth of some amphibia (Noguchi and Kobayashi (1977), the ophthalmic rete of birds (Wingstrand and Munk 1965; Richards 1967; Lucas 1970; Baumel 1975; Kilgore et al. 1976), the maxillary rete of felids (Davis and Story 1943; Daniel et al. 1953; Gillilan and Markesbery 1963; Gillilan 1976), the carotid and orbital retia of artiodactyls (Daniel et al. 1953; Cerny and Najbrt 1970; Bamel et al. 1975; Carlton and McKean 1977; McGrath 1977), the carotid rete of lorisoids (Kanagasuntheram and Krishnamurti 1965) and the vertebral rete of pholidotes (du Boulay and Verity 1973). In birds and mammals, most of these plexuses are closely associated with veins or with venous sinuses and are thermoregulatory in function, or have thermoregulatory properties. Cerebrally related retia of the magnitude found in the Cetacea are unique to this group, with the possible exception of the Sirenia (Nurie 1872 - see plates). The most popular function attributed to the cetacean rete is that of maintaining a uniform flow of blood to the brain during a dive (Morgane and Jacobs 1972).

That this is the sole, or even the major function of the cetacean retial system has not been convincingly demonstrated. Though a dampening of the pressure pulse, and hence a smoothing of flow, does indeed occur (Nagel et al. 1968), this may be an effect of structure and not a primary function. Hemodynamic functions were among the first suggested for the carotid rete of artiodactyls. Closer inspection revealed an involvement with
cerebral temperature control. We should not "explain away" the cetacean rete on the basis of mechanical properties of constituent vessels without critically evaluating all functional possibilities.

At least three observations support the view that functions other than pressure related ones may occur. First, of diving vertebrates, only cetaceans have massive cerebrally related retia. This is true even though all groups are presumably exposed to similar hemodynamic problems. Second, the retial system is huge and appears in excess of that required for a pressure reservoir. Finally, blood returning to the heart from the body must pass through two "organs" before reaching the brain - the lung and rete mirabile. Each of these structures is in a strategic position for carrying out functions other than respiration or smoothing of blood flow.

At present, there exists no complete anatomical description, from the gross to the ultrastructural level, of the retial system. Nor are there sufficient data available for comparison between species. Comparative information may allow us to relate the rete to the diving habit, and might also provide information about specific function.

The approach used in this study is a comparative anatomical one involving a detailed description of cerebrally related retia in the two constituent species of the family Monodontidae - Monodon monoceros and Delphinapterus leucas. I chose these whales for study since they are (1) closely related, (2) of similar size (brain weight), (3) suspected to differ in diving capabilities and (4) both domestically harvested.
My study focuses on the following questions:

(1) Is the internal carotid artery involved with cerebral blood supply in the Monodontidae?

(2) What is the distribution and extent of the retial system? Are there differences between species and, if so, can they be related to diving ability?

(3) What structures does the retial system supply with blood? Does the system supply only the brain, or does it supply the entire central nervous system?

(4) What is the microanatomy of the rete mirabile? Are retial arteries associated with veins in any part of the system? Are retial arteries the same as arteries in general? If not, what are the differences and do they suggest anything about retial function?

(5) What is retial function?
GENERAL MATERIALS AND METHODS

I obtained all samples for this study from whales domestically harvested in the Canadian Arctic.

Each year, during July and August, a population in excess of 4,000 Delphinapterus leucas moves into the warm waters of the Mackenzie Delta and is hunted by local natives. Except for residents of Tuktoyaktuk, most hunters and their families move into temporary hunting camps scattered around the perimeters of small bays in which the whales concentrate. Hunting is done from canoes or speed-boats equipped with outboard motors. Generally the technique involves attaching a float to a whale, then "shooting to kill". After a successful hunt, the animal is towed either to the base camp or to the nearest shore-line and butchered. Though the meat is eaten, by far the most important food commodity is the skin or muktuk.

In late July, large numbers of Monodon monoceros follow receding ice into waters surrounding northern Baffin Island. They remain in the various fjords, bays, inlets and sounds until fall. Local people from coastal settlements and traditional hunting camps harvest the whales for muktuk and ivory.
In both above areas I was able to sample whales by accompanying native people on hunting trips. All sampling was done as stipulated in permits issued by the Commissioner of the Northwest Territories\(^1\) and the Government of Canada.\(^2\)

Locations of hunting camps in the Mackenzie Delta and Pond Inlet regions are indicated in Fig. A and B respectively of Text-Fig. 1. Also included in these figures are locations of hunting grounds and the numbers of whales sampled at each location. I obtained measurements and/or tissue samples from a total of 17 *Delphinapterus leucas* and 60 *Monodon monoceros*. One additional sample (head) of the latter species was obtained from D. E. Sergeant of the Arctic Biological Station in Ste-Anne de Bellevue, Quebec. The length, sex and identifying number of each of these whales are presented in Table 1.

Names of all anatomical structures are given in English throughout the text. Occasionally, when a structure is first mentioned or appears in headings, the standardized Latin term\(^3\) is also given. Latin terminology is used in all figures.

\(^{1}\)Science and Explorers Ordinance: 1654; 1751; 1920; 2020; 2210.

\(^{2}\)Federal permit - File #: 1375-7; 5624-2-81/N3; 5624-82; 5642-82.

Text-Fig. 1. Locations of seasonal hunting camps.

Fig. A. Mackenzie Delta. Collecting site for *Delphinapterus leucas*. Black circles with white centres indicate approximate area where whales were killed. Numbers refer to numbers of whales sampled. Solid black circles indicate locations of seasonal hunting camps. Black squares are permanent settlements.

Fig. B. Pond Inlet area of northern Baffin Island. Collecting site for *Monodon monoceros*. Notations are as in Map A. Insert shows approximate location of the Mackenzie Delta (A) and Pond Inlet area (B) in the Canadian arctic.
Table 1. Specimens of *Monodon monoceros* and *Delphinapterus leucas* sampled during five field seasons.

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* Specimen (fetus) was collected at Arctic Bay by personnel of the Arctic Biological Station, Ste. Anne de Bellevue, P.Q.
CHAPTER 1

Status of the Internal Carotid Artery

(*A. carotis interna*)

Introduction

Is the internal carotid artery (*A. carotis interna*) involved with cerebral blood supply in the family Monodontidae?

In other cetaceans, this artery is considered degenerate (Slijper 1936; Walmsley 1938; Fraser 1952; Galliano et al. 1966; Morgane et al. 1966; Viamonte et al. 1968; Moris 1969; Morgane and Jacobs 1972). Evidence supporting carotid occlusion is from gross anatomical observation of (1) reduced vessel diameter along its course, and (2) an apparent superceding cerebral supply via an extensive intravertebral route (the *rete mirabile*). In *Tursiops truncatus*, Galliano et al. (1966) describe the internal carotid as a "solid cord" as it enters the cranium. Similarly, Sharpey (1835) states that the artery is "scarcely thicker than a pin" in the same area of a porpoise. Though angiographic studies also suggest vessel closure (Viamonte et al. 1968), histological documentation of non-patency is lacking. Boenninghaus (1904), in a study of the cetacean ear, concludes that the vessel is patent in fetuses, but occluded in adults. However, his histological sections do not convincingly demonstrate absence of a lumen. De Kock (1959) describes cervical and otic portions of the internal carotids in
Globicephala melaena and Phocoena phocoena. Finding no evidence of closure he suggests a regulatory or "intermittent" function.

The internal carotid artery in mysticete whales appears to have the same status as in odontocete whales. Walmsley (1938) briefly reviews the findings of previous authors and describes the lumen of the artery in a fetal Balaenoptera physalus as "obliterated in the anterior part of the tympanic cavity."

The objectives of this chapter are to (1) add completeness to a discussion of cerebral supply in the family Monodontidae, and (2) establish the status of the internal carotid artery in Delphinapterus leucas and Monodon monoceros.
Materials and Methods

Information on the position and distribution of the internal carotid artery was obtained from vascular perfusion casts and gross anatomical dissections.

Animals used in detailed dissections (*Delphinapterus leucas* #15; *Monodon monoceros* #1) were frozen in Arctic settlement freezers, transported to the lab in Vancouver, thawed, then hardened in 10% formalin. Only the head, neck and thorax were dissected.

Perfusion casts were obtained by injecting the arterial circulation of freshly killed animals (*Delphinapterus leucas* #14; *Monodon monoceros* #6) with a polyester resin\(^1\) using the apparatus in Text-Fig. 2. Each animal, after beaching, was positioned ventral side up and the sternal plate removed to expose the heart. A cut was made in the left ventricle through which a cannula was inserted and tied into place at the base of the aorta. To prevent filling of visceral arteries, the abdominal aorta was tied just distal to the diaphragm. Following this, the right atrium was cut and vascular perfusion at 150-200 mmHg pressure initiated. A saline wash of approximately 5 gallons preceded plastic injection. When perfusion was complete, the ascending aorta was tied distal to the cannula and the cast allowed to harden for approximately one hour. That portion of the carcass caudal to the diaphragm was then discarded and the

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\(^1\) Esterex 103 manufactured by Hallcraft.
Text-Fig. 2. Perfusion apparatus for vascular casting.
Manometer

Jar

Clamp

Cannula
cephalic portion stripped of all excess tissue. The head, neck and thorax were transported as a unit to the nearest settlement and frozen to prevent breakage during shipment to Vancouver where all tissues were removed by immersion in 10% KOH.

Details of wall structure and luminal status were obtained using histological techniques. Cervical (bifurcation to occiput), otic (middle ear and sinuses), and cranial (carotid canal) lengths of the left and right arteries were excised from twelve *Monodon monoceros* and fixed in 10% buffered formalin. In the lab, samples corresponding to proximal, central and distal positions along the vessel's cervical and otic courses were processed using standard histological techniques and treated with Verhoeff's stain for elastin and collagen (Thompson 1966). Also processed were sections corresponding to positions within the carotid canal.

Animals and the levels at which samples were taken are given in Table 2. Damage during hunting and flensing prevented sampling of entire vessels in many cases.
Table 2. Levels at which the A. carotis interna was sampled for histology in 12 *Monodon monoceros*. 
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Observations

Gross Anatomy

Monodon monoceros

A) Dissection:

The left internal carotid artery bifurcates dorsally from a short common carotid at a level corresponding to the base of the thyroid gland. It passes dorsal to the plane of the external carotid artery and over much of its cervical length lies medio-ventral to the vagus nerve. The vessel tapers in its cephalic third. No branches occur in the neck (Plate 1, Fig. B).

In the ear, the vessel's course and relationship to other structures are as described and/or illustrated in other species (see Beauregard 1894; Boenninghaus 1904; Reysenbach de Haan 1957; Fraser and Purves 1960, and Ridgway et al. 1974). The left internal carotid enters the otic region via the incessura parabasioccipitalis (Fraser and Purves 1960) and follows a semi-circular path medio-dorsally through the middle ear and anterior sinus. With veins of the corpus cavernosum and dorsally related cranial nerves, the vessel contributes to formation of a mucus epithelium covered cord-like structure suspended by its dorsal aspect from the roof of the middle ear and sinus (Plate 2, Fig. A). Numerous small branches occur in this region (Plate 2, Fig. F).
Leaving the ear via the carotid canal, the artery courses rostro-dorso-medially and emerges lateral and slightly postero-caudal to the hypophysis and connects with the carotid rete (Plate 1, Fig. C).

The right internal carotid artery bifurcates from a short common carotid at a slightly higher level than on the left side. Its course and distribution are as described above. No cervical branches occur.

Gross cross section of the vessels on both the left and right side demonstrated patency.

B) Perfusion Cast (Plate 3, Fig. A)

The left internal carotid artery arises dorsally from the brachiocephalic trunk (truncus brachiocphalicus sinistra) caudal to the high cervical origin of the subclavian artery (A. subclavia sinistra). The cast of the vessel terminates in the neck above the level of the cranial thyroid artery (A. thyroidea cranialis sinistra).

The right vessel bifurcates dorsally from a short common carotid artery. Further information is not available because of breakage during the clearing process.

Delphinapterus leucas

A) Dissection
The internal carotid on both the left and right side bifurcates from a short common carotid (Plate 1, Fig. A) and courses into the cranium as described in *Monodon monoceros*. The left vessel originates at a slightly higher level than on the right side.

A major difference between the two species is the presence in *Delphinapterus leucas* of cervical branches originating from the internal carotids at about the level of the atlanto-occipital joint and passing cranio-medially dorsal to the larynx to supply pre-vertebral muscles. Retial branches occur along their lengths.

Patency of cranial portions of the arteries was evident only on the left side.

B) Perfusion Cast

The left internal carotid bifurcates dorso-laterally from a short common carotid at a lower level than on the right, passes dorso-lateral then medial to the external carotid, and terminates at the level of the cranial thyroid artery (Plate 3, Fig. C and D).

The right vessel bifurcates dorsally from a short common carotid, passes dorso-medial to the external carotid, and divides at a level approximating the atlanto-occipital joint (Plate 3, Fig. B). The larger ramus gives rise to retial branches along its length and courses dorso-medially then cranially to supply pre-vertebral muscles. On the left side,
this area is supplied by a vessel branching from the brachiocephalic trunk. The smaller branch passes cranially and ends in an area corresponding to the incessura parabasioccipitalis.

Position of the carotid sinus is indicated, on both the left and right side, by an expanded portion of the internal carotid artery cranial to its origin.

Histology

**Monodon monoceros**

The cervical portion of the internal carotid changes from an elastic to a muscular artery of smaller diameter. Proximal sections are characterized by a unicellular endothelium overlying a tunica media of alternating layers of elastin and vascular smooth muscle (Plate 4, Fig. A). The division between media and adventitia is indistinct with a gradual increase in collagen and a separation of elastic lamellae adventitially. Central sections are similar to more proximal ones except for increased muscularity of the media (Plate 4, Fig. B). The most dramatic change in size and structure is observed in distal sections. A distinct muscular media and thick adventitia are present as is a more recognizable internal elastic lamella (Plate 4, Fig. C).

In the ear, muscular status is maintained; however progressive deterioration of the adventitia and internal elastic
layers is evident. In many cases, separation of adventitial elastin occurs with apparent intrusion of medial smooth muscle into these areas (Plate 5, Fig. B). A similar process occurs with internal elastin (Plate 5, Fig. A). Sub-endothelial (or possibly endothelial) proliferation is evident, and in at least two of the studied vessels, leads to apparent closure of the vessel (Plate 5, Fig. D).

Though layers of collagen on the tunica media side of the internal and external elastic lamellae sometimes occur in distal cervical portions of the internal carotid, these layers are distinct in the ear. In some cases, proliferation of collagen and the presence of organized elastin separates the media into two layers (Plate 2, Fig. C).

Absence of a lumen and disruption and disorientation of elastin characterize cranial sections of the artery. Depending on section level, non-patency is effected by a cellular plug (Plate 5, Fig. E), blood clot (Plate 5, Fig. F), or complete absence of any recognizable lumen. In all cases except the calf, the internal carotid arteries were histologically non-patent at the level of the carotid canal (Plate 6).
Discussion

The internal carotid artery is similar in the Monodontidae to that described in other cetaceans.

Tapering of the vessel is well documented (Sharpey 1835; Boenninghaus 1904; Walmsley 1938; Galliano et al. 1966). In the neck, a progressively reduced diameter is associated with a structural change from a wall elastic in nature to one more muscular. This is reported by De Kock (1959) for Phocoena phocoena, and is documented in this study for Monodon monoceros and Delphinapterus leucas.

Cervical branches are reported in Balaenoptera musculus (Turner 1870), Delphinus delphis (Fraser 1952) and Tursiops truncatus (Galliano et al. 1966). In Tursiops truncatus, Viamonte et al. (1968) describe the internal carotid artery as trifurcating. One branch enters the cranium, another supplies the rete, and the last vascularizes cervical musculature. A single large branch occurs in Delphinapterus leucas, however the degree of its development is reciprocal with that of a branch from the ascending cervical artery (A. cervicalis ascendens). No cervical branches occur in Monodon monoceros.

Retention of a large internal carotid artery, in at least part of its cervical course, is probably related more to maintenance of a carotid sinus than to the vascular supply of cervical structures. Ask-Upmark (1935) and De Kock (1959) document the position of the sinus just distal to the bifurcation and along the cervical course of the artery. In my
study a swelling representing the sinus was observed in the Delphinapterus leucas cast and noticed in at least two Monodon monoceros dissected in the field.

Though Burnes (Fraser 1952) shows the internal carotid as degenerate at the apex of the neck, other authors consider the vessel patent at least into the ear. Fraser and Purves (1960) and Purves (1966) consider patency in the ear related to active filling of the corpus cavernosum to accommodate middle ear volume changes during a dive. Small muscular vessels do branch from the artery in the ear, but they are probably more important in nutrition of surrounding tissues than in active filling of the corpus cavernosum. Filling via connections with cranial sinuses (noted by Reysenbach de Haan 1957) is more likely.

Observations of internal carotid occlusion in this study are consistent with the conclusions of Boenninghaus (1904), and generally with the views held by more recent anatomists. Discrepancies are mainly the result of using fetal animals as subject material (Jackson 1845; Mackay 1886; Ask-Upmark 1935; Nakajima 1961), and of not studying the entire length of the vessel (De Kock 1959). Though exact age of closure is unknown, I agree with Moris (1969) in that it probably occurs post-natally during the first year.

The level at which anatomical closure occurs in Monodon monoceros corresponds with the level at which Viamonte et al. (1968) demonstrated cessation of filling with radio-opaque dye in a post-mortem Tursiops truncatus, and with the level at which Sinclair (1967) reports narrowing in Stenella sp. embryos.

Reasons for complete lack of carotid involvement in
cerebral supply is unclear since the pressure reservoir, or "windkessel", theory of retial function does not in itself necessitate carotid closure. Though Reysenbach de Haan (1957) suggests, as causal factors, acoustic problems associated with having a large artery passing through the ear, the fact that other mammals having cerebrally related retial systems also have degenerate carotids casts doubt on this. One explanation may be that having two vascular channels (carotids and rete) supporting the cerebral circulation might result in flow reversals and/or pressure peaking during the cardiac cycle, particularly if the two channels vary in their hemodynamic properties. By closing the internal carotids, a more uniform flow results.

This study conclusively demonstrates anatomical closure of the internal carotid artery at a position within the carotid canal, and hence its complete lack of involvement with cerebral supply in the Monodontidae.
CHAPTER 2

Origin and Distribution of Cerebrally Related Retia: Retia and Their Afferent Vessels

Introduction

If the internal carotid artery is not the source of cerebral blood supply, what is?

The existence of a retial complex in Cetacea has been known for three hundred years. Tyson (1680), in his monograph on the anatomy of a common porpoise (Phocoena phocoena), is the first to describe the rete in odontocetes, and does so in the following way:

"...before I leave the Thorax I must take notice of a seeming Glandulous body that did lye of each side the Spine about two inches broad and the length of ten or eleven Ribs. It was continued likewise a little over some of the Sanguinary Vessels that went to the head. It was a curious contexture of sanguinary vessels variously contorted and winding, emerging from the Medulla Spinalis at the holes where the Nerves come out between the Ribs, and as we afterwards observed the same substance likewise for a good thickness covered the Medulla Spinalis throughout. In the Thorax in some places 'twas above a quarter of an Inch thick, but every where it appeared of the same Contexture, a winding and convolution of blood-Vessels."

In a general discussion of Cetacea, Hunter (1787) describes intercostal arteries as dividing into "a vast number of branches" that line the thorax and "probably" anastomose with a plexus surrounding the spinal cord. Sharpey (1835), adding to
Hunter's earlier description, implicates arteries in the head and neck of a porpoise as also forming plexuses, but offers no details.

The most noteworthy historical account of the rete mirabile, based mainly on dissections of Phocoena phocoena, is that by Breschet (1836). In addition to demonstrating the system's arterial nature, he describes and diagrams the thoracic rete and its boundaries, the spinal rete and its continuity with that of the thorax, and extensions from one or both these plexuses into cervical areas, particularly dorsal to the cervical vertebrae and in the fascia of the scalene muscles. Retial masses between transverse processes of lumbar vertebrae, and extensions of the spinal rete into the cranium are also indicated. Though retial distribution is well described, vessels from which the retia take origin are not.

In the porpoise, Owen (1868) describes the two posterior thoracic arteries (named by Stannius 1841) as supplying the first five intercostal spaces and complementing aortic intercostals in forming thoracic retia. He also states that branches from internal and external carotids for plexuses in the head and neck.

Murie (1874) briefly documents the presence of thoracic, cervical, and spinal retia in Globicephala melaena and offers a more detailed description of an arterial plexus situated dorsal to the "inferior lumbo-caudal muscles" (M. psoas) and extending laterally from intervertebral communications with the spinal rete to the ends of vertebral transverse processes. Afferent vessels are not discussed.
Wilson (1879) restricts his study of retia in *Monodon monoceros* mainly to the thorax, but does comment on their extensions into cervical areas. Among vessels described directly involved with retial formation are posterior thoracic, aortic intercostal and lumbar arteries, and a vessel of suggested homology with the ascending cervical artery of man.

A major historical reference to odontocete retial systems is in an account of the cephalic arteries in *Phocoena phocoena*. Mackay (1886) describes the thoracic rete and its origin from posterior thoracic, aortic intercostal and "inferior thyroid" arteries, and also comments on a plexus, at the "back of the skull", supplied by the dorso-cervical or deep cervical trunk and "branches from the subclavian and from the small vessel ["deep thyroid"] which springs from the aortic arch upon the left side, and from the first part of the posterior trunk on the right."

Bouvier's (1889) thesis on cetacean anatomy is also noteworthy since it contains descriptions of the thoracic rete in two odontocetes ("Dauphin" and "Marsouin") and a mysticete (*Balaenoptera acutorostrata*). Intercostal vessels branching from either the aorta and/or thoracic arteries ("arteres thoraciques") are described as major supply vessels. His account includes diagrams.

More recent works referring, in part, to the anatomy of retial systems in odontocetes are those by Slijper (1936, 1938), Fraser (1952), Harrison and Tomlinson (1956), Boice et al. (1964), Barone (1972), and Yablokov et al. (1978).
Nakajima (1961), using radiographic injections, cross sections and gross dissections of *Grampus griseus* and *Tursiops truncatus*, defines thoracic, lumbar, numerous cervical, spinal and intra-cranial plexuses, as well as numerous retia of other probable significance. Among pertinent supply vessels named are omocervical, vertebral, internal carotid, transverse colli, profunda cervical, supreme intercostal and aortic intercostal arteries.

In a series of later studies on *Tursiops truncatus*, Morgane et al. (1966), Galliano et al. (1966), Viamonte et al. (1968), and Morgane and Jacobs (1972) confirm the presence of thoracic, spinal, cervical and intra-cranial retia in this species, and demonstrate angiographically the brain's dependence on these systems for arterial supply. Named arteries from which plexuses take origin are internal carotid, supreme intercostal, aortic intercostal, profunda cervical and omo-occipital arteries, and a small cervical vessel termed first the profunda thyroid and later the cervical retial artery.

A retial system also exists in mysticete whales, however reported observations suggest that it is less extensive than in odontocetes (Bouvier 1889). Hunter (1787) briefly mentions the system in a piked whale (*Balaenoptera* sp.), and notes that vessels (posterior thoracic arteries) branching from the subclavian contribute to its formation. A more detailed account occurs in an anatomical study of *Balaenoptera acutorostrata* by Carte and MacAlister (1868). They describe the system as "extending from the first cervical to the fourth dorsal vertebra, lying on the heads of the ribs, and passing also
upwards into the large spaces formed by the transverse processes of the cervical vertebrae; a portion of this plexus likewise passed in the interval between the two heads of the trachelomastoid muscle, and in the cup-like cavities or interspaces between the necks of the ribs." They also remark that the thoracic plexus does not "extend so far outwards on the ribs as in the Porpoise and Dolphin." The system is considered mainly venous and to be continuous with vessels in the neural canal and cranium. The internal carotid artery is described as supplying "the brain through the medium of its rete mirabile, where its inosculating branches interlaced with those of the venous plexus at the base of the skull."

In the blue whale (*Balaenoptera musculus*), Turner (1870) documents retia origins from posterior thoracic and internal carotid arteries. Thoracic and cervical retia, and their extensions into the neural canal are also identified. Though no details are presented, he considers these arterial retia to be the source of cerebral and spinal vascular supply.

In fetal *Balaenoptera physalus*, Ommanney (1932) reports the system to be mainly venous and to exist as a solid mass from the first cervical to fourth thoracic vertebra, and as isolated masses between the transverse processes of the fourth to sixth vertebrae. Supply vessels are all veins in contact with the retia. The small arterial component is supplied mainly by the posterior thoracic arteries which course up to the fifth intercostal space. Though connections with spinal plexuses are described, vessels in the cervical portion of the neural canal and passing through the foramen magnum are considered totally
venous. No connection between cerebral supply and the arterial portion of the system is identified. Working with adult and fetal specimens of the same species, Walmsley (1938) clearly describes and illustrates the continuity between these systems and the cerebral circulation - arterial and venous.

In addition to differences in retial size between odontocete and mysticete whales there are also differences within each cetacean order. Slijper (1958) considers the rete largest in small species. This he relates to a greater lung volume relative to body size and, therefore, to more abrupt thoracic pressure changes during the respiratory cycle. Walmsley (1938) views the system as most extensive in species with the best diving ability. Consistent with this argument are the occurrence of extensive retia in the accomplished diver Phocaenoides dalli (Ridgway 1966) and of a "poorly developed" system in Inia geoffrensis (Mann - in Slijper 1968), a shallow diving freshwater species. In the only quantitative study to date, Nakajima (1961) demonstrates no difference between retial extent in Grampus griseus and Tursiops truncatus, but does comment that the system appears larger in Physeter macrocephalus, a champion odontocete diver.

Available information on Monodon monoceros and Delphinapterus leucas suggests that these species differ from each other in retial extent and diving capacity. Wilson (1879) describes a well developed thoracic rete in Monodon monoceros, while Wyman (1863) comments that the system is "barely noticeable" in Delphinapterus leucas. Unfortunately, we have little information on the diving habits of these animals, and
that which does exist is not conclusive. Using the amount of harpoon line taken out as an indication of diving depth, Scoresby (1820) records that *Monodon monoceros* "descend to about 200 fathoms" (370 meters). Kleinenberg et al. (1964) consider a diving depth of 14-40 meters not rare for *Delphinapterus leucas*. Comparative information on diving times is also scant. Vibe (1950) states that a submergence time of 15 minutes is common when *Monodon monoceros* are being pursued. When undisturbed, members of this species have recently been observed to dive for up to 28.5 minutes (H. Silverman pers. comm.). Recorded values for *Delphinapterus leucas* are lower and average 5-10 minutes (Tomilin 1957). Though incomplete, these data suggest that retial size may indeed be related to diving capacity - the system being largest in the best divers.

Specific aims of this portion of my study are (1) to determine retial extent and distribution in each species for comparison with each other and with systems reported in the literature, (2) to define the major arteries from which retia take origin, (3) to investigate the hypothesis that retial size varies with diving capacity, and (4) to establish a vascular foundation from which cerebral and spinal circulatory supply can be described in a subsequent chapter.
Materials and Methods

Data on retial distribution and on vessels giving rise to retia were obtained from the gross dissections and plastic perfusion casts discussed in Chapter 1.

To acquire data for statistical comparison of thoracic retial size, measurements of those dimensions used by Nakajima (1961) were recorded from nine animals of each species. Retial length was measured from the first rib caudally on both left and right sides. Along each recorded length, and between every other rib, width was measured laterally from the midline by following the curvature imposed on the system by the thoracic wall. At the same levels, retial thickness (depth) was measured at a point approximately mid-way between the vertebral column and lateral retial border. Because of lesions incurred during the hunting and/or flensing processes, all measurements could not always be obtained nor recorded consistently at similar locations.

Data were analyzed statistically as follows. To test the null hypothesis that retial length is the same in the two species, regressions of average retial length (right+left/2) on body length were tested for equality of slope and equality of equation (UBC-SLTEST). To test for equality of retial widths, ratios of total retial widths (right+left/2) were compared using a T-test (UBC-STRP). When a width value was missing, a value was determined by averaging the measurements around it. A preliminary test was run to see if retial widths and lengths were correlated (UBC-STRP). A similar set of tests was run on
ratios of retial lengths to body lengths.
Observations and Results

Retial Distribution

The following description pertains to both *Monodon monoceros* and *Delphinapterus leucas* since their retial distributions are similar.

Nomenclature

Nomenclature for various sections of the system is as follows:

1. Thoracic rete - *(Rete arteriales mirabile thoracica)* - (RAMT) - located within the boundaries of the thorax

2. Lumbar rete - *(Rete arteriales mirabile lumbaris)* - (RAML) (Slijper 1936) - that portion of the plexus in the lumbar region dorsal to the psoas muscles and between successive transverse processes

3. Spinal rete - *(rete arteriales mirabile spinalis)* - (RAMS) - *(Rete arteriales mirabile columnae vertebralis)* of Slijper 1936) - that portion of the rete within the neural canal

4. Cervical rete - *(Rete arteriales mirabile cervicalis)* - (RAMC) - located in the cervical region - does not include that portion of the plexus within the neural canal - consists of three parts:
   a) RAMC Dorsalis - dorsal cervical rete (Slijper
b) RAMC Lateralis - lateral cervical rete - located laterally in the neck and is closely associated with the scalene muscles - Nakajima (1961) describes this plexus as part of the RAMCV

c) RAMC Ventralis - ventral cervical rete - located in the prevertebral fascia dorsal to the oesophagus - Reté arteriales mirabile cervicalis anteriores of Viamonte et al. (1968); reté arteriales mirabile basis cranis of Slijper (1936) and Nakajima (1961) - this term is not used here since it has been used ambiguously (see Green (1972), Walmsley (1938), and Ommanney (1932)) - it also implies a relationship with the cranium rather than with the neck

(5) Cranial rete - (Reté arteriales mirabile cranialis) - (RAMCr) - will be used to define that portion of the plexus connecting the RAMS with the RMCI

(6) Carotid rete - (Reté mirabile carotis interna) - (RMCI) - reté arteriales mirabile ophthalmica interna of Galliano et al. (1966) - probably homologous with the Reté arteriales mirabile epidurale rostrale in other mammals - RMCI is used here to emphasize its association with the internal carotid artery

(7) Ophthalmic rete - (Reté arteriales mirabile ophthalmica) - (RAMO) - Reté arteriales mirabile ophthalmica externa of Galliano et al. 1966. - extends
along the optic nerve

(1) Thoracic Rete

The thoracic rete occurs in the endothoracic fascia of the dorsal thoracic wall (Plate 2, Fig. A and B; Plate 7, Fig. A and B). Constituent vessels arise from major systemic arteries (Plate 1, Fig. E), become tortuous (Plate 1, Fig. C) and anastomotic (Plate 1, Fig. F), and are of a uniform diameter of about 1 mm (Plate 1, Fig. D - vessels range from about .9 to 1.2 mm in outer diameter after being fixed and processed for histology, and depending on the size of the animal). Distribution of the plexus and its relation to surrounding structures are similar to those described by Breschet (1836). The rete extends laterally to a level approximating the angle of the ribs and is continuous cephalically with cervical retia and caudally with the lumbar rete. Ventrally it is related to the pleura except at the mid-line where it extends a short distance into the posterior mediastinum. Its dorsal relations include the intercostal muscles, ribs, vertebral centrae and caudally, the psoas muscles. Left and right sides anastomose with each other ventral to the vertebral column, and with the spinal rete via intervertebral foramina. Structures embedded in and/or emerging from the plexus include the intercostal veins and arteries, spinal nerves, splanchnic nerves and the sympathetic chain.
Three distinct, but interconnected plexuses constitute the cervical rete in the family Monodontidae.

A) Ventral Cervical Rete

The ventral cervical rete is a cephalic extension of the thoracic plexus into the fascia between the prevertebral muscles dorsally and the oesohagus and larynx ventrally (Plate 8, Fig. A and B; Plate 3, Fig. A). It extends anteriorly to a level approximating the atlanto-occipital joint and laterally to the scalene muscles where the ascending cervical artery forms its lateral boundary. Retial vessels course dorsally between ventral scalene muscle masses and the pre-vertebral muscles, anastomose with vessels derived from the lateral cervical rete, and pass through cervical intervertebral foramina to connect with the spinal rete. Vessels also extend dorsally from either side of the mid-line (Plate 9, Fig. A). Relations of these arteries to other retia are not clear.

B) Lateral Cervical Rete (Plate 8, Fig. A and B; Plate 9, Fig. A)

The lateral cervical rete occurs in and proliferates superficial to the plane between anterior
and posterior scalene masses. It is continuous caudally with the thoracic rete, ventrally with the ventral cervical rete (via a few vessels coursing laterally over the anterior scalene muscles), and dorsally with the dorsal cervical rete, via arteries coursing around the atlanto-occipital joint. Retial extensions course with spinal nerves through intervertebral foramina to connect with the spinal rete.

C) Dorsal Cervical Rete (Plate 16, Fig. B)

The dorsal cervical rete lies within the fascia of epaxial musculature dorso-lateral to the neural arches of the cervical vertebrae and proliferates mainly around the profunda cervical artery. In addition to a connection with the lateral rete, it is continuous caudally with the thoracic plexus via vessels accompanying the profunda cervical artery, and with the spinal rete via vessels accompanying at least the first two cervical nerves.

(3) Lumbar Rete (Plate 10, Fig. B)

The lumbar rete lies ventral to the lumbar vertebrae and in the fascia dorsal to the psoas muscles. It is continuous, dorsal to the aorta, with the thoracic rete, and, through the
intervertebral foramina, with the spinal rete.

(4) Spinal Rete

The spinal rete is continuous, via intervertebral foramina, with all previously discussed retia and also appears to receive branches directly from dorsal rami of aortic vessels distal to the lumbar rete. Though most of the plexiform mass lies dorsal to the spinal cord and is composed of left and right halves separated by a fascial plane (Plate 12, Fig. C), vessels do occur ventrally and appear continuous between the two sides (Plate 12, Fig. D). Ventrally, retial vessels are related to large intravertebral veins that constitute most, if not all, drainage from the central nervous system.

Vessels of the spinal rete increase in size dorsally, however a plexiform nature is retained (Plate 12, Fig. A and B) except at the foramen magnum where two distinct and large vessels predominate (Plate 13, Fig. A). These latter vessels probably correspond to the spinal meningeal arteries of Viamonte et al. (1968).

(5) Cranial Rete (Plate 5)

As spinal vessels approach and pass through the foramen magnum they assume a more ventral position relative to the spinal cord, and become intradural (Plate 13, Fig. B). In the cranium, retial vessels pass laterally over the cerebellar
hemispheres, course through the transverse sinuses (Plate 13, Fig. C), loop around the temporal lobe (of the cerebrum), and course medially to anastomose with the carotid rete (Plate 13, Fig. D). Though cranial vessels are indeed plexiform, there is a tendency to form large trunks as they cross the transverse sinuses on each side.

Large dural vessels, previously noted by Galliano et al. (1966), arise from the cranial rete, particularly in an area opposing the lateral cerebral sulcus (Plate 13, Fig. C and D).

(6) Carotid Rete

The carotid rete proliferates in the dura lateral to and around the hypophysis (Plate 14, Fig. E). In addition to its major association with vessels of the cranial rete (Plate 14, Fig. A), it is connected ventro-laterally with the degenerate internal carotids (Plate 14, Fig. C), and may, at least in some cases, have a communication with the maxillary artery via a middle meningeal vessel (noted only in the dissection of Monodon monoceros). Structures related to the carotid rete include cranial nerves, the hypophysis, and veins of the cavernous sinus. Plexiform vessels extend along the optic nerve (ophthalmic rete - Plate 14, Fig. B and D) and other nerves of the orbit (Plate 14, Fig. B).
(7) Ophthalmic Rete

This plexus presumably vascularizes the retina, and possibly other structures of the orbit (Plate 14, Fig. D).
Major Systemic Vessels That Give Origin to Retia

In the following section, and for each species, the vascular cast and dissection are described separately.

**Delphinapterus leucas**

Results of Perfusion Cast (Text-Fig. 3)

Except for aortic intercostals, all major arteries of the head, neck and thorax originate via two brachiocephalic trunks.

(A) Right Brachiocephalic Trunk (Truncus brachiocephalicus dextra)

The right brachiocephalic trunk arises ventro-laterally from the aortic arch (Arcus aorta). It courses 10 cm dorso-laterally in a cephalic direction and terminates as the common carotid artery (A. carotis communis dextra) and subclavian artery (A. subclavia dextra). Two branches originate from its dorsal aspect.

The first branch, the profunda thyroid artery (A. thyroidea profunda of Mackay 1886), arises 6 cm from the origin of the brachiocephalic trunk, passes 4 cm dorsally, and bifurcates. One vessel, the broncho-esophageal artery (A. broncho-esophagea dextra), passes caudally along the esophagus supplying branches to this structure and to structures in the region of the hilus of the lung. It also contributes to the thoracic rete directly,
Text-Fig. 3. Major arteries giving rise to cerebrally related retia in *Delphinapterus leucas*. Drawn from a vascular perfusion cast (*Delphinapterus leucas* #14). Retial arteries take origin from stippled vessels. Solid black area indicates region from which retial vessels are suspected to arise, but could not be documented to do so because of cast breakage.

AA - Arcus aorta
AAXD - A. axillaris dextra
AAXS - A. axillaris sinistra
AaCD - A. (aorta) costoabdominalis dorsalis
AaID - A. (aorta) intercostalis dorsalis
  RD1 - ramus dorsalis 1
  RD2 - ramus dorsalis 2
AaL - A. (aorta) lumbus
AACCD - A. carotis communis dextra
ACED - A. carotis externa dextra
ACES - A. carotis externa sinistra
ACIS - A. carotis interna dextra
ACID - A. carotis interna sinistra
ACICD - A. carotis communis dextra
ACICD - A. carotis communis dextra
ACID(cr) - ACID cranial ramus
ACIS - A. carotis interna sinistra
ACOD - A. cervico-occipitalis dextra
ACOS - A. cervico-occipitalis sinistra
ACPD - A. cervicalis profunda dextra
ACPS - A. cervicalis profunda sinistra
AISD - A. intercostalis suprema dextra
AISDID - A. intercostalis suprema sinistra
tercostalis dorsalis
  RD1 - ramus dorsalis 1
  RD2 - ramus dorsalis 2
AISS - A. intercostalis suprema sinistra
AILD - A. lingualis dextra
AILS - A. lingualis sinistra
AOD - A. occipitalis dextra
AOS - A. occipitalis sinistra
ASD - A. subclavia dextra
ASS - A. subclavia sinistra
AT - Aorta thoracica
ATCaS - A. thyroidea caudalis sinistra
ATCr - A. thyroidea cranialis
ATID - A. thoracica interna dextra
ATIS - A. thoracica interna sinistra
ATPD - A. thoracica posterior dextra
ATPS - A. thoracica posterior sinistra
DA - Ductus arteriosus
TBD - Truncus brachiocephalicus dextra
TBS - Truncus brachiocephalicus sinistra

* APTr (A. profunda thyroidea) - note cranial branch (A. cervicalis ascendens) and caudal branch (A. broncho-esophagea)
via branches at its origin, and indirectly, via an anastomotic connection with a small vessel from the ventral aspect of the thoracic aorta (Aorta thoracica). The other vessel, the ascending cervical artery (A. cervicalis ascendens dextra of Wilson 1879) courses cephalically dorso-lateral to the brachiocephalic trunk and common carotid. Branches include those to cervical muscles and to the ventral cervical rete.

The second and smaller branch arises slightly cephalic to the above vessel and appears to supply the thymus gland and dorsal aspect of the thyroid gland.

(A1) Right Subclavian Artery (A. Subclavia dextra)

The right subclavian artery arises ventro-laterally from the brachiocephalic trunk, courses a short distance cephalically, then recurs caudally. Two vessels, representing divisions of the caudal thyroid artery (A. thyroidea caudalis), branch from its origin and pass medially to the thyroid gland and larynx. A third trunk, the cervico-occipital artery (of Mackay 1886; A. omo-occipitalis of Slijper 1936), takes origin from the genu (bend) of the subclavian and passes dorsally distributing branches to adjacent muscles and to the lateral cervical rete in the plane between anterior and posterior scalene masses. Continuing caudally, the subclavian artery gives rise to the internal thoracic artery (A. thoracica interna) and the posterior thoracic artery (A. thoracica posteria), then passes over the first rib as the small axillary artery (A. axillaris).

The posterior thoracic artery curves dorsally over the
cupula plurae to reach the dorsal thoracic wall. It gives rise to the profunda cervical artery (A. cervicalis profunda) between the first and second ribs then continues caudally as the supreme intercostal artery (A. intercostalis suprema dextra) to supply the first five intercostal spaces and the thoracic rete. Shortly after its origin, the profunda cervical vessel gives rise to the transverse colli artery (A. transversa colli dextra of Slijper 1936). Both vessels contribute to the thoracic rete and penetrate the dorsal thoracic wall to supply epaxial musculature and the dorsal cervical rete.

Intercostal spaces are supplied by dorsal intercostal arteries arising from either the aorta or branches of the posterior thoracic artery. In a typical space, lateral muscular branches and two dorsal rami occur (Plate 10, Fig. A). Though the medial ramus (RD2) corresponds to that in other mammals, the more lateral ramus (RD1) appears to have no counterpart. When one or both rami are missing, supply occurs via arteries in the preceding or following space.

(A2) Right Common Carotid Artery (A. carotis communis dextra)

The right common carotid arises dorsal to the origin of the right subclavian. It courses 2 cm cephalically before bifurcating into the external and internal carotids. A single vessel, the cranial thyroid artery (A. thyroidea cranialis), branches from its ventral aspect mid-way along its course.

(A2a) Right Internal Carotid Artery (A. carotis interna dextra)

Course and distribution of the internal carotid artery are
described in Chapter 1. It contributes to the ventral cervical rete via its cervical branch.

(A2b) Right External Carotid Artery (*A. carotis externa dextra*)

Over most of its cervical course the external carotid artery lies ventro-lateral to the internal carotid. A small branch arises 6 cm cephalic to the bifurcation and gives origin to both a deep and a superficial laryngeal vessel. Another branch arises medially from the external carotid 3 cm cephalad to the above artery and supplies an area dorsal to the hyoid. The third and fourth branches are the occipital (*A. occipitalis dextra*) and lingual (*A. lingualis dextra*) arteries respectively.

(B) Left Brachiocephalic Trunk (*Truncus brachiocephalicus sinistra*)

This trunk arises from the apex of the aortic arch and in a plane dorsal to its right counterpart. It courses 3 cm in the neck and bifurcates into the subclavian and the common carotid arteries. Glandular vessels (thymus and thyroid) and the ascending cervical and broncho-esophageal arteries arise from a common trunk on the dorsal aspect of the brachiocephalic trunk. The ascending cervical artery courses cephalically dorsal to the carotid plane and terminates in the dorsal aspect of the pharynx. It supplies cervical and pre-vertebral muscles and contributes to the ventral cervical rete. Branches from the base of the broncho-esophageal artery supply the thoracic rete.
(B1) Left Subclavian Artery (A. subclavia sinistra)

The left subclavian artery arises at a more caudal level than on the right, but does have the same course and distribution. The cervico-occipital, internal thoracic and posterior thoracic arteries are its respective branches before continuing over the first rib as the axillary artery. The posterior thoracic vessel gives rise, between the first and second ribs, to the profunda cervical artery and continues caudally as the supreme intercostal to supply up to and including the fourth intercostal space. Unlike on the right, the profunda cervical penetrates the thoracic wall before giving rise to the transverse colli artery. Retial vessels arise from the cervico-occipital (to the lateral cervical rete), posterior thoracic (to the thoracic rete), supreme intercostal (to the thoracic rete), and profunda cervical (to the thoracic and dorsal cervical retia) arteries.

(B2) Left Common Carotid Artery (A. carotis communis sinistra)

The left common carotid courses 2 cm cephalically then bifurcates to form the external and internal carotids. No branches occur along its short cervical length.

(B2a) Left Internal Carotid Artery (A. carotis interna sinistra)

No cervical or retial branches arise from this vessel. Its course and distribution are discussed in Chapter 1.

(B2b) Left External Carotid Artery (A. carotis externa sinistra)
The external carotid courses first ventro-medial then ventro-lateral to the internal carotid. In order of their occurrence, branches include the cranial thyroid artery, an unnamed artery to the muscles associated with the hyoid, the lingual artery and the occipital artery. Only the latter vessel gives rise to retial vessels (to the lateral cervical rete).

(C) Thoracic Aorta (Aorta thoracica)

The first two dorsal branches of the thoracic aorta are completely retial and arise at the level of the eighth and ninth intercostal spaces. A similar cephalically directed large retial branch arises from the right dorsal intercostal artery of the ninth intercostal space. All intercostal spaces not supplied by the supreme intercostal artery on each side are supplied by aortic intercostals in the manner diagrammed in Text-Fig. 3. A pair of costoabdominal arteries (Aa. costoabdominalis dorsales) and at least one pair of lumbar arteries (Aa. Lumbales) are also illustrated. Retial branches occur from all the above vessels.
Results of Dissection (Text-Fig. 4)

Two brachiocephalic trunks and the left profunda thyroid artery arise from the aortic arch.

(A) Right Brachiocephalic Trunk (Truncus brachiocephalicus dextra)

As in the cast, the right brachiocephalic trunk arises ventro-laterally from the aortic arch and terminates a short distance cephalically at its bifurcation into the subclavian and common carotid arteries. A single large branch arises dorsally, gives origin to the ascending cervical and broncho-esophageal arteries, then courses dorso-laterally over the cupula plurae as the posterior thoracic artery. The latter vessel gives origin, between the first and second ribs, to the profunda cervical artery and continues caudally to the third intercostal space as the supreme intercostal (Plate 15, Fig. A). The posterior thoracic artery and its branches contribute to the thoracic rete, the ascending cervical artery to the ventral cervical rete, and the profunda cervical artery to the dorsal cervical rete. I could not demonstrate retial origins from the broncho-esophageal artery.

(A1) Right Subclavian Artery (A. subclavia dextra)

The right subclavian artery branches laterally from the brachiocephalic trunk. As the vessel arches caudally, numerous small muscular branches and the large cervico-occipital vessel
Text-Fig. 4. Major arteries giving rise to cerebrally related retia in *Delphinapterus leucas*. Drawn from a dissection (*Delphinapterus leucas* #15). Retial arteries take origin from stippled vessels. Solid black area indicates region from which retial vessels are suspected to arise, but could not be documented to do so because of lesions in the animal.

AAxD - A. axillaris dextra
AAxS - A. axillaris sinistra
AaCD - A. (aorta) costoabdominalis dorsalis
AaID - A. (aorta) intercostalis dorsalis
  RD1 - ramus dorsalis 1
  RD2 - ramus dorsalis 2
ABED - A. broncho-esophagea dextra
ABES - A. broncho-esophagea sinistra
ACA - A. cervicalis ascendens
ACED - A. carotis externa dextra
ACES - A. carotis externa sinistra
ACCS - A. carotis communis sinistra
ACI (ce) - A. carotis interna (cervical branch)
ACI (cr) - A. carotis interna (cranial ramus)
ACID - A. carotis interna dextra
ACIS - A. carotis interna sinistra
ACOD - A. cervico-occipitalis dextra
ACOS - A. cervico-occipitalis sinistra
ACPd - A. cervicalis profunda dextra
ACPS - A. cervicalis profunda sinistra
AITD - A. intercostalis suprema dextra
AISS - A. intercostalis suprema sinistra
AID - A. lingualis dextra
ALS - A. lingualis sinistra
AOD - A. occipitalis dextra
AOS - A. occipitalis sinistra
APTrD - A. profunda thyroidea dextra
APTrS - A. profunda thyroidea sinistra
ASD - A. subclavia dextra
ASS - A. subclavia sinistra
AT - Aorta thoracica
ATCa - A. thyroidea caudalis
ATCrD - A. thyroidea cranialis dextra
ATCrS - A. thyroidea cranialis sinistra
ATID - A. thoracica interna dextra
ATIS - A. thoracica interna sinistra
ATPD - A. thoracica posterior dextra
ATPS - A. thoracica posterior sinistra
RMCI - Rete mirabile carotis interna
take origin. The latter vessel passes dorsally between the superior costal surface of the scapula and the body wall supplying adjacent muscles and ending in muscles of the back. Retial branches occur in the plane between anterior and posterior scalene masses. The subclavian artery continues caudally branching into the internal thoracic artery and passing over the first rib as the axillary artery.

(A2) Right Common Carotid Artery (A. carotis communis dextra)

This artery courses a short distance cephalically and bifurcates into the external and internal carotids. No branches occur along its length.

(A2a) Right Internal Carotid (A. carotis interna dextra)

The internal carotid artery bifurcates from the common carotid and passes cranially dorsal to the plane of the external carotid artery. A single large medial branch occurs at a level approximating the atlanto-occipital joint and supplies pre-vertebral and possibly pharyngeal muscles. It also contributes to the ventral cervical rete. Otic and cranial portions of the internal carotid artery are discussed in Chapter 1.

(A2b) Right External Carotid Artery (A. carotis externa dextra)

The external carotid artery gives origin to the caudal and cranial thyroid arteries, then divides into an arterial loop superficial to the cranial end of the stylohyoid. The occipital and lingual arteries branch from the dorso-lateral portion of the loop. Retial branches occur along the former vessel as it
courses across the intra-scalene plane.

(B) Left Brachiocephalic Trunk (*Truncus brachiocephalicus sinistra*)

The left brachiocephalic trunk originates from the aortic arch dorsal to the level of the right trunk. It passes ventrolaterally giving rise dorsally to a small glandular branch and bifurcates into the subclavian and common carotid arteries at a level caudal to the same bifurcation on the right.

(B1) Left Subclavian Artery (*A. subclavia sinistra*)

Arising in the neck and passing cephalo-laterally then caudally, the subclavian artery gives origin to the cervico-occipital, internal thoracic and posterior thoracic arteries respectively, then passes over the first rib as the axillary artery. The posterior thoracic artery supplies up to and including the fourth intercostal space via the supreme intercostal (Plate 15, Fig. A), and to epaxial musculature via the profunda cervical artery and its branch, the transverse colli. The posterior thoracic and its branches contribute to the thoracic rete. The dorsal cervical rete is supplied by the profunda cervical artery.

(B2) Left Common Carotid Artery (*A. carotis communis sinistra*)

The left common carotid artery has a short course in the neck and gives origin to no branches.
(B2a) Left Internal Carotid Artery (A. carotis interna sinistra)

The internal carotid artery courses and branches as on the right. An anastomotic connection exists between its cervical branch and the ascending cervical artery.

(B2b) Left External Carotid Artery (A. carotis externa sinistra)

Branches corresponding to caudal and cranial thyroid arteries occur as diagrammed in Text-Fig. 4. The lingual and occipital arteries take origin from a common trunk. As on the right side, the left occipital contributes to retia in the plane between anterior and posterior scalene masses.

(C) Left Profunda Cervical Artery (A. cervicalis profunda sinistra)

Unlike in the cast, the profunda cervical artery arises dorsally from the ascending portion of the aortic arch. One branch, the ascending cervical artery, passes cranially to supply cervical muscles and the ventral cervical rete, and anastomose with the cervical branch of the internal carotid. The other branch, the broncho-esophageal artery, courses as on the right.

(D) Thoracic Aorta (Aorta thoracica)

As in the cast, intercostal spaces not supplied by branches of the posterior thoracic artery on each side are supplied by aortic intercostals. The three most cephalic branches of the thoracic aorta are totally retial, as are three other more caudal intercostals. All these vessels contribute to the
thoracic rete, as do two costoabdominal arteries as diagrammed in Text-Fig. 4.

(E) Abdominal aorta (*Aorta abdominalis*).

Though the abdominal aorta was not followed in this dissection, the dorsal ramus of a lumbar artery between the seventh and eighth vertebrae caudal to the last thoracic vertebra of an adult male was dissected in the field. Branches arising adjacent to the intervertebral foramina passed medially into the neural canal and contributed to the spinal rete (Plate 16, Fig. A).
**Monodon monoceros**

Results of Perfusion Cast (Text-Fig. 5)

Four vessels, the right brachiocephalic trunk, the left brachiocephalic trunk, the left profunda thyroid artery and the left posterior thoracic artery arise from the aortic arch.

(A) Right Brachiocephalic Trunk (*Truncus brachiocephalicus dextra*)

Arising ventro-cephalically from the aortic arch, the brachiocephalic trunk divides almost immediately into the subclavian and common carotid arteries. No branches occur along its length.

(A1) Right Subclavian Artery (*A. subcalavia dextra*)

The right subclavian artery courses laterally from its origin and gives rise first to the posterior thoracic artery and secondly to the internal thoracic artery before continuing, as the axillary artery, over the first rib. In addition to these major arteries is a small vessel that arises opposite the origin of the posterior thoracic artery and loops cranially dorsal to the subclavian. It becomes mainly retial. The posterior thoracic artery passes dorso-laterally, gives rise, between the first and second rib, to the profunda cervical artery, and continues caudally as the supreme intercostal artery to supply at least up to and including the eighth intercostal space. Retial arteries
Text-Fig. 5. Major arteries giving rise to cerebrally related retia in *Monodon monoceros*. Drawn from a vascular perfusion cast (*Monodon monoceros* #6). Retial arteries take origin from stippled vessels. Solid black areas indicate regions from which retial vessels are suspected to arise, but could not be documented to do so because of cast breakage.

AA - Arcus aorta
AAXD - A. axillaris dextra
AAXS - A. axillaris sinistra
AaID - A. (aorta) intercostalis dorsalis
ABED - A. broncho-esophagea dextra
ABES - A. broncho-esophagea sinistra
ACAD - A. cervicalis ascendens dextra
ACAS - A. cervicalis ascendens sinistra
ACCD - A. carotis communis dextra
ACC S - A. carotis communis sinistra
ACED - A. carotis externa dextra
ACES - A. carotis externa sinistra
ACID - A. carotis interna dextra
ACIS - A. carotis interna sinistra
ACPD - A. cervicalis profunda dextra
ACPS - A. cervicalis profunda sinistra
ACOD - A. cervico-occipitalis dextra
ACOS - A. cervico-occipitalis sinistra
AISD - A. intercostalis suprema dextra
  RD1 - ramus dorsalis 1
  RD2 - ramus dorsalis 2
AISS - A. intercostalis suprema sinistra
ALD - A. lingualis dextra
ALS - A. lingualis sinistra
AOD - A. occipitalis dextra
AOS - A. occipitalis sinistra
APTrD - A. profundus thyroidea dextra
APTrS - A. profunda thyroidea sinistra
ASD - A. subclavia dextra
ASS - A. sublavia sinistra
AT - Aorta thoracica
ATCa - A. thyroidea caudalis
ATCr - A. thyroidea cranialis
ATCD - A. transversa colli dextra
ATCS - A. transversa colli sinistra
ATID - A. thoracica interna dextra
ATIS - A. thoracica interna sinistra
ATPD - A. thoracica posterior dextra
ATPS - A. thoracica posterior sinistra
TBD - Truncus brachioccephalicus dextra
TBS - Truncus brachioccephalicus sinistra
arise from these vessels as in Delphinapterus leucas. Unfortunately, breakage during the clearing process prevented documentation of supply to the dorsal cervical rete from the profunda cervical artery.

(A2) Right Common Carotid Artery (A. carotis communis dextra)

The right common carotid has a long course in the neck prior to its high cervical bifurcation into the internal and external carotids. Just cephalic to its origin and arising from its dorsal aspect is the profunda thyroid artery. The latter vessel divides into a cranial branch, the profunda cervical artery, and a caudal branch, the broncho-esophageal artery. The profunda cervical artery contributes to the ventral cervical rete and anastomoses with a medial branch of the cervico-occipital artery (possibly the cranial thyroid artery). The broncho-esophageal artery courses caudally and has no evident retial branches (probably lost during the clearing process).

Two vessels branch from the external carotid mid-way along its cervical course. The larger of the two, the cranial thyroid artery, originates ventrally and slightly cephalad to the smaller unidentified vessel which arises dorsally.

The last branch of the common carotid is the cervico-occipital, from which arises the cranial thyroid at its base. The latter vessel contributes to the ventral cervical rete via a pharyngeal branch and also via an anastomotic connection with the ascending cervical artery.
(A2a) Right Internal Carotid Artery (A. carotis interna dextra)

The right internal carotid bifurcates dorsally from the common carotid just cranial to the origin of the cervico-occipital artery. Unfortunately, breakage during the clearing process prevents a description of its course and distribution.

(A2b) Right External Carotid (A. carotis externa dextra)

The external carotid courses cephalically ventral to the plane of the internal carotid. A small unidentified medially directed vessel, the occipital artery, and the lingual artery branch as diagrammed in Text-Fig. 5.

(B) Left Brachiocephalic Trunk (truncus brachiocephalicus sinistra)

Unlike in all other specimens of this study, the left brachiocephalic trunk has a relatively long cervical course and gives rise to three major vessels before terminating as the external carotid and subclavian arteries. The first branch, coursing medio-ventrally from its origin, is the caudal thyroid artery. The second branch, the internal carotid artery, arises cephalo-dorsal to the caudal thyroid artery and terminates slightly above the level of the subclavian. The last branch is the cranial thyroid artery which contributes to formation of the cervical rete and also gives origin to a branch corresponding to the terminal end of the ascending cervical artery described in the following dissection.
(B1) Left Subclavian Artery (A. subclavial sinistra)

Branching laterally from the left brachiocephalic trunk, the subclavian artery recurs caudally and bifurcates to form the internal thoracic and axillary arteries at a level corresponding to the first rib. The cervico-occipital artery (broken during the clearing process) arises laterally just as the subclavian recurs caudally.

(B2) Left External Carotid (A. carotis externa sinistra)

The external carotid artery passes cephalically from its origin and gives rise to the lingual and occipital arteries respectively. As the latter vessel crosses the intra-scalene plane, it contributes to the lateral cervical rete.

(C) Profunda Thyroid Artery (A. thyroidea profunda)

The third aortic branch, the profunda thyroid artery, arises dorsally from the descending portion of the aortic arch and bifurcates, shortly after its origin, to form the broncho-esophageal artery and a branch representing the basal portion of the ascending cervical artery. The latter vessel becomes totally retial.

(D) Posterior Thoracic Artery (A. thoracica posteria)

The posterior thoracic artery is the fourth major aortic trunk and originates from the dorsal aspect of the aortic arch at approximately the level of the third intercostal space. It passes cephalically, loops dorso-laterally over the cupula plurae, bends caudally, giving origin to the profunda cervical
artery between the first and second rib, and continues caudally as the supreme intercostal to supply up to and including the seventh intercostal space and anastomose with the aortic intercostal of the eighth space. Retial vessels originate along the posterior thoracic, supreme intercostal and the base of the profunda cervical arteries.

(E) Thoracic aorta (*Aorta thoracica*)

As previously described for *Delphinapterus leucas*, intercostal spaces not supplied by the posterior thoracic artery on each side are supplied by aortic intercostals. In this specimen, two remnants of aortic intercostals cephalad to that supplying the eighth and ninth left spaces are totally retial. More distal vessels were lost during the clearing process.
Results of Dissection (Text-Fig. 6)

As in the cast, four trunks branch from the aortic arch and supply the head, neck and most of the thorax.

(A) Right Brachiocephalic Trunk (Truncus brachiocephalicus dextra)

The right brachiocephalic trunk passes cephalo-laterally from its origin on the aortic arch and, at a level corresponding to the base of the thyroid gland, divides into the subclavian and common carotid arteries. Three branches occur along its short cervical course.

Almost at its base and from its dorso-lateral aspect arises the posterior thoracic artery. Passing laterally, it gives origin to the profunda thyroid artery, then, via a small anastomotic branch which courses between the sternomastoid and scalene muscles, communicates with the axillary artery. It then passes dorsally over the cupula plurae and, distal to the origin, in the first intercostal space, of the profunda cervical artery, continues caudally as the supreme intercostal artery to supply the first nine intercostal spaces (Plate 15, Fig. B). The profunda cervical artery passes medially, then penetrates the thoracic wall dorsally between the necks of the first and second ribs to supply epaxial musculature and the dorsal cervical rete (Plate 16, Fig. B). No retial vessels could be demonstrated from its caudal branch, the transverse colli artery. The posterior thoracic artery and its branches contribute to the
Text-Fig. 6. Major arteries giving rise to cerebrally related retia in *Monodon monoceros*. Drawn from a dissection (*Monodon monoceros* #1). Retial arteries take origin from stippled vessels. Solid black areas indicate regions from which retial vessels are suspected to arise, but could not be documented to do so because of lesions in the animal.

AA - Arcus aorta
AAxD - A. axillaris dextra
AAxS - A. axillaris sinistra
AaID - A. (aorta) intercostalis dorsalis
AAMS - A. alveolaris mandibularis sinistra
ABES - A. broncho-esophagea sinistra
ACA - A. cervicalis ascendens
ACED - A. carotis externa dextra
ACES - A. carotis externa sinistra
ACI - A. carotis interna
ACP - A. cervicalis profunda dextra
ACOD - A. cervico-occipitalis dextra
ACOS - A. cervico-occipitalis sinistra
AISD - A. intercostalis suprema dextra
RD1 - Ramus dorsalis 1
RD2 - Ramus dorsalis 2
AISS - A. intercostalis suprema sinistra
ALD - A. lingualis dextra
ALS - A. lingualis sinistra
AMMS - A. meningea media sinistra
AMS - A. maxillaris sinistra
AOD - A. occipitalis dextra
AOS - A. occipitalis sinistra
APTrD - A. profunda thyroidea dextra
APTrS - A. profunda thyroidea sinistra
ASD - A. subclavia dextra
ASS - A. subclavia sinistra
AT - Aorta thoracica
ATCa - A. thyroidea caudalis
ATCr - A. thyroidea cranialis
ATIS - A. thoracica interna sinistra
ATPD - A. thoracica posterior dextra
ATPS - A. thoracica posterior dextra
RMCI - Rete mirabile carotis interna
TBD - Truncus brachiocephalicus dextra
TBS - Truncus brachiocephalicus sinistra
The ascending cervical artery passes cephalically dorsal to the carotid plane and just ventral to the division between the scalene and pre-vertebral muscles. Before terminating at the level of the occiput, it supplies branches to these and possibly pharyngeal muscles, and to the ventral cervical rete. I did not follow the broncho-esophageal artery caudally; however retial branches did appear to arise from its base.

The second branch of the right brachiocephalic trunk is small and arises laterally, courses ventrally and supplies the thymus.

The third branch is nutritive to the thymus and base of the thyroid. It arises medial to and just caudal to the origin of the subclavian artery.

(A1) Right Subclavian Artery (A. subclavia dextra)

The subclavian artery arises ventro-laterally from the distal end of the brachiocephalic trunk, arches laterally between the sternomastoid and scalene muscles, and continues caudally over the first rib as the axillary artery. Five branches occur along its length.

Arising medially from its base, the first branch courses cephalically over the ventral aspect of the thyroid gland as this structure's largest supply vessel. A second branch originates just distal to the above artery and is nutritive to the lateral aspect of the gland.

Two vessels, corresponding to the cervico-occipital artery of the cast, take origin from the apex of the cervical arch
formed by the subclavian artery. The first, and largest of the two, gives origin to a vessel that courses cephalically between and supplies the sternohyoid and sternomastoid muscles, then passes between the sternomastoid muscle and the scalene mass. Numerous peripheral vessels arise at this level as do medially directed retial vessels (ventral cervical rete). Continuing dorsally at a level slightly cephalad to the gleno-humeral joint, the main artery appears to contribute branches to muscles of the shoulder, neck and scapula (in particular, the subscapularis muscle), and to a retial mass (lateral cervical rete) coursing with the brachial plexus between and lying external to the anterior and posterior scalene masses. The second and smaller artery arises just distal to the first, passes dorso-laterally between the sternomastoid and anterior scalene muscles, and supplies vessels to these muscles and to cutaneous regions. It ends in the pectoral muscles and has no retial branches along its length.

Continuing caudally, the right subclavian gives rise to the internal thoracic artery then passes over the first rib and becomes the axillary artery. The latter vessel indirectly contributes to the thoracic rete via a previously mentioned anastomotic connection with the posterior thoracic artery.

(A2) Right Common Carotid Artery (A. carotis communis dextra)

The common carotid has no branches and courses only a short distance before bifurcating to form the internal and external carotid arteries.
(A2a) Right Internal Carotid Artery (A. carotis interna dextra)

Origin and distribution of the right internal carotid artery are discussed in Chapter 1. No cervical branches occur along its length.

(A2b) Right External Carotid Artery (A. carotis externa dextra)

Four major branches occur along the cervical course of the external carotid artery. The first, the cranial thyroid artery, arises medio-ventrally at the base of the larynx. Its branches supply the strap muscles, thyroid gland and larynx. The second branch, originating ventrally at a level corresponding to the middle of the thyroid cartilage, supplies the strap muscles and muscles of the hyoid apparatus, and distributes vessels to the sternomastoid muscle. The occipital artery branches dorso-laterally from the external carotid at the cephalic end of the thyroid cartilage. Passing deep to the sternomastoid muscle it gives origin to peripheral vessels, to branches penetrating adjacent muscles and to retial vessels (lateral cervical rete). Its terminal branches contribute to supply of epaxial muscles. The fourth and final cervical branch, the lingual artery, arises approximately at the mastoid process and courses mainly into the tongue.
(B) Left Brachiocephalic Trunk (*Truncus brachiocephalicus sinistra*)

The left brachiocephalic trunk takes origin from the aortic arch dorsal to its counterpart on the right and at a slightly higher level. It terminates at the base of the thyroid as the subclavian and common carotid arteries. A single medially directed branch occurs just caudal to the subclavian artery and distributes vessels to the thymus and base of the thyroid gland.

(B1) Left Subclavian Artery (*A. subclavia sinistra*)

The left subclavian artery branches ventro-laterally from the brachiocephalic trunk. Three major branches occur along its length. Near its base and from its medio-ventral aspect, a large vessel arises and continues medially as the largest nutritive artery of the thyroid gland. The second branch is the cervico-occipital artery. As on the right side, it sends a vessel cephalically ventral to the carotid plane and between the sternomastoid and sternohyoid muscles to supply these muscles and more superficial areas. Coursing dorsally between the sternomastoid and scalene muscles, the main trunk distributes vessels to muscles of the shoulder, scapula and neck, and to cutaneous regions. Retial vessels originate from branches coursing across the sternomastoid and scalene plane (Plate 16, Fig. C), and the intra-scalene plane, as defined by emergence of the brachial plexus.

Continuing caudally, the subclavian gives origin to a small subscapular branch and terminates in a vessel which contributes equally with a branch from the internal thoracic artery in
forming the axillary artery. Both constituent vessels of the
axillary trunk appear to contribute to retial formation in the
transition zone between thoracic and cervical retia. Numerous
tortuous vessels (brush retia) occur in the axilla, but they
appear to be nutritive to cutaneous areas in the floor of the
axilla.

(B2) Left External Carotid Artery (A. carotis externa)

The external carotid artery courses as on the right.
Thyroid and laryngeal branches occur medially from its base and
two vessels supplying muscles of the hyoid apparatus occur more
distally. The occipital artery arises dorso-laterally from the
carotid at about the level of the mastoid and courses dorsally
to supply adjacent musculature and rete (lateral cervical rete)
(Plate 16, Fig. D). The last branch is the lingual artery,
arising just cephalad to the occipital artery.

Though a description of the cranial course of the external
carotid artery is not presented here, it is pertinent to note
that a small vessel arising from the internal maxillary artery,
and representing the middle meningeal artery (A. meningea media)
anastomoses with the carotid rete. This vessel was apparent only
in this specimen.

(C) Left Profunda Thyroid Artery (A. thyroidea profunda
sinistra)

The third major branch of the aortic arch is the left
profunda thyroid artery. Its two branches, the ascending
cervical and broncho-esophageal arteries, course as previously
described. I could demonstrate retial branches from only the common trunk and the ascending cervical artery.

(D) Left Posterior Thoracic Artery (A. thoracica posteria sinistra)

The left posterior thoracic artery is the last branch of the aortic arch. It arises just caudal and lateral to the above vessel, courses cephalically then laterally over the cupula plurae where it gives rise to the internal thoracic artery, then courses caudally as the supreme intercostal to supply the first eight intercostal spaces (Plate 15, Fig. B). The profunda cervical and transverse colli arteries arise separately from the posterior thoracic artery and course dorsally between the first and second rib. Though both contribute to the thoracic rete, only the profunda cervical appears to contribute to the dorsal cervical rete.

A branch taking origin from the internal thoracic artery courses laterally over the first rib and ventral to the scalene muscles to contribute equally with a previously described branch from the subclavian in formation of the axillary artery.

(E) Thoracic aorta (Aorta thoracica)

From the fifth to ninth intercostal space nine vessels, representing reduced aortic intercostals, take origin from the thoracic aorta and become totally retial. Distally, a pair of aortic intercostals, branching from a common trunk, and a single costoabdominal artery take origin. Both give rise to retial branches.
Size Of The RAMT

The thoracic rete is larger in Monodon monoceros than in Delphinapterus leucas. Length, width, and depth measurements are included in Table 3 and 4. Regression lines of retial length on body length are the same for each species, as are the ratios of retial length to body length (Text-Fig. 7A). However, ratios of retial width to retial length are significantly different at the four rib positions examined (alpha = .05) (Text-Fig. 7B). Hence, the difference in retial size is due mainly to a greater lateral extent in Monodon monoceros than in Delphinapterus leucas. (Depth data are incomplete, so were not analyzed statistically. No gross differences are apparent.)

Hematology

Blood data are generally consistent with, but do not prove, the hypothesis that Monodon monoceros is a "better" diver than Delphinapterus leucas. Red blood cell counts, hematocrits and hemoglobin concentrations for eight Monodon monoceros are presented in Table 5. Also included in this table are mean values recorded by Geraci et al. (1968) for 17 Delphinapterus leucas. Mean red blood cell counts do not differ between the two species (Tp = .073). However, mean hematocrit values and mean hemoglobin concentrations certainly do (tp = 0.00). Probably the most indicative character for use as a diving index is hematocrit since its measurement is subject to the least error.
(equipment and observer).
Table 3. Thoracic retial measurements in *Monodon monoceros*. Numbers enclosed by double lines refer to ribs. Arrows indicate columns of values used for statistical analyses. Underlined numbers are estimated from surrounding values. Measurements are in cm.
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Note: The table above lists the dimensions of rectangular shapes in millimeters. Each row represents a different combination of depth, width, and height, along with the corresponding diagonal length and volume.
Table 4. Thoracic retial measurements in *Delphinapterus leucas*. Numbers enclosed by double lines refer to ribs. Arrows indicate columns of values used for statistical analyses. Underlined numbers are estimated from surrounding values. Measurements are in cm.
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Text-Fig. 7. Size comparisons of the rete arteriales mirabile thoracica in *Delphinapterus leucas* and *Monodon monoceros*.

Fig. A. Regression of rete arteriales mirabile thoracica (RAMT) length on body length. Solid circles are *Monodon monoceros*. Hollow circles are *Delphinapterus leucas*. The asteryx indicates an animal for which only one side was measured. Insert is a comparison of ratios of RAMT length to body length (notations are as in Fig. B.).

Fig. B. Comparison of ratios of RAMT with to RAMT length at four levels in the thorax. Solid circles are *Monodon monoceros*. Hollow circles are *Delphinapterus leucas*. Bars refer to standard deviations. Stars indicate that width and length measurements are correlated.
Table 5. Hematology - Erythrocyte values (RBC, hemoglobin concentration and hematocrit) for Monodon monoceros and Delphinapterus leucas.
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$\bar{X} \pm SD \quad 2.94 \pm 0.26 \quad 22.5 \pm 1.4 \quad 57.5 \pm 3.0$

**Delphinapterus leucas** (Geraci et al. 1968)

$\bar{X} \pm SD \quad 3.16 \pm 0.23 \quad 19.1 \pm 0.6 \quad 42.4 \pm 2.1$

(n = 16) (n = 17) (n = 17)
Distribution of cerebrally related plexuses in the family Monodontidae is generally as described in smaller odontocetes. Peripheral sections of the system occur in the thorax, neck and lumbar region, and take origin from most systemic arteries with which they are associated. These plexuses extend into the neural canal and anastomose with the spinal rete which in turn is continuous with cranial and carotid retia within the cranium. Arteries supplying the brain originate from the carotid rete. Worthy of note is the extensive development of cervical plexuses in this family. This is probably related to the occurrence of a "longer" neck in Monodontidae than in other groups in which the system has been studied.

Location of the retial system partly reflects the distribution of spinal nerves. In the neck, the rete is associated mainly with the scalene plane, as are nerves of the brachial and cervical plexuses. Spinal nerves and retial vessels are also distributed together in the thorax and lumbar regions. Given that the carotid rete is homologous with the epidural rete of artiodactyls, and that the cetaceans and artiodactyls are related (Gaskin 1976), it is tempting to envisage development of the rete mirabile from a small intracranial plexus which grew out of the foramen magnum into the neural canal, and from this area, along paths of least resistance to expansion. These paths were the same as those used by the spinal nerves, and include (1) the endothoraic fascia, (2) the fascial plane dorsal to the
psoas muscles, (3) the fascial plane between the anterior and posterior scalene masses and (4) the fascia of epaxial cervical musculature. Probably a more realistic approach is to view the cetacean rete as an extreme modification of a vascular pattern common to all mammals.

This view is supported by the fact that most of the arteries from which retial vessels take origin contribute to vascular supply of the brain, spinal cord and/or meninges in other mammals. Vessels identified as contributing to retial formation in *Monodon monoceros* and *Delphinapterus leucas* are the: (1) internal carotids, (2) occipitals, (3) cervico-occipitals (probably homologous with the supra-, sub-, and dorsal scapular arteries in man), (4) posterior thoracics, (5) profunda cervicals, (6) supreme intercostals, (7) aortic intercostals, (8) costoabdominals, (9) lumbers, (10) ascending cervicals, (11) broncho-esophageals (at their bases) and (12) middle meningeals. All except homologues of vessels (3) and (11) are cited as having branches to the meninges and/or central nervous system in man (Warwick and Williams 1973) and other mammals (Getty 1975). It appears, then, that the cetaceans have magnified a route of cerebral supply that is present, but inconspicuous, in other orders. This has been accomplished at the expense of the more classically described routes in mammals - the internal carotid and vertebral arteries.

Though vessels giving rise to the rete are basically the same in *Monodon monoceros* and *Delphinapterus leucas*, there is one characteristic that is species dependent - size of the supreme intercostal arteries. In *Monodon monoceros*, this vessel
supplies 7 to 9 intercostal spaces (Wilson 1879: 8-9 spaces), while in *Delphinapterus leucas* it supplies half this number (3-5). This may be related to the larger width of the retial system in *Monodon monoceros*.

Results of my study are consistent with the hypothesis that better divers have more extensive retial systems. In *Monodon monoceros*, hemoglobin concentration and hematocrit are higher than those in *Delphinapterus leucas* recorded in the literature (Geraci *et al.* 1968). The comparative blood data presented here are in agreement with those reported by MacNeill (1975) for two captive individuals of each species, except that my red blood cell counts are low. This may be due to observer error since I have no reason for expecting red blood cell size to be larger in this species than in *Delphinapterus leucas*, though this is certainly a possibility. Overall, hematological findings support the view that of the two species, *Monodon monoceros* is the better diver. This species also has the larger thoracic rete. Together, these data suggest that the retial system is indeed linked to diving ability. We may gain some insight into the nature of this link by closely examining retial vessels themselves and by defining the structures for which retial blood is ultimately destined.

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'The vessel in the latter species resembles closely that described for other cetaceans in which the rete mirabile has been studied.'
CHAPTER 3

Supply of the Central Nervous System:
Retial Efferents

Introduction

The basic pattern of blood supply to the vertebrate central nervous system is bilateral and segmental (Gillilan 1967). This is particularly evident in vasculature of the spinal cord. In the head, a segmental arrangement is established in the embryo, but is lost with further development (Padget 1948).

Arteries of the neural canal and spinal cord are best described in mammals (Voris 1928; Suh and Alexander 1939; Sahs 1942; Woollam and Millen 1955; Gillilan 1958; Knox-Macaulay et al. 1960; Tokioka 1973; diagramed by Clemente 1975 and Netter 1975) where they are arranged in the following manner. Among vessels originating from segmental arteries of the aorta (and other trunks) are spinal rami that course medially and enter the neural canal. Three groups of vessels arise from these rami:

(1) pre-laminar arteries that course dorsally and contribute to the epidural plexus which supplies the walls and contents of the epidural space

(2) anterior and posterior radicular arteries that penetrate the dura and accompany roots of the spinal nerves to the spinal cord

(3) post-central arteries that run ventrally and form ventral portions of the epidural plexus.
Radicular arteries form a plexus on the surface of the spinal cord and most often establish prominent cranially and caudally directed channels. These anastomose with those of preceding and succeeding radicular arteries to form a single anterior spinal artery ventrally and two posterior spinal arteries dorsally. Intrinsic vessels of the spinal cord take origin from the surface plexus and from the longitudinal channels.

Though spinal supply in mammals is obviously based on a segmental and bilaterally symmetrical pattern, vessels do vary in size along the cord. Anterior radicular arteries, or those accompanying ventral spinal roots, are generally more prominent than radicular arteries associated with dorsal roots. Also, some of both the anterior and posterior vessels are larger than others, and consequently have a greater area of supply. This is particularly noticeable in lower thoracic and lumbar regions where a single anterior radicular artery (A. radicularis magna) provides circulation to the entire caudal end of the spinal cord.

Vessels supplying the vertebrate brain consist primarily of terminal branches of the internal carotid artery (Abbie 1934; Gillilan 1967). Within the cranium, and just lateral to the hypophysis, the internal carotids bifurcate. One branch courses rostrally to the forebrain (telencephalon and diencephalon), while the other is directed caudally to the midbrain (mesencephalon) and hindbrain (metencephalon and myelencephalon). The manner in which these vessels ramify varies with structural complexity of the brain.
In fish and amphibians, the mesencephalon functions as the major association centre. Other areas of the brain are responsible for transmitting information to and from this area or in reflex control of vital functions. The telencephalon is concerned almost exclusively with olfaction and consists of at most three types of "cortex": paleopallium (olfactory lobes), archipallium (hippocampus of mammals) and basal nuclei (corpus striatum).

Circulation to the telencephalon is affected mainly by lateral and medial olfactory arteries which, together with small diencephalic branches, constitute the rostral carotid division. As their names indicate, these arteries supply lateral and medial portions of the archipallium and paleopallium. The lateral vessels also associate with the corpus striatum and may send branches dorsally over posterior portions of the cerebrum (Gillilan 1967) to supply this structure and parts of the diencephalon.

Caudal carotid rami supply branches to the optic lobes and parts of the cerebellum, then unite to form a single basilar artery. This vessel runs caudally to supply the rest of the brainstem and cerebellum.

The reptilian brain is characterized by the appearance of a small dorsally situated neopallial association cortex in the telencephalon, by a more distinct corpus striatum than in fish or amphibians, and by movement of cell bodies externally.

In most reptiles, branches of the rostral carotid division are arranged into anterior, middle and posterior cerebral
vessels thought to be homologous with branches of the olfactory arteries of fish and amphibians, and similar to the more complex pattern observed in mammals. Posterior cerebral arteries course dorsally over the cerebral cortex to supply this structure as well as the diencephalon. Middle vessels ramify laterally over the piriform cortex and general cortex, and also distribute vessels to the corpus striatum. The anterior cerebral arteries course medially to supply portions of the olfactory area, then enter the longitudinal cerebral fissure to supply adjacent cortex.

As in amphibians, the caudal carotid divisions distribute large vessels to the optic tectum and cerebellum then anastomose to form a caudally directed basilar artery.

Extensive development of the corpus striatum and cerebellum, and lack of neopallial cortex are distinguishing features of the avian brain. Associated circulatory adjustments include enlargement of middle cerebral vessels, and development of distinct inferior cerebellar arteries from the basilar trunk. Also, rostral carotid divisions are larger than caudal ones, and extensive extra-cranial anastomoses occur (Baumel 1975).

In mammals, cerebral hemispheres are the most prominent features of the brain. This is due mainly to enlargement of the neopallium to form the "cortex", and ascendance of this area as a major association centre. Also present is a large cerebellum. The resulting increase in neural mass is no doubt partly responsible for the most noteworthy feature of intracranial circulation in this group - the involvement of vessels other than the internal carotids in brain supply.
Generally, circulation to the mammalian brain is characterized by the following features:

1. a vertebral basilar system to augment carotid supply,
2. a sub-dural circle of Willis formed by a connection between the two anterior cerebral arteries rostrally, and between the carotids and the vertebro-basilar system caudally,
3. a shift in origin of the posterior cerebral arteries to the caudal carotid rami,
4. establishment of the anterior choroidal artery as a discrete vessel and its acquisition of choroidal branches from the posterior cerebral artery,
5. extensive proliferation of cortical branches from stem cerebral arteries to supply the neopallium.

Though the most obvious branches of the cerebral arteries are those to the neopallium, the "stems" of these vessels retain their association with more primitive regions. Hence, proximal segments of the anterior cerebral arteries supply parts of the archipallium (hippocampus) and paleopallium (rostral portions of the olfactory lobes). Middle cerebral arteries supply the paleopallium (piriform portions of the olfactory lobes) and, in addition, most of the corpus striatum (basal nuclei). One striatal vessel, represented in reptiles by channels supplying the amygdala and caudal parts of the basal nuclei, arises directly from the rostral ramus of the carotid and, because of its association with the choroid plexus of the lateral ventricles, is termed the anterior choroidal artery. Stem
vessels of the posterior cerebral arteries vary, and can take origin from either the rostral or caudal carotid rami. Hofmann (1900) defines four types (after du Boulay and Verity 1973):

1. Posterior cerebral artery alpha (A. cerebri caudalis alpha) - the anterior choroidal artery in most mammals
2. Posterior cerebral artery beta (A. cerebri caudalis beta) - a diencephalic vessel branching from the caudal carotid ramus and supplying the medial geniculate body and pulvinar
3. Posterior cerebral artery gamma (A. cerebri caudalis gamma) - also a diencephalic branch, but arises caudal to beta
4. Posterior cerebral artery delta (A. cerebri caudalis delta) - courses rostral to cranial nerve III and is usually associated with an anterior tectal artery.

Of the arteries arising caudal to the above, those of the cerebellum are the largest. On the basis of their location with respect to cranial nerves and other structures of the brainstem, five types have been identified (Hofmann 1900): alpha, beta, gamma, delta and epsilon. The basilar artery gives origin to numerous small vessels that penetrate the hindbrain, and is continuous along the ventral surface of the spinal cord with the anterior spinal artery.

Lengthy reviews of brain vasculature in mammals are those by Tandler (1899), Hofmann (1900), De Vriese (1905) and du Boulay and Verity (1973).

In cetaceans, the brain receives its blood supply via
cranial related retial systems; however the way in which vessels arise from the carotid rete and distribute themselves to the brain is not clear. Mackay (1886) describes cerebral vessels of Phocoena phocoena as "exactly similar to the corresponding vessels of human anatomy." He continues to describe "posterior cerebral arteries" as "entirely derived from the internal carotid trunk" and, after supplying the cerebellum and medulla, to anastomose with vessels derived from the spinal rete. In the same species, Boenninghaus (1904) later describes four vessels originating from the carotid rete: (1) "A. corporis callosi" (anterior cerebral artery), (2) "A. fossae Sylvii" (middle cerebral artery), (3) "A. chorioidea", and (4) "Art. cerebelli superior" (rostral cerebellar artery which gives rise to other cerebellar arteries and vessels of the brainstem). In Tursiops truncatus, Morgane and Jacobs (1972) suggest cerebral vessels to have no apparent homologies with the typical mammalian pattern. However, in a later angiographic study, du Boulay and Verity (1973) were able to demonstrate the presence of anterior cerebral arteries which they describe as uniting to form a single "artery of the corpus callosum".

The only description of cerebral vessels in a mysticete whale is that by Walmsley (1938) of Balaenoptera physalus. He describes anterior and middle cerebral arteries as taking origin from a common trunk that penetrates the dura lateral to the hypophysis. The posterior cerebral artery and a small superior cerebellar artery arise separately at more distal levels.

Though vascular supply of the cetacean spinal cord is also believed to occur via the retial system (Turner 1870; Cunningham
1877; Wilson 1879; Mackay 1886) this has not been documented.

In this chapter I describe the origin and distribution of vessels directly involved with vascular supply of the brain and spinal cord. Specific aims are to determine whether or not (1) the entire central nervous system is supplied via the retial system, and (2) there exists a basic mammalian pattern of supply to the central nervous system.
Materials and Methods

Information on spinal cord vascularity was obtained by gross dissection of the system in a single Monodon monoceros calf (#57). In the field, all tissues of the neural canal were removed as a unit and fixed in 10% formalin. Subsequent dissection involved carefully exposing and longitudinally excising the dura mid-ventrally and mid-dorsally to expose the spinal cord. Arteries supplying the cord were identified by the thickness of their walls and were traced to their epidural origins. Patterns of venous drainage were noted, but not dissected in detail.

Patterns of cerebral supply in Monodon monoceros and Delphinapterus leucas were determined by gross dissection of intracranial arteries in two individuals of each species. The two Delphinapterus leucas (#15, 4) were decapitated and their heads cleaned of all extra-cranial tissue, frozen for shipment, and subsequently fixed in 10% formalin. Monodon monoceros material consisted of the flensed head of a calf (#57) and an entire term fetus (#61), both of which were fixed in the field by immersion in 10% formalin. Each brain and surrounding dura were removed from the cranium. After noting the distribution of retial vessels, the dura was carefully removed to expose arteries of the brain and their pattern of origin from the carotid rete.
Observations

Spinal cord (Plate 17 and 18)

The entire spinal cord receives circulatory supply via vessels that take origin directly from the spinal rete. On each side, vessels arise from larger retial arteries and course medially to the dura mater. Each vessel then divides into numerous meningeal arteries and a penetrating branch that continues through the dura and arachnoid to the spinal cord. Though penetrating branches are most evident ventrally where they occur mid-way between successive spinal roots, they also occur dorsally and in association with spinal roots. Anterior and posterior spinal arteries are not apparent, nor does any penetrating branch appear dominant over others. Rather, these uniformly distributed vessels form a plexus on the cord's surface from which intrinsic vessels of the spinal cord take origin.

Spinal drainage occurs via a venous plexus on the cord's surface. Unlike with the arterial side of the circulation, anterior and posterior external spinal veins are evident, and vessels are most pronounced dorsally. Though efferent veins penetrate the meninges both "intersegmentally" and with ventral spinal roots (ventral radicular veins) the most prominent vessels leave the cord in association with dorsal spinal roots (dorsal radicular veins). Undoubtedly spinal drainage ultimately occurs via the large epidural venous plexus, though this was not
confirmed.

Brain (Text-Figs. 8 and 9.)

In both Delphinapterus leucas and Monodon monoceros four vessels take origin from the carotid rete and penetrate the outer meninges to supply the brain (Plate 19). The rostral pair (RC -cranial rami) give rise to vessels of the forebrain. The smaller and more caudal pair (RCA - caudal rami) supply mainly the mid- and hindbrain.

Each rostral vessel penetrates the meninges lateral to the adenohypophysis, crosses the subarachnoid space, and assumes a position caudal to the olfactory lobe and medial to the uncus. Hypophyseal arteries and vessels that course into the telodiencephalic sulcus dorsal to the optic tract take origin at this level. The main trunk curves laterally, gives rise to the anterior choroidal and anterior cerebral arteries, then continues into the lateral fissure or Sylvian fissure as the middle cerebral artery.

The anterior choroidal artery (or A. cerebri caudalis alpha of Hofmann (1900); A. choroidea rostralis) passes dorsally around the cerebral peduncle to enter the choroid fissure of the inferior horn of the lateral ventricle (Plate 20, Fig. B). It follows the medial curvature of the choroid plexus to a level approaching the body of the ventricle, then divides into numerous branches that emerge from the fissure and loop over the splenium of the corpus callosum to supply dorso-medial portions
Text-Fig. 8. A and B. Subdural circulatory pattern in two specimens of *Delphinapterus leucas*. All vessels of the brain arise from two pairs of vessels that take origin from the rete mirabile carotis interna. Arteries supplying most of the forebrain arise from the rostral pair (RCD, RCS) while other brain regions are supplied by the caudal pair (RCaD, RCaS). Note the absence of communicating vessels between rostral and caudal vessels, and the lack of union between the two Aa. cerebri rostralis (ACRD, ACRS).

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<tr>
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<td>A. cerebri caudalis alpha dextra</td>
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<tr>
<td>ACC alpha S</td>
<td>A. cerebri caudalis alpha sinistra</td>
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<tr>
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<tr>
<td>ACC MS</td>
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<td>ACRS</td>
<td>A. cerebri rostralis sinistra</td>
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<td>Cerebellum</td>
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<tr>
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<tr>
<td>RCS</td>
<td>Ramus cranialis (rostralis) sinistra</td>
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<td>NS</td>
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<td>O</td>
<td>Oliva</td>
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<td>P</td>
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<tr>
<td>TCH</td>
<td>Telencephalon cerebrum hemispherium</td>
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<td>N. accessorius</td>
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<td>12</td>
<td>N. hypoglossus</td>
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Text-Fig. 9 A and B. Subdural circulatory pattern in 2 specimens of *Monodon monoceros*. As in *Delphinapterus leucas*, all vessels of the brain arise from two pairs of vessels that take origin from the rete mirabile carotis interna. Note the lack of a complete subdural circle of Willis and the absence of Aa. vertebrales.

AB - A. basilaris
ACe alpha D - A. cerebelli alpha dextra
ACe beta S - A. cerebelli beta sinistra
ACe gamma D - A. cerebelli gamma dextra
ACe gamma S - A. cerebelli gamma sinistra
ACC alpha D - A. cerebri caudalis alpha dextra
ACC alpha S - A. cerebri caudalis alpha sinistra
ACMD - A. cerebri media dextra
ACMS - A. cerebri media sinistra
ACRD - A. cerebri rostralis dextra
ACRS - A. cerebri rostralis sinistra
CB - Cerebellum
NS - Nn. spinales
O - Oliva
P - Pons
TCH - Telencephalon cerebrum hemispherium
2 - N. opticus
3 - N. oculomotorius
5 - N. trigeminus
6 - N. abducens
7 - N. facialis
8 - N. vestibulocochlearis
9 - N. glossopharyngeus
10 - N. vagus
11 - N. accessorius
12 - N. hypoglossus
of the cerebral hemispheres. As the anterior choroidal artery enters the choroid fissure, a large branch takes origin, travels a short distance with its parent trunk, then recurs to supply tentorial surfaces of the cortex. Another vessel, arising either from the anterior choroidal artery or the middle cerebral artery, courses to the uncus and cortex of the temporal lobe. Smaller branches of the anterior choroid artery supply the choroid plexus and walls of the lateral ventricle.

From its origin, the anterior cerebral artery (A. cerebrai rostralis) courses medially to reach the central or longitudinal cerebral fissure. The vessel curves dorsally and loops over the genu of the corpus callosum to supply antero-medial portions of the cerebral hemisphere (Plate 20, Fig. A). No anterior communicating artery occurs between vessels of opposite sides, nor do these arteries combine to produce a single artery. Proximal branches include striatal arteries and vessels that course laterally with middle cerebral vessels.

The middle cerebral artery (A. cerebrai media) is the largest of the three major vessels branching from the rostral trunk. It courses laterally into the Sylvian fissure and branches profusely (Plate 20, Fig. A). Ramifications loop over the insula and adjacent cortex to emerge from the fissure and run superficially over lateral surfaces of the cerebral hemisphere. Numerous striatal vessels take origin from proximal portions of the artery as it crosses the anterior perforated substance.

The distal pair of trunks arise medio-caudal to the rostral pair and lateral to the posterior lobe of the hypophysis. After
crossing the subarachnoid space, they assume a position ventral to the junction of the pons and cerebral peduncles. Proximal branches most likely represent non-cortical branches of the posterior cerebral arteries described for man (Stephens and Stilwell 1969). These include (1) vessels (thalamic) to the posterior perforated substance of the interpeduncular fossa and (2) vessels coursing dorsally around the mesencephalon and rostral to the third cranial nerve (these arteries associate with the geniculate bodies, tectal surface of the midbrain, and dorsal areas of the diencephalon), and (3) a vessel that runs caudal to the third cranial nerve and continues dorsally to reach tectal surfaces of the midbrain. The largest vessels branching from proximal regions of the caudal trunks are the superior cerebellar arteries or the cerebellar arteries alpha of Hoffman (1900). These course in a lateral direction then loop dorsally over the superior surface of the cerebellum which they supply. Continuation of the caudal trunks occurs via two small vessels that course caudally over the ventral surface of the pons. An anastomosis consistently occurs between these vessels; however the level at which it occurs and its size are variable (see the Text-Figures). Caudally, a small basilar artery continues over the remainder of the brainstem and terminates in the "anterior spinal plexus" at approximately the level of origin of the first cervical nerve. Originating from either the paired vessels or single artery of the basilar system are three pairs of cerebellar arteries and numerous small vessels which supply the pons and medulla. Cerebellar arteries beta, accompany the seventh and eighth cranial nerves laterally, then recur to
supply the inferior aspect of the cerebellum and the choroid plexus of the third ventricle. Cerebellar arteries \textit{gamma} arise caudal to the sixth cranial nerve and supply the cerebellum, as do cerebellar arteries \textit{delta}, which originate in association with caudal portions of the olive. The latter vessels were distinct in only one specimen of \textit{Delphinapterus leucas}. 
Discussion

Vascular supply to the central nervous system in Monodontidae is a distinct variation of the basic mammalian plan. In addition to originating from extensive retia, arteries of the spinal cord and brain differ from the norm in their collateral associations and in those vessels on which circulatory emphasis is placed.

In *Monodon monoceros*, vessels supplying the spinal cord arise from the spinal or vertebral rete. They penetrate the dura between successive spinal roots (mainly ventral) and not in association with them, unlike the radicular arteries of other mammals. Also, these vessels are uniformly distributed and contribute equally to a plexus surrounding the cord. An A. radicularis magna is not present nor are distinct anterior and posterior spinal arteries. Hence, the arterial pattern is one having uniform "intersegmental" supply and not requiring large longitudinal anastomotic channels to ensure adequate circulation.

Circulation to the brain is effected by two pairs of arteries originating from the carotid rete. The rostral pair supplies most of the forebrain while the more caudal vessels vascularize mainly the midbrain and hindbrain. The circulatory pattern is characterized by:

1. complete independence of anterior cerebral arteries (no anastomoses),
2. extensive supply of "posterior cerebral areas" by the
anterior choroidal arteries,

(3) absence of subdural communicating vessels between rostral and caudal trunks arising from the carotid rete,

(4) union of caudal trunks to form a small basilar artery, and

(5) absence of vertebral arteries, and hence of a vertebral basilar system.

Brain vasculature in *Phocoena phocoena*, as described by Boenninghaus (1904), differs from the above in that constituent vessels arise from four pairs of subdural trunks. Another minor difference is the presence of duplicate basilar arteries.

The absence of a vertebral basilar system, lack of a complete circle of Willis, and extensive proliferation of the anterior choroidal arteries into cortical areas are notable differences from the general mammalian scheme. However, unlike the situation suggested by Morgane and Jacobs (1972), a basic pattern is recognizable and constituent vessels do appear homologous with those of terrestrial mammals. Consistent with the latter point is a striking similarity between the adult cetacean pattern and the embryonic stage in man prior to establishment of a connection between the caudal ramus of the internal carotid artery and the neural plexus. At this stage, the forebrain is supplied by terminal branches of the internal carotid while more caudal areas are supplied by segmental trigeminal arteries.

This is by no means an exhaustive study of central nervous
system vasculature in the Cetacea, but it does serve to clarify vessel origins from the retial system. It also suggests that the observed circulatory pattern is simply a modified mammalian one. Combined with observed retial associations with various cranial nerves (Chapter 2), the results of this chapter indicate that the entire central nervous system and its derivatives are supplied via the extensive retial system.
SUMMARY OF GROSS ANATOMY:

The Rete - Afferents and Efferents

All blood destined for the central nervous system passes through an arterial plexus or *rete mirabile* (Text-Fig. 10). Retial vessels take origin from most systemic arteries of the body, particularly those which in other mammals supply the central nervous system and/or its membranes. Blood passes from thoracic, cervical and lumbar retia into the spinal rete of the neural canal. The latter plexus extends cephalically into the cranium and is continuous with the carotid rete at the base of the brain. Efferent arteries, or those vessels leaving the retial system to supply central nervous tissues, include: (1) two pairs of vessels that emerge from the carotid rete and penetrate the dura to supply the brain and (2) an estimated thirty-two pairs of vessels that arise from the spinal rete and vascularize the spinal cord. Other efferents are those to cranial nerves, eyes (ophthalmic retia) and dura mater.
Text-Fig. 10. Summary of blood flow through cerebrally related retia. Stippled structure is the retial system. Afferent retial arteries are illustrated as branching from a systemic artery in the thoracic region of the plexus. Blood flows from thoracic, lumbar and cervical retia into the spinal rete within the neural canal and from here either (1) into the spinal cord, or (2) into plexuses (cranial and carotid) within the cranium. Arteries leaving the spinal and carotid retia to supply the spinal cord and brain respectively are colored black in the diagram. Arrows indicate direction of blood flow.
DORSAL

VENTRAL

Systemic Arteries

SPINAL

LUMBAR

THORACIC

CERVICAL:
1 Ventral
2 Lateral
3 Dorsal

Brain

Spinal Cord

OPHTHALMIC

CAROTID

VENTRAL
CHAPTER 4

Retial Microanatomy

Introduction

Many accounts of retial anatomy exist in the literature, however few deal with histology (Ivanova 1971; Nakajima 1961; Simpson and Gardner 1972; Slijper 1962; Walmsley 1938), and only one includes ultrastructural data (Voql and Fisher 1976). This is rather surprising since most theories of retial function are mechanical ones and can be indirectly investigated using the tools of microanatomy.

Summarizing from the brief accounts that do exist, the retia consist of muscular arteries interlaced with veins, nerves and fatty connective tissue. Vessels of the neural canal (spinal rete) are usually described as larger than those of the thorax, and include a greater proportion of veins. Of intracranial retia (RAMCr and RHCI), Walmsley (1938) comments:

"The structure of the intracranial [cerebral] rete is essentially similar [to the spinal rete] in all its parts ... and ... is formed of rather thin-walled arteries and extremely thin-walled veins. In the region of the hypophysis, however, these vessels are rather smaller and are very tortuous..."

This description is reminiscent of accounts dealing with the rete mirabile epidurale rostrale of ungulates, a system demonstrated to have thermoregulatory properties. Though suggestive of a similar functional potential for the carotid rete of cetaceans, there exists no data adequate for comparison
with the ungulate system.

Retial arteries themselves have well defined elastic membranes and a distinct muscular media. Ivanova (1971) describes thoracic vessels in *Phocoena phocoena* as having a thick "uninterrupted" external elastic membrane, and an adventitia containing no collagen. She also notes, as does Murie (1874), a close association between retial arteries and lymphatic vessels. Retial arteries are considered well innervated (Walmsley 1938; Ommanney 1932; Morgane and Jacobs 1972), however this conclusion is based on the presence of large nerve trunks in retial tissue, and not on the occurrence of nerve endings around retial vessels.

The object of this chapter is mainly to provide background information for detailed discussion of retial function in Chapter 5. Emphasis is placed on defining those features associated with (1) elasticity, (2) blood storage capacity, and (3) thermoregulation. Specific objectives are to:

a) describe retial arteries, emphasizing the arrangement of elastic membranes and the structure of the tunica media,

b) determine the ratio of lumenal area to total tissue area in order to estimate blood storage capacity (in chapter 5),

c) determine retial innervation and hence the potential for nerve induced changes in blood flow and volume, and

d) determine the structure of the carotid rete and compare it with its homologue in an ungulate ie: is
there any indication that the system may be related to thermoregulation in some way.
Materials and Methods

Retial tissue for general histology was obtained from animals roughly 15 min to 2 hrs post-mortem. Samples were fixed in either 10% buffered formalin (Monodon monoceros) or 2% buffered paraformaldehyde (Delphinapterus leucas), and later processed using standard histological techniques. Verhoeff's stain (Thompson 1966) was used to accentuate elastin and collagen. Sections were examined and photographed with a Zeiss photomacrographic unit and a Wild photomicroscope.

Sample sites in the thorax corresponded with those at which retial measurements were taken, as described in Chapter 2. Section areas of .5 x 1 cm were photographed and a planimeter used to calculate arterial and lumenal areas from the photographs. Mean values for the two species were tested for significant differences using "the randomization test for independent samples" described by Siegel (1956).

My sampling of other retia was limited, and consisted of vessels taken at various levels in the neural canal (Delphinapterus leucas) and from the lateral, ventral and dorsal cervical retia (Monodon monoceros). The carotid rete was also sampled (Monodon monoceros). For comparison, I obtained material from the epidural rete of a single Ovis aries (domestic sheep). The latter tissue was fixed by perfusion with 5% glutaraldehyde in .1M cacodylate buffer at pH 7.3.

Tissue for general ultrastructural observation was primarily taken from three Monodon monoceros (#20,30,38) and,
because of the time factor and ease of sampling, consisted only of thoracic retia from the fourth or fifth intercostal space. Samples were fixed for 2-4 hrs in 5% glutaraldehyde in 0.1M cacodylate buffer at pH 7.3. After washing and storage in buffer for up to three weeks, samples were postfixed in buffered 1% osmium tetroxide, dehydrated, then embedded in Epon 812. Sections were cut on a Porter-Blum MT2 ultramicrotome, and stained for 30 min in uranyl acetate and 10 min in lead citrate. Sections were studied and photographed on a Zeiss EM 10. All tissue was fixed within 10 min post-mortem.

The mammalian vascular system is innervated by the autonomic nervous system, and primarily, though not exclusively, by sympathetic adrenergic nerves. Hence, in this study, the fluorescence method of Falck and Owman (1965; as modified by M. Todd pers. comm.) was used to determine the presence of adrenergic nerve endings in selected retial and other vessels. Basically the method involves conversion of non-fluorescent mono-amines, enclosed in dried protein layers, to fluorescent derivatives by condensation with mildly humid formaldehyde gas (see Corrodi and Jonsson 1967 for review).

Material for fluorescence was obtained from a single Monodon monoceros (#58). Vessels were sampled from the following plexuses:

a) thoracic rete (4th to 5th intercostal space)
b) spinal rete (caudal portion)
c) spinal rete (cervical portion)
d) ventral cervical rete
e) caudal rete (Rete mirabile caudalis). This system is
structurally different than cranial related retia. It lies in the haemal canal ventral to the caudal vertebrae and consists of longitudinally arranged arteries (caudal aorta and its ramifications) immersed in a plexus of veins (Plate 21, Fig. A to D). In this study, I sampled both the caudal aorta and the smaller vessels. These were chosen for comparison with arteries of other retia since they could be obtained easily and had the potential for being well innervated (vascularize peripheral tissues and are part of a counter-current heat exchange system). Also, the smaller arteries are of similar size to vessels of the thoracic rete.

I began collecting and processing vessels, in the above order, roughly 5 min post-mortem, and the sequence was completed within an hour. Samples were quenched in supercooled isopentane then stored in liquid nitrogen. In the lab, tissues were freeze-dried for a minimum of 24 hrs then exposed, for 2 hrs, to hot (80°C) formaldehyde vapour in a desiccator. A relative humidity of 80% was attained in the desiccator by sitting paraformaldehyde over H_2SO (122ml H_2O + 78ml H_2SO) for seven days prior to its use. Following vapour treatment, samples were embedded in paraffin and the resulting blocks sectioned for analysis.

To document conclusively fluorescence of mono-amines, and to aid in differentiating nerves from brightly autofluorescent elastin, I used the borohydride reduction method of Corrodi et al. (1964). This procedure involves observing tissues after (1) exposure to formaldehyde vapour, (2) treatment with sodium borohydride (reduces fluorescent derivatives of mono-amines to non-fluorescent forms, but does not effect non-specific autofluorescence), and (3) re-exposure to formaldehyde vapour. Tissue damage and loss were reduced by coating sections with
Parlodion (.5% in 1:1 ether/isopropanol) and by mounting cover-slips as shown in the procedural diagram in Text-Fig. 11. Chemistry of the method is illustrated in Text-Fig. 12.

After each treatment, the same area of each section was photographed using a Zeiss fluorescence photomicroscope set up in the darkfield mode. Use of a #2 primary (exitor) filter and a 530nm secondary (barrier) filter gave the best contrast. I used Tri-X film (Kodak) and developed it in Beseler FD2.

Pieces of rat tail artery, a vessel known to be well innervated, were embedded in the same blocks as whale vessels and served as controls for method. Also, duplicate sections were processed using 95% isopropanol without sodium borohydride in Step 2 to control for diminished fluorescence due to factors other than the borohydride (see flow chart).

Results using the fluorescence technique were not overly satisfying; however the information obtained using this method was consistent with that obtained ultrastructurally.

Ultrastructural documentation of nerves was accomplished using material from a single adult Monodon monoceros (#56). Among tissues collected were vessels of the thoracic rete, ventral cervical rete, cervical and caudal portions of the spinal rete, and caudal rete (caudal aorta and accompanying arteries). Samples were processed as described previously except that I used 2.5% glutaraldehyde in .1M cacodylate and .1M sucrose at pH 7.3.
Text-Fig. 11. Procedural diagram for fluorescent demonstration of adrenergic nerve endings.
1. **Exposure**
   - Expose freeze-dried tissue to formaldehyde gas.
   - Embed in paraffin and section.
   - Melt sections onto clean glass slides.

2. **Photograph**
   - Rat tail artery.

3. **Coat with paraffin**
   - Coat with .5% paraffin.
   - Mount.

4. **Photograph**
   - Grade #1 cover slip.

5. **Mount**
   - Photographic.

6. **Test**
   - Remove cover slip.
   - 2 x 100% xylene: 2.5 min.
   - 2 x 100% isopropanol: 2.5 min.
   - .01% - .03% sodium borohydride in 95% isopropanol: 2.5 min.
   - 3 x 100% isopropanol: 2.5 min.
   - 100% xylene: 2.5 min.

7. **Control**
   - Mount as above.
   - Photograph.
   - Remove cover slip.
   - 100% isopropanol: 5 min.
   - Dry on warm hot-plate.
   - Expose to formaldehyde gas.
   - Mount as above.
   - Photograph.
Text-Fig. 12. Chemistry of the fluorescence method of detecting adrenergic nerve endings. Noradrenalin is converted to fluorescent derivatives by treatment with formaldehyde gas in Step (1). Treatment with sodium borohydride (Step (2)) converts these derivatives back to non-fluorescent forms. Exposure to formaldehyde gas in Step (3) re-establishes fluorescence.
FORMALDEHYDE

OH

NH₂

TVS

NORADRENALIN

Non-fluorescent

FORMALDEHYDE IN A PROTEIN LAYER

FORMALDEHYDE IN A PROTEIN LAYER

SODIUM BOROHYDRIDE

FORMALDEHYDE IN A PROTEIN LAYER
Fluorescent
Results

A) Microanatomy

Thoracic Rete (Rete arteriales mirabile thoracica)

Retial histology is the same in both Monodon monoceros and Delphinapterus leucas. The system consists mainly of small muscular arteries embedded in fatty connective tissue (Plate 22, Fig. A and B). Veins are present, but are not nearly as numerous as arteries. Interstitial tissue consists of white fat cells, mats of collagen fibers (that are continuous with adventitial layers of surrounding blood vessels), nerve trunks and small vascular channels (Plate 23, Fig. D). Intercostal arteries and veins, and spinal nerves pass through the rete (Plate 22, Fig. C), and the entire system is limited medially by the pleura (Plate 22, Fig. D and E).

As is generally characteristic of vertebrate blood vessels, retial arteries consist of three tunicae (Plate 23, Fig. A and B). The tunica intima is comprised of a single layer of endothelial cells (Plate 24, Fig. C), a thick subendothelial stratum of filamentous material and elastin (Plate 25, Fig. C and D) and a fenestrated internal elastic lamina (Plate 24, Fig. C). In addition to basic organelles, pinocytotic vesicles, and filaments (Plate 25, Fig. A), endothelial cells contain substantial deposits of glycogen. This was implied ultrastructurally (Plate 24, Fig. A and B) and confirmed with
Best's Carmine stain (Thompson 1966). Though poor fixation prevents a complete description of connections between endothelial cells, gap junctions appear numerous (Plate 25, Fig. B).

The tunica media consists of roughly 12-14 layers of vascular smooth muscle cells embedded in an electron translucent matrix (Plate 26, Fig. A). Intra-media strands of elastin are present as are a few collagen fibers (Plate 26, Fig. C). Vascular smooth muscle cells, identified by their dense intracellular contractile filaments, numerous surface caveolae, and well defined basement membranes, are connected by simple apposition in the manner described by Henderson (1975a) (Plate 26, Fig. D and E) (also see Henderson 1975b for a general review of connections between smooth muscle cells). At no time did I observe nexus or gap junctions between retial smooth muscle cells. Areas of apposition are characterized by loss of basement membranes and by an intercellular gap of around 10 nm (Hendersen 1975a). Often, caveolae, multivesicular bodies, and mitochondria associate with junctional areas as do occasional extensions of one cell into another.

The most distinctive feature of retial smooth muscle is the presence of large glycogen deposits (Plate 27, Fig. A, B, and D) (Vogl and Fisher 1976), confirmed, as in endothelial cells, with Best's Carmine stain. These deposits, or "pools", are usually perinuclear and often found in relation to membrane swirls (Plate 27, Fig. F) and mitochondria (Plate 27, Fig. E). Glycogen particles are of the alpha type, identified ultrastructurally by their rosette appearance (Plate 27, Fig. B) (Revel 1964; also
see De Bruijn 1973 and De Bruijn and Breejen 1975).

The tunica adventitia consists of three or more fenestrated and interconnected lamellae of elastin separated by layers of collagen fibers (Plate 24, Fig. D and E). The most luminal stratum of elastin, on which smooth muscle of the media rests, is the external elastic lamella.

Dorsal (Plate 28, Fig. A.), Lateral (Plate 28, Fig. B), and Ventral (Plate 28, Fig. C) Cervical Rete (Rete arteriales mirabile cervicales, dorsalis, lateralis, and ventralis)

Histologically, cervical retia appear similar to the thoracic plexus. Though veins are present, small muscular arteries are again the most distinctive vascular components. Interstitial tissue consists mainly of collagen interlaced with fat cells.

Spinal Rete (Rete arteriales mirabile spinalis)

This system differs from those previously discussed in that vessels are generally larger and tend to consist of proportionately more veins. The latter feature is particularly noticeable in cranial cervical regions where arteries are thin walled and associate with plexiform veins. Arteries in cervical areas of the neural canal (Plate 26, Fig. B; Plate 28, Fig. D) contain more elastin (and collagen) than caudal spinal vessels and vessels in the thorax. This was evident from histology,
ultrastructure and fluorescence. Caudal to the cervical region, vessels gradually become smaller, thicker walled and more muscular (Plate 28, Fig. E, F, and G).

Carotid Rete (**Rete mirabile carotis interna**)

Unlike the ungulate system, composed of thin-walled arteries surrounded by venous blood of the cavernous sinus (Plate 29, Fig. B), the carotid rete of *Monodon monoceros* is characterized by thick walled muscular arteries surrounded by a matrix of fatty connective tissue (Plate 29, Fig. A, C, and D). Vessels of the cavernous sinus are distinct veins and are not numerous.

B) Innervation

Fluorescence

Results of a control series, using rat tail artery, are presented in Plate 30, Fig. A to F. Treatment with sodium borohydride completely eliminates fluorescence of adrenergic nerves at the adventitia-media border. Fluorescence is only partially restored by treatment with formaldehyde vapour. In the sections using 95% isopropanol without reducing agent, a partial loss of emitted light occurs both at step 2 and step 3, probably due to diffusion of neurotransmitter out of the synaptic vesicles. Hence, the intensity of neuro-fluorescence is
diminished by factors other than the sodium borohydride, but not to the extent of overshadowing the specific effect of the reducing agent.

Of the vessels examined in this study, the caudal aorta was the most heavily innervated. An adrenergic plexus exists at the adventitia-media border from which numerous nerves extend into the abluminal third of the media (Plate 31, Fig. M to D; Plate 32, Fig. D to I). Small arteries associated with the aorta are also innervated, though more weakly so (Plate 33, Fig. D to F). From fluorescence, nerves in these vessels appear distributed in the adventitia and not directly against the media. Vessels in caudal portions of the spinal rete are weakly innervated (Plate 33, Fig. G to I). I could demonstrate no adrenergic endings in vessels of the thoracic rete (Plate 31, Fig. D to F, and J to L), ventral cervical rete (Plate 33, Fig. J, K, N and O), or cervical portions of the spinal rete (Plate 30, Fig. G to I, and L to N).

Ultrastructure

In the caudal aorta, vesiculated varicosities (swellings) occur both at the adventitia-media border (Plate 34, Fig. A, B, C) and within the media (Plate 34, Fig. D). Though nerves containing small granular vesicles predominate, varicosities composed exclusively of empty vesicles also occur. Varicosities do not directly oppose smooth muscle cells. Rather, they are separated by a gap of variable magnitude.
Varicosities associated with small arteries of the caudal rete are found abluminal to the external elastic lamina and are therefore removed from direct association with muscle cells of the media (Plate 35, Fig. C, D, and E). Varicosities containing small granular vesicles predominate.

Vessels chosen, for ultrastructural examination, from the caudal portions of the spinal rete differed from those examined by fluorescence in that the external elastic lamina was poorly defined and adventitial extensions, containing nerves, appeared to protrude into the media. As in other vessels, varicosities containing granular vesicles were most numerous (Plate 35, Fig. A, and B).

Though preterminal axons, recognized by their small diameters, absence of varicosities and close association with Schwann cells (Plate 36, Fig. D), and terminal axons, identified by their varicose nature, do occur in association with retial arteries, they are not numerous and are always found in the most abluminal layers of the adventitia (Plate 36, Fig. A). At no time during the course of this study did I observe nerves at the adventitia-media border or directly abluminal to the external elastic lamina. The varicosities that I did observe consisted mainly, though not exclusively, of small empty vesicles.

Nerve trunks occur infrequently in the adventitia of arteries from cervical regions of the spinal rete (Plate 36, Fig. E). I observed no varicosities in material examined in this study.
Values of luminal and vascular (arterial) areas in .5cm$^2$ of retial tissue (thoracic rete) are presented in Tables (6) and (7) respectively. There is no difference between the mean measurements in the two species ($\alpha = .1$). Means (calculated using pooled data) for luminal and vascular areas are $10.93 \pm 3.4\text{mm}^2$ per 50mm$^2$ rete and $25.64 \pm 3.8\text{mm}^2$ per 50mm$^2$ rete respectively.
Table 6. Luminal area in $50\text{mm}^2$ of thoracic retial tissue. Means are in $\text{mm}^2$. 

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<th>Luminal Area</th>
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<tr>
<td>Animal</td>
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<td>5 8</td>
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<td><em>Monodon monoceros</em></td>
<td>7 10</td>
</tr>
<tr>
<td></td>
<td>9 7</td>
</tr>
</tbody>
</table>

$\bar{X}$ (pooled data) = 10.93 ± 3.40 (SD)
Table 7. Arterial area in $50\text{mm}^2$ of thoracic retial tissue. Means are in $\text{mm}^2$. 
<table>
<thead>
<tr>
<th>Animal</th>
<th>Sections</th>
<th>Observed</th>
<th>$\bar{X}$</th>
</tr>
</thead>
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<td>10</td>
<td>24.52</td>
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<tr>
<td></td>
<td>2</td>
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<td>8</td>
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<td>6</td>
<td>22.80</td>
</tr>
<tr>
<td><em>Monodon monoceros</em></td>
<td>7</td>
<td>10</td>
<td>23.91</td>
</tr>
<tr>
<td></td>
<td>9</td>
<td>7</td>
<td>25.01</td>
</tr>
</tbody>
</table>

$\bar{X}$ (pooled data) = 25.64 ± 3.80 (SD)
Discussion

Retia related to supply of the central nervous system in the family Monodontidae are histologically similar to those described in other odontocetes: that is, small muscular arteries embedded in fatty connective tissue. Of total thoracic retial volume, about 50% is actually composed of vascular tissue and roughly 21% is luminal or is blood destined for the central nervous system. Among other considerations, discussed fully in the next chapter, these data make this system an unlikely candidate for blood storage. Also, there are no obvious indications that the system, as a whole, has a thermoregulatory function. Apart from an intermingling of arterial and venous plexuses in cervical portions of the spinal rete, no countercurrent mechanism exists, nor is there an association of vessels with thermogenic tissues (brown fat). That the cetacean rete is functionally different from most other retia interposed between the heart and brain in mammals is emphasized by comparative anatomy of the carotid rete. In ungulates, thin-walled arteries are bathed in venous blood from peripheral tissues (nasal mucosa and horns) of the head. In Monodon monoceros, the homologous system consists of thick walled arteries surrounded by fatty connective tissue.

Though retial arteries in different anatomical locations do vary in size and elastic content, they are, for the most part, muscular, not elastic, in nature. Their most distinguishing feature is almost always a well defined media composed mainly of
vascular smooth muscle. This feature, combined with the observed association between the thoracic rete and sympathetic nerve trunk suggest that retial arteries might be well innervated. That this is so does not, in fact, appear to be the case.

A comprehensive survey of smooth muscle innervation, and more specifically, of vascular smooth muscle innervation, is contained in a series of papers by Burnstock and co-workers (Burnstock et al. 1970; Burnstock and Iwayama 1971; Burnstock 1975a). Summarizing studies by these and other authors (Dolezel 1973; Devine 1978; Khor'kov 1978), neuromuscular junctions of the type found in skeletal muscle do not generally occur in smooth muscle. Rather, sympathetic nerves secrete neurotransmitter "en passage" from numerous varicosities or swellings along terminal portions of their axons. The gap between varicosity and muscle cell varies from 20 nm to several microns (Devine 1978; Khor'kov 1978). Vascular innervation occurs mainly at the media-adventitia border, with a few axons extending into the media in larger vessels (Dolezel 1973). Though both adrenergic and cholinergic innervation occur, the former predominates and usually causes constriction. Ultrastructurally, and depending on the fixation, adrenergic varicosities are identified by an abundance of small granular vesicles (Burnstock and Robinson 1967; Burnstock 1975b). Vesicles in cholinergic axons appear agranular. Amplification of the vascular response to neurotransmitters is achieved in part through electrical coupling of smooth muscle cells. In vessels not containing discrete gap junctions, coupling may occur in areas of simple appositon by a diffuse arrangement of gap
junction subunits (Fry et al. 1977).

Retial arteries are at best poorly innervated. When present, varicosities and pre-terminal axons usually occur in outer layers of the adventitia where they probably have a greater effect on cells of this layer and on extra-arterial tissues than on smooth muscle cells of the media. Since varicosities were not observed fluorescently in thoracic retial arteries, and the few that were observed ultrastructurally contained empty vesicles, it is tempting to suggest the presence of cholinergic innervation. However, because of the method of fixation, this is only speculative.

Of all extra-cranial retial vessels, only those in caudal portions of the spinal rete have clearly defined adrenergic nerves associated with smooth muscle of the media. In general, retial arteries appear passive with respect to nervous control. Any vasomotion that does occur, probably does so in response to factors circulating in the blood.

The walls of retial arteries are as described for muscular arteries in general. The only aspect of arterial substructure that dramatically differs from vessels in other mammals is the occurrence of large glycogen deposits. Glycogen concentrations do reach high levels in vascular smooth muscle of the mammalian uterus (York and Hillman 1968; Sype and Hillman 1970) but they are transitory and appear related to constriction during the birth process. Though endothelial cells in rat vessels contain the machinery for glycogen synthesis (Numano et al. 1974), extensive stores of this carbohydrate are not known to occur.

Extensive vascular glycogen deposits suggest the following
functional possibilities:

1) retial vessels are very active and at times need energy in excess of that which can be obtained from "normal" amounts of stored glycogen or substrate from the blood. This appears unlikely since retial arteries are poorly innervated, located centrally and are associated with no obvious function that would necessitate rapid and widespread vaso-motion.

2) retial arteries undergo prolonged periods of hypoxia and need large glycogen reserves for continued function. That glycogen reserves are generally more prolific in tissues of marine mammals than in those of their terrestrial counterparts is well known (DuBois et al. 1948; Kerem et al. 1973). It is also accepted that deposits occur mainly in tissues that maintain metabolism anaerobically during periods of ischemic hypoxia resulting from blood re-distribution during the diving response (Hochachka and Storey 1975). At first glance, then, it would not appear unusual to find extensive carbohydrate reserves in vascular tissues. However, unlike viscera and skeletal muscle, or even the heart, the rete mirabile can not be "removed" from the circulation since efferent vessels supply the central nervous system. Also, vascular smooth muscle normally obtains a large proportion of its energy from glycolytic metabolism. Yet, even in large arteries where hypoxic stress is usual (because the media generally lacks a blood supply) one does not
find glycogen reserves of the magnitude found in retial vessels of *Monodon monoceros* (this may be related to continued rather than intermittent stress in this species). Of even greater interest than glycogen deposits in vascular smooth muscle is their presence in endothelial cells. There is no indication that these cells are very active metabolically. Also, they are continually in contact with blood destined for the central nervous system. Vascular tissues undoubtedly use carbohydrate reserves for their own metabolism during periods of stress (diving), however, this is not inconsistent with the following two possibilities.

3) Retial vessels may contribute to maintenance of blood sugar levels during a dive. Supporting this view is the position of the rete with respect to the central nervous system and the large mass of retial tissue. Also, the fact that smooth muscle normally stores glycogen pre-adapts it for the function proposed here.

4) the rete may act as a "buffer" during the recovery phase of a dive, or when aerobic metabolism is re-established, by converting lactate to glucose or glycogen, thereby contributing to reduction of increased lactate levels that normally occur during this period in diving birds and mammals (Scholander 1940).
The latter two hypotheses will be considered in detail when discussing retial function - the focus of the next chapter.
CHAPTER 5

Retial Function

General Introduction

The cerebrally related retial system described in previous chapters is a massive organ that (1) extends into at least four regions of the body (head, neck, thorax and abdomen), (2) is composed of tissues (vascular and fatty connective tissues) known to have multiple properties, (3) is associated with a variety of anatomical structures (lungs, larynx, muscles and nerves) and (4) is strategically positioned between the heart and central nervous system. Also, the animals in which it occurs are "top of the line" examples of marine mammal aquatic adaptation. They spend their entire lives in the water and, at least in some cases, extend both the time and depth parameters of a "dive" to unparalleled limits (*Physeter macrocephalus*: depth - 1100 to 1199 m; time - 55 to 60 min Lockyer 1977; *Hyperoodon ampullatus*: time - 2 hrs Scholander 1940). For all the above reasons, it is not surprising that there are as many functions ascribed to the retial system as there are literary references to its anatomy. Though diverse, most of these hypotheses fall into two general categories: (1) those involving changes in blood chemistry, and (2) those of a purely mechanical nature.
Chemical Hypotheses

General Review

At numerous times during the past three hundred years anatomists have suggested the rete mirabile to function as a gland, or to in some way alter the chemistry of blood flowing through the system. This hypothesis, together with a thermal one, first appears in The Anatomy of a Porpess by Tyson (1680), and was presented in the following nebulous, but interesting, manner:

"But whether it may be that the heat of so much blood contained in so many vessels may serve for the invigorating the Animal Spirits in the Medulla Spinalis, or whether it may not be a Glandulaous body and so serve for the draining of the serosities of the blood and thereby render it fitter for generating Spirits, or what other uses it may have, is to me yet obscure."

Murie (1867), was a little more specific in his approach. He suggested an exchange of "nutrients" between blood vessels and lymphatics, and that this was related to breath holding:

"I apprehend that the countless divisions, subdivisions, and minute vascular osculations, by coming in close contact with the lymphatic system, conduces to an interchange or exudation of their constituents.

Do the retia and lymph-sacs, then, supplant the necessity for frequent respiration, or substitute by subsidiary function a reserve force where depuration or nutritive quality of the blood is interfered with?"
Since Murie's time, functions of the lymphatic system have been shown to be those of returning fluids to the circulation and of immunity. Moreover, lymphatic vessels and nodes are not usually prominent features of retial anatomy in healthy animals. Hence, Murie's ideas do not seem plausible as originally stated.

More recently, Ommanney (1932) considered the rete to function as an "accessory lung" by absorbing oxygen from the blood while the whale is at the surface, and by later liberating this gas during a dive. In support of his argument, he cites the high solubility of oxygen in fat. Similarly, Harrison (1972), on the basis of unpublished ultrastructural studies, suggested that retial vessels may absorb circulating carbon dioxide. Both these ideas have no precedent and are theoretically difficult to support.

Contribution to Blood Sugar Levels: A Hypothesis

Introduction

In Chapter 4, I presented a number of possible uses for the large glycogen deposits that occur in retial tissues. Most interesting is the suggestion of free glucose release during a dive (Vogl and Fisher 1976). This hypothesis is not totally without support since:

(1) tissues other than those of the liver, kidney, and intestine can release free glucose (lung of *Leptonychotes weddelli* - Hochachka et al. 1977;
(2) vascular tissues normally contain small amounts of glycogen and are hence pre-adapted for the storage function proposed here,

(3) the system has a large surface area which favors exchange,

(4) retial arteries are on a direct pathway to the central nervous system which depends on glucose as an energy source,

(5) the rete is not removed from the circulation during a dive (a "heart - lung - rete - brain" machine),

(6) biologically, it may be inefficient to completely "lock" carbohydrate reserves in one tissue at the possible expense of another.

Unfortunately, the definitive test of this hypothesis (measurement of glucose levels in afferent and efferent retial arteries before, during, and after a dive) proved unfeasible for a number of reasons. Hence, an indirect approach involving biochemical and ultrastructural analyses had to be used.

Biochemical investigations were focused on two enzymes: glucose-6-phosphatase and lactate dehydrogenase.

Glucose-6-phosphatase catalyses reaction (A) and is part of the mechanism by which glucose is released from cells.

\[
(A) \text{ Glucose-6-P + H}_2\text{O} \rightarrow \text{Glucose} + \text{Pi}
\]
It is generally accepted that if a tissue, or cell, releases free glucose, then it has glucose-6-phosphatase. This implies that if retial tissue does not have this enzyme, it can not release free glucose. It does not mean, however, that if retial tissue has glucose-6-phosphatase it releases free glucose. Nor does it logically follow that if retial tissue does not release free glucose it will not have glucose-6-phosphatase. Hence, in the biochemical and ultrastructural studies below, I will simply demonstrate that retial tissue has or does not have the potential for free glucose release. I will not be able to show that the rete actually does contribute directly to blood sugar levels. If indeed the enzyme is present, measurement of its activity, and comparison of this value with activity values in other tissues may allow some comment on the likelihood of free glucose release.

Lactate dehydrogenase (LDH) catalyses reaction (B), the last step in the glycolytic pathway.

(B) Pyruvate + NADH + H+ <--> Lactate + NAD+

This enzyme consists of four subunits of two types, a muscle type (M) and a heart type (H). By varying the proportion of M and H subunits in the enzyme, five basic isozymes can result. Tissues having a high capacity for anaerobic metabolism usually have isozymes with a large proportion of M type subunits. LDH isozymes with predominantly H type subunits usually characterize tissues with high aerobic capacity (Everse and Kaplan 1973). One might expect then, that if retial tissues have proportionately
greater amounts of M than H subunits in their LDH isozymes, they use stored glycogen themselves rather than release it as free glucose.

Ultrastructurally, the problem was approached two ways: (1) Are glycogen deposits present in arteries other than those of the rete? (substantial concentrations in non-retial vessels would argue against the hypothesis); (2) Are glycogen deposits present in retial vessels of species other than *Monodon monoceros*? (Lack of deposits in other species would suggest that free glucose release is not a significant retial function.)

Materials and Methods

Glucose –6-Phosphatase

a) Ultrastructural localization

Tissues for ultrastructural localization of G-6-Pase were obtained from a single *Monodon monoceros* calf (#59). Samples of liver and thoracic rete were excised 2-5 min post-mortem, placed in fixative (2.5% glutaraldehyde in .1m cacodylate + .1M sucrose at pH 7.3), and cut into small pieces. After 3-5 min tissues were washed in buffer (.1 m cacodylate + .1 m sucrose at pH 7.3), then incubated for one hour at 37°C in media containing either G-6-P (test) or B-Glycerophosphate (control) as described by Borgers et al. (1971). Subsequently, samples were fixed for 2 1/2 hrs (same as above), then washed and stored in buffer. In
the lab, tissues were post-fixed for 1 hr (0.1M Osmium tetroxide in 0.1M cacodylate + 0.1M sucrose at pH 7.3), then processed for ultrastructural observation. Cut edges of samples were examined for enzyme specific lead deposition.

Buffers for incubation media were prepared in the lab prior to my departure for the arctic. All other ingredients, pre-weighed and stored dry, were not added until just prior to use.

A custom built portable water bath was used to maintain the required incubation temperature.

B) Activity

Tissue for determining G-6-Pase activity was obtained from one adult *Monodon monoceros* (#58). Blocks of tissue, excised 5 min. to one hour post-mortem, from the thoracic rete, lung, heart (right ventricle), liver, epaxial muscle, and brain (cerebral cortex), were frozen in liquid nitrogen and later transferred to a -60°C freezer until they could be assayed.

The assay technique, described fully in Appendix I was generally as described by Nordlie and Arion (1966) except that all preparations were incubated at 31°C and that no attempt was made to isolate the microsomal fraction from the homogenate. Inorganic phosphate was determined by the Fiske and Subbarow (1925) method using the ready-made reducing reagent sold by Sigma (Cat# M-0878). For each reaction tube, two sets of controls were run: (1) zero time control, and (2) no substrate + no enzyme control. From each of at least two homogenates per
tissue, three assay runs were made. To control for method, rat
tissues (liver, lung, heart, brain and muscle) were assayed and
compared with values recorded in the literature.

In the above assay, no attempt was made to control the time
between making the homogenates and measuring activities. Since
usually three tissues were assayed per day, and the homogenates
were run in sequence three times, the interval between preparing
the tissue and making the last activity measurement was as long
as 10 hours. To control for possible effects of time, a sample
from each tissue was thawed and assayed as quickly as possible
(roughly 20 min later). Also, heart, lung, brain and rete were
assayed (time controlled) once under conditions which more
closely resembled physiological ones (incubated at 37°C and
buffered to pH 7.3).

Lactate Dehydrogenase

A qualitative indication of the types of LDH isozymes
present in heart, brain, liver, muscle and rete of Monodon
monoceros (#58) was obtained using disc gel electrophoresis in
the manner described by Dietz and Lubrano (1967). Approximately
equal parts by volume of tissue and buffer (.1M Tris-HCL/pH 7.0)
were homogenized, then centrifuged for 20 min at 34,800 G and 4°C
(Sorval 4.25 head). From the resulting supernatants, 10 ul
aliquots were extracted and added to the tops of 5.5% acrylamide
gels prepared earlier. Electrophoresis was run in a Tris-Glycine
buffer system (pH 8.5/4°C) at 250 V and 2 mA/tube.
Gels were stained in the dark and at 5°C with a solution containing 1 ml 75% DL-lactate, 23 mg nitroblue tetrazolium, 23 mg NAD+, 1 mg phenazine methosulphate, and 75 ml 100mM Tris-HCl buffer (pH 8.0) (Moon et al. 1977). When patterns had developed, gels were removed from the stain and stored in 7% acetic acid.

Ultrastructural material

Tissue collected for nerve studies and general ultrastructural analysis was also examined specifically for glycogen deposition. Vessels were from the caudal rete (terminal aorta and accompanying vessels), flipper (counter-current network), and the spinal rete. Also examined were small vessels within interstitial tissues of the thoracic rete. No attempt was made to quantify glycogen in any vessel.

Also examined was material from the thoracic rete of Tursiops truncatus collected and processed by Dr. J. C. Fanning, Queensland (Australia).

Results

Glucose-6-Phosphatase

(b) Ultrastructural localization

Since blocks rather than thin sections of tissue were incubated, staining was far from optimal. However, differences
between the density of G-6-Phosphohydrolase specific lead precipitation in retial and hepatic tissues were consistent with measured differences in activities: that is, liver stained "better" than rete. In hepatocytes (Plate 37, Fig. A and B) and in retial smooth muscle cells (Plate 37, Fig. C to G), specific staining occurred in the nuclear envelope and endoplasmic reticulum. Non-specific precipitation, indicated by positive staining in controls, occurred in the mitochondria and cytoplasm of both cell types, and in association with the caveolae of retial smooth muscle. Staining of retial endothelial cells was unsuccessful due to poor fixation.

(a) Activity

G-6-Pase activities in all tissues examined are presented in Text-Fig. 13. Because of the small sample sizes, no inferential statistics were done on the data. However, there is no obvious difference between values calculated using zero time controls and those using no enzyme plus no substrate controls. Mean activities of retial tissue were .44 ± .07 units (zero time control) and .39 ± .1 units (no substrate plus no enzyme control). These values were slightly lower than those determined for heart and brain, and greater than those recorded for muscle. Activity values in pulmonary tissue were 1.15 ± .24 and 1.06 ± .34 units. Values measured at pH 7.3 and 37 °C generally corresponded with those measured at pH 6.5 and 31 °C, except possibly in the lung where they were slightly higher. Enzyme
Text-Fig. 13. Glucose-6-phosphatase activities in tissues of *Monodon monoceros*. For each tissue, values calculated using zero time controls are on the left. Those calculated using no enzyme plus no substrate controls are on the right.

For each homogenate assayed at 31°C and pH 6.5, measurements were made in triplicate. Maximum and minimum values are indicated by vertical lines. The small horizontal lines represent means. Mean values for homogenates in each control group were pooled. Means of these values are indicated by the large stippled circles.

Values obtained for rat tissues (one measurement - one homogenate) are indicated by black circles with starred centres. Only the assay of liver was time controlled.

Solid circles are values (one measurement - one homogenate) obtained for whale tissues in time controlled assays.

Solid stars are the results (one measurement - one homogenate) of assays done at 37°C and pH 7.3 (whale tissues).
Glucose-6-Phosphatase Activity
(Monodon monoceros)
activities determined in rat tissues were generally in agreement with values in the literature (liver - Nordlie 1974; brain - Hawkins and Miller 1978)

Lactate Dehydrogenase

An electrophoretic profile of LDH isozymes in Monodon monoceros tissues (heart, brain, liver, lung, rete and muscle) is presented in Plate 38. In retial arteries, the majority of subunits are of the M type, and the most evident isozyme appears to be HM3 (or LDH-4). Heart and muscle characteristically band out at opposite ends of the isozyme spectrum while other tissues occupy intermediate positions. The proportion of M subunits appears to increase from brain to liver and again to lung.

Ultrastructural Data

Glycogen deposits were observed in all vessels examined from Monodon monoceros (Plate 39). No deposits were found in retial arteries of Tursiops truncatus.

Discussion

The demonstration of G-6-Pase in retial vessels is consistent with the occurrence of a potential for free glucose release, and is in agreement with the finding of this enzyme in
vascular tissues of other species (Borgers et al. 1971). However, that activities in retial tissues are low and of the same orders of magnitude as those found in heart and brain do not overwhelmingly support the hypothesis of direct retial contribution to blood sugar levels as a major function. Moreover, the mere presence of this enzyme does not necessarily mean that, under normal conditions, it functions as a glucose-6-phosphohydrolase, since it is known to be multifunctional (Nordlie 1974). Even if it does function in the classical manner, we possibly should regard it as part of a mechanism for regulating net glucose flux.

Metabolically, vascular smooth muscle uses mainly carbohydrate as an energy source (Paul and Ruegg 1978; RQ=.91 ± .28 in human aorta and .99 ± .24 in dog aorta, Kirk et al. 1954; RQ=.9 ± .01 in dog femoral artery, Kosan and Burton 1966), normally functions with a high level of aerobic glycolysis (Kirk et al. 1954; Paul et al. 1974; Peterson and Paul 1974; Hellstrand 1977; Paul and Ruegg 1978), and does, depending on the vessel, demonstrate a Pasteur effect (Lundholm and Mohemelundholm 1960; Hellstrand 1976). That this is also true of retial smooth muscle is in part supported by the presence, in this tissue, of electrophoretically slow moving LDH isozymes, slower in fact, than in "healthy" pig or human arteries (Zemplenyi 1975). This agrees with the conclusions of Shoubridge et al. (1976) that cetacean tissues generally have larger proportions of M than H type subunits, and that this is related to hypoxic stress (diving).

At present we know little about the respiratory metabolism
of endothelial cells (Roberson and Rosen 1977), except, perhaps, that they are more active than smooth muscle cells and more closely resemble "typical" somatic cells (pronounced Pasteur effect and low rate of aerobic glycolysis - Morrison et al. 1977).

From a metabolic point of view then, the rete probably fits into the classical "heart-lung-(rete)-brain" model as an organ which has only minor effects on blood oxygen levels and circulating metabolites. Its metabolic rate is undoubtedly low, since vascular smooth muscle is generally not very active (Kirk et al. 1954) and vessels probably compensate for any loss of aerobic metabolism during periods of stress (diving) by increasing glycolysis at the expense of stored glycogen (see Hellstrand et al. 1977). However, this does not totally rule out the possibility of some free glucose release during a dive, nor the metabolizing of lactate during recovery periods. Also, an indirect contribution to blood sugar levels may occur via the production of lactate and its recycling as glucose by the lung, a tissue known to have gluconeogenic properties in Leptonychotes weddelli (Hochachka et al. 1977, Hochachka and Murphy in press; note that G-6-Pase activities in Text-Fig. 13 are twice as high in the lung as in all tissues except liver). This would provide a mechanism by which carbohydrate reserves "locked" in retial cells could be fully utilized elsewhere (CNS and lung) during periods when hepatic tissues, normally responsible for regulating metabolite levels, are short-circuited (Bron et al. 1966).

In summary, though the considerations discussed above are
not inconsistent with the hypothesis of direct retial contribution to blood sugar levels, this function is, at best, a minor one for the following reasons:

a) large glycogen reserves are present in vascular tissues other than in those of the rete,
b) retial glycogen pools are not present in all species,
c) G-6-Pase activities are low, and
d) LDH profiles are indicative of a tissue having a high capacity for anaerobic metabolism, hence suggesting that the rete uses most, if not all, glycogen reserves itself.

At present there is no overwhelming support for chemical hypotheses of retial function. Any changes in blood chemistry are most likely minor and of secondary importance to functions related to vessel mechanics.

(2) Mechanical Hypotheses

General Review

Mechanical hypotheses of retial function are numerous and are currently the most popular. Among the more notable suggestions are those related to filling of non-collapsible air spaces, temperature regulation, equalizing pressure differences between body regions, maintenance of a uniform blood flow to central nervous tissue, and dampening of potentially damaging pressure pulses.
Filling Non-collapsible Air Spaces

The first function considered here is that of filling non-collapsible portions of the thorax during deep dives (Walmsley 1938). The only work remotely connected with this line of thought is that by Hui (1976) who found that the presence of an engorged thoracic rete does affect the nature of thoracic collapse. However, apart from the lack of extensive innervation reported in my study, we know nothing of how, or even if, vessels of the rete alter during a dive. It also seems pertinent at this point to mention that in the middle ear (a large non-collapsible air space) volume accommodation, over and above that achieved by the eustachian tube, occurs by engorgement of veins, not arteries. Moreover, it seems likely that once expanded at physiological pressure, volume changes are not that great, or at least not as great as those which occur in veins. If expansion of retial tissue is indeed involved with accommodating decreased pulmonary volume during diving, this is not the whole story since it does not account for the presence of retial vessels in the neural canal, cervical region, or cranium. That the system is so extensive leads us to the next proposition - that of blood storage.
Blood Oxygen Reservoir

Introduction

A popular belief during the 17th and 18th centuries was that the cetacean rete functioned as a blood oxygen reservoir. Hunter (1787) introduced this idea in the following manner:

"Animals of this tribe, as has been observed, have a greater proportion of blood than any other known, and there are many arteries apparently intended as reservoirs, where a larger quantity of arterial blood seemed to be required and vascularity could not be the only object."

Owen (1868) later added:

"Thus the neural axis can receive its appropriate stimulus of oxygenated blood during the periods of long submersion and consequent interruption of respiration, to which the Cetacea are subject."

Other anatomists perpetuating this hypothesis included Breschet (1836), Wilson (1878) and Mackay (1886).

More recently, Morgane and Jacobs (1972) include in their possibilities of retial function that of a "vascular reservoir".

Since no quantitative estimate of retial blood volume exists in the literature, and because this information is necessary to evaluate the blood oxygen reservoir hypothesis, I decided to estimate retial vascular capacity in Monodontidae.
Materials and Methods

In the field, retial measurements (lengths and widths) and body lengths were recorded from six *Delphinapterus leucas* (#4,5,6,9,10,11) and eight *Monodon monoceros* (#7,9,12,13,14,21,26,34). I used these data to estimate thoracic and spinal retial volumes. To provide models for the general shape of the system, and hence data from which volumes could be determined from the recorded linear measurements, one specimen of each species was dissected and measured in detail (*Delphinapterus leucas* #15; *Monodon monoceros* #1). Model specimens were cut into sections between successive pairs of ribs and the resulting sections photographed. Outlines of retial tissues were traced from the prints onto paper, then depth, width and area measurements made as in Text-Figs. 14 and 15. Other necessary values (body lengths, retial lengths, distances between sections) were added to the models using appropriate magnification factors.

I then wrote a program to calculate retial volumes using the above models as baselines. Cross sectional areas of field specimens were calculated by using recorded width and estimated depth measurements in combination with area formulae (for each area value) derived from standard animals, then the volumes between these areas were determined using the equation for the volume of a truncated cone:
Text-Fig. 14. Detailed measurements of the thoracic and spinal retia in the "model" specimen of *Delphinapterus leucas*.

Measurements in the figure refer to the following:

Distances (in cm) between sections are indicated in the lower diagram of the figure.
Text-Fig. 15. Detailed measurements of the thoracic and spinal retia in the "model" specimen of *Monodon monoceros*. See Text-Fig. 14 for notations.
For sections in which no width value was recorded, this value was estimated by multiplying the corresponding value in the model by an average magnification factor determined from those of recorded widths. Distances between sections were considered to be of the same proportion of total retial length as in model animals. "Segmental" volumes were then summed to arrive at totals. Volumes of right and left sides were calculated separately, as were those of thoracic and spinal portions of the system. Total thoracic and spinal volumes were then plotted against body length and a t-test (UBC SLTEST) used to test the hypothesis of similar slopes and equations of regression lines for the two species. Errors inherent to the above analyses are:

1. Volume values are not totally independent of each other since they were, in essence, extrapolated from the two model animals,

2. Extrapolation assumes that retial proportions do not change with body length (i.e., shape of the rete is the same in all age classes).
(3) Because of the small sample size, retial volume is simply assumed to be linearly related to body length.

In spite of these faults, the method probably gives the best estimate possible of retial volumes in animals from which only retial lengths and widths were recorded, and does provide at least some sort of foundation for comparison between species.

To approximate retial blood volume and to express this value as a percentage of total blood volume, the following method was used. Thoracic and spinal retial volumes of an animal 350 cm long were calculated using regression lines of volume on length. These values were summed and the result multiplied first by 4/5 to account for non-retial tissue (bone; intercostal nerves, arteries, and veins) and second by the proportion of luminal area in a retial cross section (21%) to obtain an estimate of total retial blood volume (rest). Body weight of the above animal was determined using the regression line of weight on length determined for *Monodon monoceros*¹ (Keith Hay pers. comm.), then total blood volume estimated using data for three small cetaceans² (Ridgway and Johnston 1966). Retial blood volume (rest) was then expressed as a percentage of the animal's estimated total blood volume.

\[ \log \text{wt. (Kg)} = 2.3692 \log \text{L (cm)} - 3.2511 \]

¹ *Phocoenoides dalli* - 143 ml/Kg; *Lagenorhynchus obliquidens* - 108 ml/Kg; *Tursiops truncatus* - 71 ml/Kg.
Results

Differences in thoracic retial width between species are to some extent reflected in the volume estimates. Though there are no statistically significant differences between regression lines of volume on length for either the thoracic (Text-Fig. 16A) or spinal (Text-Fig. 16B) retia, the probability of common equations for the thoracic rete is an order of magnitude smaller than for the spinal rete. Such results are expected since the neural canal is of similar dimensions in both species and is filled with retial tissue, whereas the thoracic rete occurs only along the dorsal thoracic wall and differs in width between the two species. In this study, width differences do not have a significant effect on volume. Hence, equations common to the two regression lines in each of Text-Fig. 16A \( (V \, \text{cm}^3 = -1453 + 17.62 \, L \, \text{cm}) \) and Text-Fig. 16B \( (V \, \text{cm}^3 = -718.5 + 7.853 \, L \, \text{cm}) \) were used in calculating total retial volume \( (6734.05 \, \text{cm}^3) \).

Retial blood volumes, expressed as a percentage of total blood volume, are 1.4%, 1.8%, 2.8% calculated using data for *Tursiops truncatus*, *Lagenorhynchus obliquidens*, and *Phocoenoides dalli* respectively. No attempt was made to compensate for vascular collapse at death or for any shrinkage during histological preparation.
Text-Fig. 16. Regressions of retial volumes on body length.

Fig. A. Regression of thoracic retial volume on body length.

Fig. B. Regression of spinal retial volume on body length.

Solid circles and lines are values for *Monodon monoceros*.

Hollow circles and segmented lines are values for *Delphinapterus leucas*.

Asterisk - refers to an animal for which only measurements for the dextral side were recorded (volume for dextral side was doubled for use in this analysis).

Boxed values - Model animals
**Common Slope**

- Prob. = 0.600

**Common Equation**

- Prob. = 0.074

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**Common Slope**

- Prob. = 0.308

**Common Equation**

- Prob. = 0.601

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Body Length (cm.)
Discussion

It is unlikely that the retial system functions primarily as a "blood-oxygen" reservoir. In relation to total blood volume, retial capacity is low, ranging from 1% to 3% depending on how total blood volume is calculated. These figures are far below the proportion of blood normally in systemic veins (59% in man, Guyton 1977) - the site of most volume storage in mammals.

Marine mammals in general have larger blood volumes than their terrestrial counterparts (see Ridgway 1972 for marine mammal values and Prosser 1972 for those of terrestrial mammals), and they appear to accommodate most of this increase by expanding the venous side of the circulation, not the arterial side. The presence of enlarged hepatic veins, expanded and sometimes duplicated venae cavae, enlarged epidural veins, and at least in pinnipeds, the development of distinct "hepatic sinuses" support this view (see Harrison and Tomlinson 1956; King 1965; Harrison and King 1965; Ronald et al. 1977; Hilton and Gaskin 1978).

That it is veins and not arteries that form volume reservoirs is no doubt related to problems associated with maintaining pressure on the arterial side of the circulation. It is far more efficient to simply "hang a bag" onto an unpressurized system than to incorporate a "volume reservoir" into a highly pressurized one.

Though presence of the rete does increase volume capacity of the vasculature, this increase is small, at least in
comparison to total blood volume, and does not appear to justify expense. If indeed the system is functioning as a reservoir, it is more likely doing so as a pressure rather than as a volume one.

Pressure / Flow Hypotheses

Discussion

The first functions attributed to *retia mirabilia* in general were those related to blood pressure and flow (see Ask-Upmark 1935 for review). Willis (1486 - cited by Ask-Upmark 1935) believed carotid retia to supply blood to the brain "slowly and with a gentle and almost even stream". He related their presence in ungulates to a head-down stance and its absence in man and horse to nimbleness of mind and/or body. Ask-Upmark (1935) concisely defined the major pressure hypothesis of retial function as follows:

"The rete would thus serve, not only by transforming the pressure down to a lower absolute level, but also by moderating the changes of the pressure in the efferent vessel brought about by changes in the afferent artery(ies).....

Thus the hydrodynamic effect of the rete mirabile caroticum would be to keep the pressure in the arteries to the brain at a convenient and fairly constant level."

Though dampening of the pressure pulse, at least at hypertensive levels, has been observed (Edelman et al. 1972), any pressure
related function of the ungulate system appears secondary to a more basic function - cerebral temperature control.

When present, the epidural rete is usually embedded in the cavernous sinus which drains, among other areas, horns (Taylor 1966) and the nasal mucosa (Baker and Hayward 1968). By regulating the amount of "cool" blood returning from peripheral areas to the sinus, the amount of heat lost from blood flowing through retial arteries can be varied. A dissociation of cerebral and core temperatures is observable under "normal" conditions (Baker and Hayward 1968a; Hayward and Baker 1969) and becomes exaggerated during exercise (Taylor and Lyman 1972; Baker and Chapmann 1977) and environmental heat stress (Baker and Hayward 1968b). The ability to keep cerebral temperature lower than general body temperature allows an animal to withstand hyperthermia and hence "store" heat - one mechanism of withstanding thermal stress.

Thermal functions have also been proposed for the cetacean retial system. Tyson (1680) considered these possibilities, as did Cunningham (1877). The latter author believed retial vessels to maintain "a uniform warmth" around the spinal cord by "keeping it bathed ... in warm arterial blood". In recent literature, reference to thermal function is scant, even though part of the intracranial system (carotid rete) appears homologous to the epidural rete of ungulates, and at least one author has reported a close association between arteries and veins in this area (Walmsley 1938). However, it does appear that significant involvement with heat loss, gain, or retention is unlikely, at least in the Monodontidae. This is so for the
following reasons:

1. The entire body core is wrapped in an insulating layer of blubber, suggesting that "warm" blood could be stored in venous pools since these are within the body core,

2. Well developed vascular thermoregulating mechanisms are present in peripheral areas to regulate core temperature,

3. Retial vessels are not generally associated with veins or with any thermogenic tissues (brown fat - see Chapter 4), and

4. There is probably more of a problem of retaining heat rather than losing it, at least in the smaller cetaceans.

Though thermal functions have generally been overlooked, pressure related ones certainly have not.

For at least one hundred years, authors have thought the cetacean rete to in some way alter or regulate blood pressure and flow. Slijper (1958), and later Nakajima (1961), concluded that the system equalizes pressure differences between body regions when whales submerge or respire. Much earlier, however, Turner (1870) proposed that:

"It [the rete] serves, I believe, the purpose, by minutely subdividing the arterial stream, of distributing and equalizing the force of the blood current before it reaches those delicate organs the brain and spinal cord."
At present, the most popular hypothesis of retial function is, in essence, a more sophisticated form of Turners original one.

Recent measurements of blood pressure in spinal meningeal arteries of an anaesthetized bottlenose dolphin (*Tursiops truncatus*) indicate a leveling of the pressure pulse with only a slight reduction of mean pressure. In other words, the system is acting as a capacitor, not a resistor (Nagel et al. 1968). Hence, the rete may serve to maintain a continuous flow of blood to the brain in the face of bradycardia on diving (Morgane and Jacobs 1972). Or, using an analogy, the system is acting as a "windkessel" (bellows) or pressure reservoir—filling quickly during systole, via the numerous afferent arteries, and emptying slowly during prolonged diastole, via the relatively few efferent vessels (estimates of total cross sectional areas of retial afferents and efferents are approximately 300 mm$^2$ and 40 mm$^2$ respectively).

Retial anatomy supports the view that the system has a low resistance. An estimated total of 800 points of retial origin occur along the systemic arteries described in Chapter 2. Retial arteries have an inner diameter of about .7 mm and, in a 350 kg whale, total retial blood volume is approximately 1131$^3$ cm (Text-Fig. 17A). Using these data, and ignoring anastomoses between vessels, each of the 800 retial arteries can be calculated to have a length of 350 cm (Text-Fig. 17B). In "electrical" terms, the system appears set up as a number of resistors in parallel with a total resistance equal to one eight hundredth of the resistance of one of its constituent arteries. If estimated values of 50 cm/sec and .05 dyn sec/cm$^2$ are used
Text-Fig. 17. Retial model.

Fig. A. Estimated numbers and diameters of vessels which pass into and out of the retial system. Input vessels are those that take origin from systemic arteries and form the rete. Output vessels are those that take origin from spinal and carotid retia and pass into the spinal cord and brain respectively.

Fig. B. A simple model of the retial system is one formed of 800 vessels each 350 cm long and .7 mm ID. In this particular model anastomoses between vessels are ignored and the system can be considered a series of resistors in parallel. Total resistance is low.
Retinal Blood Volume
1131.3 cm³

Input
800 Arteries
.7 mm ID
Output

Brain
4 Arteries
3 mm ID

Spinal Cord
64 Arteries
.5 mm ID

\[ R_{\text{total}} = \frac{R_{\text{single artery}}}{800} \]
for average blood velocity through the rete and blood viscosity respectively, the Poiseuille equation predicts a pressure drop, across the total system, of about 6 mmHg - a fairly low resistance indeed.

Related to the "windkessel" hypothesis is the suggestion that the rete may serve to dampen large pressure pulses that might prove damaging if, as in *Zalophus californianus* (California sea lion), cerebral vessels dilate during a dive (Dormer et al. 1976).

The unfortunate thing about all pressure hypotheses is that what we observe physiologically to support such proposals may be nothing more than effects of structure rather than primary functions. If we accept that a system functioning primarily as a windkessel will result in a dampened pressure pulse and a smoothed flow, we cannot infer that because we observe these consequences physiologically that the system is indeed functioning primarily as a windkessel. In philosophical terms, we cannot confirm anything by "affirming the consequent" of a hypothetical proposition (Stone 1966). For example, the spermatic artery in some mammals is extremely tortuous (or retial) (Harrison 1949; Barnett and Brazenar 1958), and results in a dampening of the pressure pulse (Waites and Moule 1960; Setchell and Waites 1969). Though we would like to propose that production of a non-pulsatile flow is the major function of this structure, evidence certainly suggests that pulse changes are simply effects of structure and that the primary function is most likely regulation of testicular temperature (Harrison and Weiner 1949; Dahl and Herrick 1959; Waites and Moule 1961;
Godinho et al. 1977).

Since the cetacean retial system is basically a plexus of blood vessels which undoubtedly have mechanical properties characteristic of blood vessels in general we have to be very careful when inferring function based solely on affirming that these vessels do indeed have the mechanical properties we might have predicted. It becomes far too easy to simply "explain the system away" rather than critically evaluate it. One way to approach the problem is to prove all other propositions false, or at least unlikely. Even here we run into problems - the system could, quite possibly, be multifunctional.

That we may be overlooking something by accepting pressure hypotheses is supported by the following observations:

1) constituent vessels are not homogeneous (small muscular arteries in the thorax; large arteries with a greater content of elastin in the neural canal; a pair of large arteries coursing around the cerebellar hemispheres in the cranium; a plexus of small vessels at the base of the brain).

2) cervical vessels of the spinal rete appear closely associated with veins,

3) the system is unique to the Cetacea, even though other diving mammals would theoretically be exposed to the same "pressure" problems (this may relate in some way to the absence of a hepatic sinus and sphincter which, in seals, regulate flow of blood back to the heart during bradycardia (Ronald et al. 1977),

4) other diving mammals seem to have enough capacitance
in their vasculature to cope with dramatic changes in cardiac output and maintain a continuous flow of blood to the central nervous tissues (we may be able to account for some of the observed differences in vascular anatomy by simply recognizing that the Cetacea, particularly the odontocetes, have much larger brain/body weight ratios than other diving mammals. In other words, they may "need" pressure reservoirs over and above those which can be provided by expanding extant vessels - development of an aortic bulb - Plate 40 - see Drabek 1977 for a discussion of the aortic bulb in seals).

Of all the functions suggested to date, the windkessel hypothesis appears the most probable by virtue of the fact that other suggestions are less likely however, we must be careful in accepting this as the sole or even the major retial function on the basis of evidence produced by "the processes of elimination" since there may be factors involved of which we are as yet unaware.
SUMMARY AND CONCLUDING REMARKS

(1) The internal carotid arteries are completely degenerate as cerebral supply vessels in the family Monodontidae. These vessels are patent in the neck and ear, but are occluded within the carotid canal. There are no other channels directly connecting intracranial vessels with major systemic trunks.

(2) Blood supply to the central nervous system and its derivatives occurs indirectly via a massive rete mirabile located along the dorsal thoracic wall, in fascia of the lumbar and cervical regions and within the neural canal and cranium. Major systemic arteries that contribute to retial formation are the:

- a) internal carotids
- b) occipitals
- c) cervico-occipitals
- d) posterior thoracics
- e) profunda cervicals
- f) supreme intercostals
- g) aortic intercostals
- h) costo-abdominals
- i) lumbars
- j) ascending cervicals
- k) broncho-esophageals, and possibly the
- l) middle meningeals.

Most of these vessels supply branches to the central nervous system and/or its membranes in other mammals.
(3) Two pairs of trunks originate from the carotid rete and supply the brain. One pair supplies the forebrain while the other pair supplies mainly the mid- and hindbrain.

(4) The spinal cord is vascularized by segmentally arranged arteries which originate from retia in the neural canal. Most of these arteries occur ventrally and between successive spinal roots. Distinct anterior and posterior spinal arteries are not present.

(5) Though gross retial anatomy is similar in *Monodon monoceros* and *Delphinapterus leucas*, there are two related features that appear species specific - (1) thoracic retial width, and (2) size of the supreme intercostal arteries. Both are larger in *Monodon monoceros*, as are values of hematocrit and hemoglobin concentration, which, in this study, are used as indices of diving potential. These data are consistent with the hypothesis that the retia mirabile is in some way associated with diving capability.

(6) Retial microanatomy is the same in the two species. Though there is some variation in structure from one anatomical region to another, the system generally consists of small muscular arteries embedded in fatty connective tissue. There is no obvious association between arteries and veins in any part of the plexus,
except, perhaps, in cervical portions of the spinal rete, nor is the system well innervated. Also, retial arteries are similar in structure to mammalian arteries in general, except that large deposits of glycogen occur in endothelial and vascular smooth muscle cells. The latter observation was responsible for our generating the hypothesis that retial vessels may, in addition to using the stored carbohydrate themselves, contribute to blood sugar levels during a dive (Vogl and Fisher 1976).

(7) Though retial arteries appear to have the machinery for releasing free glucose, direct contribution to blood glucose levels is probably not significant since G-6-Pase levels are low. Also, LDH electrophoretic profiles suggest that vessels do use the stored carbohydrate reserves themselves. A small contribution to circulating metabolites may occur via release of lactate which the lung can either use as an energy source or convert to glucose for use by the central nervous system.

(8) I found no evidence that the cetacean rete is thermoregulatory.

(9) Though retial blood capacity is in the order of 3% of total blood volume, I argue that the system's major function is not one of a blood oxygen reservoir since:
(1) about 75% of the rete is connective tissue other than blood, and (2) vertebrates generally store blood in veins, not arteries.

(10) That the rete expands to fill non-collapsible air spaces is also unlikely as a major function. Vessels are found in regions where air spaces do not occur, and the potential for expansion is probably not great.

(11) My anatomical observations are generally consistent with hemodynamic hypotheses of cetacean retial function as originally stated by Turner (1870), and as later reiterated by Ask-Upmark (1935) and Morgane and Jacobs (1972). There are many afferents vessels to the rete and few efferents. Also, retial arteries generally contain a fair amount of elastin, though the variation between vessels in different regions is a little perplexing. The system does indeed appear "set up" as a "windkessel", and the lack of innervation suggests that its action is passive.

It would appear, then, that the cetacea rete mirabile is simply a modified form of the basic mammalian pattern of blood supply to the central nervous system, but is much elaborated to magnify the mechanical, and other, effects characteristic of arterial networks in general.
Plate 1. Gross anatomy of the A. carotis interna.

Fig. A. Ventral view of the neck and head showing the origin and distribution of the Aa. carotis internae in Delphinapterus leucas. (#15). Structures ventral to the carotid plane have been removed.

ACID(C) - A. carotis interna dextra (cervical part)
ACID(ce) - A. carotis interna dextra (cervical branch)
ACID(O) - A. carotis interna dextra (otic part)
ACCS - A. carotis communis sinistra
ACES - A. carotis externa sinistra
ACIS(C) - A. carotis interna sinistra (cervical part)
ACIS(ce) - A. carotis interna sinistra (cervical branch)
ACIS(O) - A. carotis interna sinistra (otic part)
AMS - A. maxillaris sinistra
M - Mandibula
MAE - Meatus acusticus externus
RAMCV - Rete arteriales mirabile cervicalis ventralis

Fig. B. Ventral view of cervical and otic regions of the A. carotis interna sinistra of Monodon monoceros (#1). Note tapering.

ACES - A. carotis externa sinistra
ACIS(C) - A. carotis interna sinistra (cervical part)
ACIS(O) - A. carotis interna sinistra (otic part)
FAO - paraoccipital process
NV - N. vagus
RAMCL - Rete arteriales mirabile cervicalis lateralis

Fig. C. Ventral view of dura mater encephali covering the hypophyseal region of the brain in Monodon monoceros (#1). Note position of the Aa. carotis internae.

ACID(O) - A. carotis interna dextra (otic part)
ACID(CR) - A. carotis interna dextra (cranial part)
ACIS(O) - A. carotis interna sinistra (otic part)
ACIS(CR) - A. carotis interna sinistra (cranial part)
H - Hypophysis
Plate 2. Otic part of the A. carotis interna in *Monodon monoceros*. Gross anatomy and histology.

Fig. A. Cross section of the otic part of the A. carotis interna and associated structures.

ACI - A. carotis interna
E - Epithelium
N - Cranial nerves
V - Veins (corpus cavernosum)

Fig. B - E. Serial sections of a branch taking origin from the A. carotis interna.

ACI - A. carotis interna
B - Branch

Fig. F. Gross dissection of the A. carotis interna to illustrate branching in the ear.

ACI - A. carotis interna
B - Branch
Plate 3. Perfusion cast of the Aa. carotes internae.

Fig. A. Vascular cast showing origin of the Aa. carotes internae in Monodon monoceros (#6). Note small size of the A. carotis interna sinistra. The A. carotis interna dextra is broken at its origin.

ACID - A. carotis interna dextra
ASD - A. subclavia dextra
ACIS - A. carotis interna sinistra
ASS - A. subclavia sinistra
TBS - Truncus brachiocephalicus sinistra

Fig. B. Vascular cast showing origin and distribution of the A. carotis interna dextra in Delphinapterus leucas (#14). Note the large cervical branch and the smaller cranial ramus. Medio-ventral view.

ACED - A. carotis externa dextra
ACID - A. carotis interna dextra
ACID(ce) - A. carotis interna dextra (cervical branch)
ACID(cr) - A. carotis interna dextra (cranial ramus)
RANCV - Rete arteriales mirabile cervicalis ventralis

Fig. C. As in Fig. B., but showing vessel on the sinistral side. The arrow marks the point at which the cast of the vessel terminates. Ventro-lateral view.

ACIS - A. carotis interna sinistra

Fig. D. Lateral view of the vessel in Fig.c.

ACES - A. carotis externa sinistra
ACIS - A. carotis interna sinistra
ACID
ACID (cr)
ACID (ce)
ASS
TBS
ACIS

ACID
ACIS

ACIS

ACIS

ACIS
ACES

5 cm

5 cm

2 cm

2 cm
Plate 4. Histology of cervical parts of the A. carotis interna in Monodon monoceros.

Fig. A. Proximal section of the A. carotis interna (cervical part). Note the predominantly elastic nature of the wall.

   End - Endothelium
   Col - Collagen
   Vv - Vasa vasorum

Fig. B. Central section of the A. carotis interna (cervical part). Note the increased amount of vascular smooth muscle in luminal portions of the wall.

   End - Endothelium
   Vsm - Vascular smooth muscle

Fig. C. Distal section of the A. carotis interna (cervical part). Note the distinct tunica media consisting predominantly of vascular smooth muscle.

   TA - Tunica adventitia
   TI - Tunica intima
   TM - Tunica media
Plate 5. Histology of otic and cranial parts of the A. carotis interna in Monodon monoceros.

Fig. A. Section from the central region of the A. carotis interna (otic part). Note duplication of the internal elastic lamina and proliferation of vascular smooth muscle between the layers.

L - Lumen

Fig. B. Section through distal region of the A. carotis interna (otic part). Note separation of external elastic laminae (arrow) and proliferation of vascular smooth muscle in the zone of separation.

L - Lumen

Fig. C. Section through central portion of the A. carotis interna (otic part). Note elastin (arrow-head) in the tunica media and the apparent separation of the media into two layers. Small arrows indicate collagen deposits.

Fig. D. Section through central portion of the A. carotis interna (otic part). Note sub-endothelial (or endothelial) proliferation (arrow).

Fig. E. Section through cranial part of the A. carotis interna. Arrow indicates a "cellular plug" in the lumen.

Fig. F. Section through cranial part of the A. carotis interna. Arrow indicates a blood clot in the luminal area. Note deterioration of internal elastic lamina.

Fig. A. Course of the A. carotis interna in the head and neck. Numbers correspond to the positions of sections in rows 1 to 7 (numbered in lower left corner of sections in Fig. (column B. 1, 2, and 3 are proximal, central, and distal portions of the cervical part of the A. carotis interna. 4, 5, and 6 are proximal, central, and distal portions of the otic part. 7 is the cranial part.

ACI - A. carotis interna
BT - Bulla tympanica
BS - Os basisphenoidale
CO - Condylus occipitalis
FM - Foramen magnum
IB - Incisura parabasioccipitale
M - mandibula
PBO - Pars basilaris occipitale
PLO - Pars lateralis occipitale
S - Sinus
V - Vomer

Fig. Column B. Series of sections through the A. carotis interna dextra of *Monodon monoceros* #43. All are at the same magnification. Note tapering.

Fig. Column C. Same series as in Fig. B., but with sections 3 to 7 magnified. Vessel in 7 is patent.

Fig. Column D. Series of sections through the ACID of *Monodon monoceros* #39. Vessel in 7 is non-patent (filled with cells).

Fig. Column E. ACIS of *Monodon monoceros* #39. Vessel in 7 is non-patent (filled with cells).

Fig. Column F. ACID of *Monodon monoceros* #22

Fig. Column G. ACIS of *Monodon monoceros* #22

Fig. Column H. - ACID of *Monodon monoceros* #20

Fig. Column I. - ACIS of *Monodon monoceros* #20

Fig. Column J. - ACID of *Monodon monoceros* #21

Fig. Column K. - ACIS of *Monodon monoceros* #21

All sections from C3 to K7 are at approximately the same magnification (indicated in C3). Note that the A. carotis interna at level 7 (cranial) is non-patent in all animals except the calf (#43).
Plate 7. Gross anatomy of the rete arteriales mirabile thoracica.

Fig. A. Ventral view of the rete arteriales mirabile thoracica in *Monodon monoceros*. Heart and lungs have been removed to expose the dorsal thoracic wall.

AISD - A. intercostalis suprema dextra  
AISS - A. intercostalis suprema sinistra  
AT. - Aorta thoracica  
MP - M. psoas  
NS. - Nn. Splanchnici  
OC - Os costale  
RANT - Rete arteriales mirabile thoracica

Fig. B. Ventro-lateral view of the rete arteriales mirabile thoracica (dextra) in *Delphinapterus leucas*. Heart and lungs have been removed to expose the dorsal thoracic wall.

OC - Os costale  
RANT - Rete arteriales mirabile thoracica

Fig. C. Vessels of the rete arteriales mirabile thoracica in *Monodon monoceros*. Note the tortuous course of constituent arteries. Vessels are viewed through the pleura.

Fig. D. Gross cross section of the rete arteriales mirabile thoracica in *Delphinapterus leucas*. Note the uniformity of vessel size.

Fig. E. Origin of retial vessels (indicated by arrows) from the A. intercostalis suprema in *Delphinapterus leucas*. Artery is excised and its wall viewed from the luminal side.

Fig. F. Vessels of the rete arteriales mirabile thoracica in *Delphinapterus leucas*. Note the anastomotic nature of the arteries.
Plate 8. Vascular cast of cervical and thoracic retia in *Delphinapterus leucas*.

Fig. A. Ventral view of major systemic arteries and associated retia.

- AA - Arcus aorta
- AT - Aorta thoracica
- RAMCL - Rete arteriales mirabile cervicallis lateralis
- RAMCV - Rete arteriales mirabile cervicallis ventralis
- RAMT - Rete arteriales mirabile thoracica

Fig. B. Dorsal view of same cast as in Fig. A. Arrows indicate positions of ribs (Os costales). The rete arteriales mirabile spinalis and rete arteriales mirabile cervicallis dorsalis are absent.

- RAMCL - Rete arteriales mirabile cervicallis lateralis
- RAMCV - Rete arteriales mirabile cervicallis ventralis
- RAMT - Rete arteriales mirabile thoracica

Fig. A. Lateral view (from dextral side) of cervical retia in *Delphinapterus leucas*.

ACID - A. carotis interna dextra  
RAMCLS - Rete arteriales mirabile cervicalis lateralis sinistra  
RAMCVD - Rete arteriales mirabile cervicalis ventralis dextra  
Arrow-head - extension of RAMCV dorsally

Fig. B. Ventral view of cervical retia and associated arteries in *Monodon monoceros*.

AA - Arcus aorta  
RAMCV - Rete arteriales mirabile cervicalis ventralis  
TBD - Truncus brachiocephalicus dextra  
TBS - Truncus brachiocephalicus sinistra  
Arrow-head - indicates continuity of cervical with thoracic retia
Plate 10. Vascular cast of thoracic and lumbar retia in *Delphinapterus leucas*. Magnified views.

Fig. A. Part of the rete arteriales mirabile thoracica showing the two dorsal rami of an A. intercostalis dorsalis. (Dorsal view).

RD1 - ramus dorsalis 1
RD2 - ramus dorsalis 2
Arrow-head - retial artery originating from a lateral branch of the A. intercostalis dorsalis.

Fig. B. Part of the rete arteriales mirabile thoracica and rete arteriales mirabile lumbus. Ventral view of dextra side.

AaL - A. (aorta) lumbus
M - ramus to the M. psoas
RAML - Rete arteriales mirabile lumbus
RAMT - Rete arteriales mirabile thoracica
Dotted line - indicates the course of the M. psoas dorsal to the RAMT and ventral to the RAaL

Fig. A to C. Cross sections of the canalis vertebralis and its contents in Delphinapterus leucas (field dissection). Section levels indicated below:

Fig. D to F. Cross sections of the canalis vertebralis and its contents in Monodon monoceros (field dissection). Section levels indicated below:

CV - Corpus vertebra
FI - Foramina intervertebralle
LAV - Lamina arcus vertebrale
MD - Musculi dorsi
MS - Medulla spinalis
PAV - Pediculus arcus vertebrale
RAMS - Rete arteriales mirabile spinalis
RMS - Rete mirabile spinalis
VE - V. epidurales

Note that most of the canalis vertebralis is occupied by vascular tissue.

Fig. A. Vascular cast of one side of the rete arteriales mirabile spinalis in *Delphinapterus leucas*. Medial view. Dorsal is up in the figure.

Fig. B. As in Fig. A. but lateral view. Note plexiform nature of vessels.

Fig. C. Dorsal view of the canalis vertebralis and its contents in *Delphinapterus leucas*. The arcus vertebrae have been removed to expose the two halves of the rete arteriales mirabile spinalis (arrows).

Fig. D. Ventral view of contents of the canalis vertebralis in *Monodon monoceros*. Note that retial arteries (arrow-head) appear continuous between the two sides. White arrows indicate Vv. epidurales. Black dots with white centres indicate sites of attachment to disci intervertebrales.

Fig. A. Monodon monoceros. Caudal view of the foramen magnum illustrating the predominance of two large arteries (A. meningea spinalis - Viamonte et al. 1968) of the rete arteriales mirabile spinalis in this area. Ventral is up in the figure.

CO - Condylus occipitalis

Fig. B. Delphinapterus leucas. Caudal view of an area slightly cranial to that Fig.A, but with all muscle and bone removed. The dura mater encephali is intact. Note the ventral concentration of arteries (recognized by the thickness of their walls). Ventral is up in the figure.

RAMS - most cranial part of the rete arteriales mirabile spinalis

Fig. C. Monodon monoceros. Similar view to that in Fig. B, but with the outer layer of dura mater encephali removed to expose vessels of the rete arteriales mirabile cranis and their association (arrow-heads) with the sinus transversus.

AM - A. meningis
RAMCr - Rete arteriales mirabile cranis
ST - Sinus transversus

Fig. D. Delphinapterus leucas. Ventro-lateral view of brain and associated vessels and meninges. Outer layer of dura mater encephali is removed to expose vessels. In some areas, the inner layer is also removed to expose cranial nerves for use as a landmarks. Note the continuity of the rete arteriales mirabile cranis and rete mirabile carotis interna.

AM - A. meningis
H - Hypophysis
RAMCr - Rete arteriales mirabile cranis
RMCI - Rete mirabile carotis interna
2 - N. opticus
5 - N. trigeminus
7 - N. facialis
8 - N. vestibulocochlearis

Fig. E. Delphinapterus leucas. Ventral view of hypophyseal region of the brain. Note that vessels of the rete mirabile carotis interna are continuous between the two sides around the hypophysis. Also note the position of the Aa. carotes internae (arrow-heads). Rostral is down in the figure.

2 - N. opticus
H - Hypophysis

Fig. A. Vascular cast of the rete mirabile carotis interna sinistra and associated vessels.

0 - artery extending from the RMCI into the ophthalmic area
RAMCr - Rete arteriales mirabile cranis
RMCI - Rete mirabile carotis interna

Fig. B. Association of retial arteries with cranial nerves. Rostral view. Ventral is up in figure.

RAMO - Rete arteriales mirabile ophthalmicus
2 - N. opticus
5 - N. trigeminus
white arrow-heads with black centres - nerves associated with muscles of the eye (N. trochlearis, N. occulomotorius, N. abducens)
white arrows - arteries associated with nerves other than 2.

Fig. C. Ventral view of the rete mirabile carotis interna and its association with the A. carotis interna dextra.

ACID - A. carotis interna dextra
0 - artery extending from the RMCI into the ophthalmic area
RMCI - Rete mirabile carotis interna

Fig. D. As in Fig. C., but at a lower magnification to illustrate extension of the rete mirabile carotis interna into the ophthalmic region.

0 - artery extending from the RMCI into the ophthalmic area
OP - Ophthalmicus
RAMO - Rete arteriales mirabile ophthalmicus
RMCI - Rete mirabile carotis interna
Plate 15. Dissection of the dorsal thoracic wall to illustrate differences between *Delphinapterus leucas* and *Monodon monoceros* in length of the A. intercostalis suprema.

Fig. A. Dorsal thoracic wall of *Delphinapterus leucas*. Retial vessels have been removed.

AA - Arcus aorta  
AaID - A. (aorta) intercostalis dorsalis  
AISD - A. intercostalis suprema dextra  
AISS - A. intercostalis suprema sinistra  
NS - N. spinalis

Fig. B. Dorsal thoracic wall of *Monodon monoceros*. Retial vessels have been removed.

AA - Arcus aorta  
AaID - A. (aorta) intercostalis dorsalis  
AISD - A. intercostalis suprema dextra  
AISS - A. intercostalis suprema sinistra
Plate 16. Anatomical documentation of retial origins from major systemic arteries.

Fig. A. Dissection of the spinal ramus (arrow) of an A. lumbus in Delphinapterus leucas. This vessel supplies the rete arteriales mirabile spinalis.

Fig. B. Origin of retial vessels (arrow-head) from the A. cervicalis profunda dextra of Monodon monoceros.

ACPD - A. cervicalis profunda dextra
ATCD - A. transversa colli dextra

Fig. C. Origin of retial arteries (arrow-head) from the A. cervico-occipitalis sinistra of Monodon monoceros.

AAXS - A. axillaris sinistra
ACES - A. carotis externa sinistra
ACOS - A. cervico-occipitalis sinistra
ASS - A. subclavia sinistra

Fig. D. Origin of retial arteries from the A. occipitalis sinistra of Monodon monoceros.

ACES - A. carotis externa sinistra
ACOS - A. occipitalis sinistra
Arrow-heads - Retial arteries
Arrows - Retial origins
Plate 17. Anatomical documentation of spinal blood supply from the rete arteriales mirabile spinalis in Monodon monoceros.

Fig. A. Ventral view of the medulla spinalis and associated structures. Note small artery (arrow) penetrating the dura mater spinalis. Also note numerous dural branches near the penetrating branch.

DMS - Dura mater spinalis
MS - Medulla spinalis
NS - N. spinalis
RAMS - Rete arteriales mirabile spinalis

Fig. B. Same area as in Fig. A, but with dura excised to show course of the penetrating branch through the dura mater spinalis to the medulla spinalis.

NS - Medulla spinalis
RAMS - Rete arteriales mirabile spinalis

Fig. C. Ventral view of the medulla spinalis and associated structures in the thoracic region. Note branch (arrow-head) originating from the rete arteriales mirabile spinalis and coursing through the dura mater spinalis to the medulla spinalis.

NS - Medulla spinalis
RAMS - Rete mirabile spinalis

Fig. D. Close-up of subdural arteries (arrow-heads) in Fig. C. Note the absence of a prominent A. spinalis ventralis.

V - V. spinalis ventralis
Plate 18. Subdural vessels of the medulla spinalis in *Monodon monoceros*.

Fig. A. Ventral view of medulla spinalis in cervical region. Note arteries (A) coursing through dura and their relation to ventral roots of the spinal nerves.

Fig. B. Ventral view of medulla spinalis and associated arteries (A) and veins (V) in the thoracic region.

Fig. C. Ventral view of medulla spinalis and arteries (A) of supply in the caudal region.

Fig. E. and D. Dorsal view of supply arteries in the cervical region.

Fig. F. Dorsal view of the medulla spinalis and associated drainage vessels (V) in the thoracic region. Note the association of veins with dorsal roots and compare with the location of arteries in Fig. B.

Fig. G. and H. Dorsal view of the medulla spinalis and associated arteries (A) and veins (V) in the caudal region.
Plate 19. Series of dissections to expose vessels supplying the brain and illustrate their mode of origin from the rete mirabile carotis interna in *Monodon monoceros*.

Fig. A. Hypophyseal region of the brain viewed from its ventral aspect. Dura mater encephali is intact. Rostral direction is up in the figure. Arrow-heads indicate the Aa. carotides internae.

H - hypophysis

Fig. B. As in Fig. A., but with the outer layer of dura mater encephali removed to expose the rete mirabile carotis interna. Note the relationship of the rete to the hypophysis, carotid arteries and cranial nerves.

H - Hypophysis
RMCI - Rete mirabile carotis interna
3 - N. oculomotorius
4 - N. trochlearis
Arrow-heads - A. carotis interna

Fig. C. Same area as in Fig. B., but with all dura mater encephali removed. Note the two pairs of subdural arteries that take origin from the rete mirabile carotis interna (removed with dura mater encephali).

AH - Adenohypophysis
NH - Neurohypophysis
RCD - Ramus cranialis (rostralis) dextra
RCS - Ramus cranialis (rostralis) sinistra
RCaD - Ramus caudalis dextra
RCaS - Ramus caudalis sinistra
2 - N. opticus
3 - N. oculomotorius
4 - N. trochlearis
5 - N. trigeminus

Fig. D. As in Fig. C., except that some of the pia-arachnoid is removed to expose major arteries of the brain. Hypophysis has also been removed.

ACC alpha D - A. cerebri caudalis alpha dextra
ACC alpha S - A. cerebri caudalis alpha sinistra
ACMD - A. cerebri media dextra
ACMS - A. cerebri media sinistra
ACRD - A. cerebri rostralis dextra
ACRS - A. cerebri rostralis sinistra
ACe alpha D - A. cerebelli alpha dextra
ACe alpha S - A. cerebelli alpha sinistra
P - Pons
Plate 20. Gross dissection of cerebral arteries in *Monodon monoceros*.

Fig. A. Dorso-lateral view of the brain showing the cortical distribution of the three major cerebral arteries. Most of the dextral cerebral hemisphere has been removed to expose the insula. Rostral direction is up.

ACC alpha - A. cerebri caudalis alpha  
ACM - A. cerebri media  
ACR - A. cerebri rostralis  
CC - Corpus callosum  
HC - Hemispherium cerebrum  
HCe - Cerebellum  
Insula - Insula

Fig. B. Dorsal view of the dextral side of the brain showing the course and distribution of the A. cerebri caudalis alpha dextra (arrow-heads). The ventriculus lateralis dextra has been opened to expose its contents.

CC - Corpus callosum  
HC - Hemispherium cerebrum  
HCe - Cerebellum  
Insula - Insula  
TB - Tentorial branch of the ACC alpha  
PCVL - Plexus choroideus ventriculi lateralis

Fig. A. Gross cross section through the peduncular region of the tail in *Monodon monoceros*. Ventral is bottom in the figure.

CV - Corpus vertebra
RMCa - Rete mirabile caudalis
RMS - Rete mirabile spinalis

Fig. B. Gross cross section through the rete mirabile caudalis in the same region as in Fig. A. (*Delphinapterus leucas*). The rete consists of the Aorta caudalis and associated small arteries.

AC - Aorta caudalis

Fig. C. Histological section of the rete mirabile caudalis in a fetal *Monodon monoceros*. Note the association between arteries and veins.

A - Artery
AC - Aorta caudalis
V - Vein

Fig. D. Histological section of the rete mirabile caudalis in an adult *Monodon monoceros*. As in Fig. C, note the association between arteries and veins. Also note small branches arising from the aorta caudalis.

A - Artery
AC - Aorta caudalis
V - Vein
Plate 22. Histology of the rete arteriales mirabile thoracica.

Fig. A. Cross section of the rete arteriales mirabile thoracica in *Monodon monoceros*.

A - Artery  
F - Fat  
V - Vein

Fig. B. Cross section of the rete arteriales mirabile thoracica in *Delphinapterus leucas*.

A - Artery  
F - Fat  
V - Vein

Fig. C. Cross section of the rete arteriales mirabile thoracica in *Monodon monoceros* to illustrate the association of retial arteries with major intercostal structures.

AI - A. intercostalis  
NS - N. spinalis  
VI - V. intercostalis

Fig. D and E. Cross section of the rete arteriales mirabile thoracica to show its relationship to the pleura (P).
Plate 23. Histology of the rete arteriales mirabile thoracica in Monodon monoceros.

Fig. A. Cross section of retial artery. Arrow indicates elastic fibre in the tunica media. Formalin fixed. Verhoeff's stain.

EEL - External elastic lamina
IEL - Internal elastic lamina
TM - Tunica media

Fig. B. Cross section (1um thick) of retial artery. Arrow indicates elastic tissue in the tunica media. Fixed in glutaraldehyde and osmium tetroxide. Embedded in Epon 812. Stained with toluidine blue.

End - Endothelium
EEL - External elastic lamina
TA - Tunica adventitia
TM - Tunica media

Fig. C. Cross section of retial origin from an A. intercostalis. Fixed and stained as in Fig. B.

AI - A. intercostalis
RAM - Retial artery

Fig. D. Cross section of retial interstitial material. Fixed in glutaraldehyde. Embedded in methyl methacrylate. Stained in hematoxylin and eosin.

A - Retial artery
Col - Collagen
F - Fat
Arrow-heads - Small vessels
Plate 24. Ultrastructure of the tunica intima and tunica adventitia in arteries of the rete arteriales mirabile thoracica in *Monodon monoceros*.

Fig. A. Endothelial cell with glycogen deposit.

GLY - Glycogen
IEL - Internal elastic lamina
L - Lumen
N - Nucleus
SEL - Sub-endothelial layer

Fig. B. As in Fig. A.

Fig. C. Tunica intima showing the endothelium and sub-endothelial layer overlying a fenestrated internal elastic lamina.

End - Endothelium
F - Fenestration
IEL - Internal elastic lamina
SEL - Sub-endothelial layer

Fig. D. Tunica adventitia. Note the alternating layers of elastin and collagen.

Col - Collagen
E - Elastin
EEL - External elastic lamina
TM - Tunica media

Fig. E. Fenestration in the external elastic lamina (arrow-head).
Plate 25. Ultrastructure of the tunica intima in arteries of the rete arteriales mirabile thoracica in Monodon monoceros.

Fig. A. Micro-filaments (MF) in an endothelial cell.

Fig. B. Gap junction (arrow-head) between two endothelial cells.

Fig. C and D. Filamentous material (arrows) in the sub-endothelial layer.

End - Endothelium
IEL - Internal elastic lamina
Plate 26. Ultrastructure of the tunica media of retial arteries in Monodon monoceros.

Fig. A. Tunica media of artery in the rete arteriales mirabile thoracica.

E - Elastin

Fig. B. Tunica media of artery in the rete arteriales mirabile spinalis (cervical portion). Note the large amounts of elastin and collagen.

E - Elastin
Col - Collagen
VSM - Vascular smooth muscle cell

Fig. C. Ground substance in the tunica media of artery in the rete arteriales mirabile thoracica.

E - elastin
Col - Collagen
N - Nucleus
SV - Surface vesicles (caveolae)

Fig. D. Junction (large arrow-head) between two vascular smooth muscle cells in the rete arteriales mirabile thoracica. Small arrow-head indicates basement membrane.

Fig. E. Junction (large arrow-heads) between two vascular smooth muscle cells in the rete arteriales mirabile thoracica. Note the extension of one cell into the other.
Plate 27. Ultrastructure of vascular smooth muscle cells in arteries of the rete arteriales mirabile thoracica of Monodon monoceros.

Fig. A. Glycogen deposit in vascular smooth muscle cell.

Gly - Glycogen  
n - Nucleus

Fig. B. Alpha glycogen particles in a vascular smooth muscle cell.

Fig. C. As in Fig. A.

Fig. D. Vascular smooth muscle cells in tunica media. Arrow indicates junction between two cells.

Gly - Glycogen  
N - Nucleus

Fig. E. Association of glycogen with mitochondria.

Gly - Glycogen  
M - mitochondria

Fig. F. Glycogen associated with a membrane swirl.

Gly - Glycogen  
MS - Membrane swirl
Plate 28. Histology of extra-thoracic retia.

Fig. A. Rete arteriales mirabile cervicalis dorsalis in Monodon monoceros.

Fig. B. Rete arteriales mirabile cervicalis lateralis in Monodon monoceros.

Fig. C. Rete arteriales mirabile cervicalis ventralis in Monodon monoceros.

Fig. D. Rete arteriales mirabile spinalis (foramen magnum) in Delphinapterus leucas.

Fig. E. Rete arteriales mirabile spinalis (C5) in Delphinapterus leucas.

Fig. F. Rete arteriales mirabile spinalis (T7) in Delphinapterus leucas.

Fig. G. Rete arteriales mirabile spinalis (24th vertebra) in Delphinapterus leucas.

A - Artery
M - Muscle
N - Nerve
V - Vein
Plate 29. Comparative histology of carotid related retia in *Monodon monoceros* and *Ovis aries*.

Fig. A. Cross section of the rete mirabile carotis interna in *Monodon monoceros*. Note the large arteries surrounded by fatty connective tissue. Also note the few veins.

A - Artery  
P - Fat  
IDM - Inner layer of dura mater encephali  
N - Nerve  
ODM - Outer layer of dura mater encephali  
V - Vein

Fig. B. Cross section of the rete mirabile epidurale rostrale of *Ovis aries*. Note that the thin walled arteries lie in a venous pool.

A - Artery  
V - Vein (Sinus cavernosus)

Fig. C. Cross section of the rete mirabile carotis interna in *Monodon monoceros*. Note fat.

A - Artery  
P - Fat

Fig. D. Cross section of the rete mirabile carotis interna in *Monodon monoceros*. As in Fig. A, note the fat deposits and few veins.

A - Artery  
P - Fat  
V - Vein

Fig. A to C. Control for method. Test series using rat tail artery (A. caudalis). In Fig. A, the artery has been treated with formaldehyde gas. Note the media-adventitial nerve plexus (arrow-head). Fig. B is the same vessel after treatment with sodium borohydride. Note the reduction in nerve fluorescence. Treatment with formaldehyde gas re-establishes fluorescence (Fig. C).

L - Lumen
TM - Tunica media

Fig. D to F. Control for method. Control series using rat tail artery (A. caudalis). Figures correspond to A, B, and C respectively, except that sodium borohydride was omitted from the isopropanol in Step (2) (Fig. E).

Fig. G to I. Test series. Artery of the rete arteriales mirabile spinalis (cervical region). No nerves are obvious.

TA - Tunica adventitia
TM - Tunica media

Fig. J and K. Test series. Rat tail artery run with vessel in Fig. L and M.

Fig. L to N. Test series. Artery of the rete arteriales mirabile spinalis (cervical region). No nerves are obvious.

TA - Tunica adventitia
TM - Tunica media

Fig. A to C. Test series. Rat vessel processed with artery in Fig. D, E and F.

L - Lumen
TM - Tunica media

Fig. D to F. Test series. Vessel of the rete arteriales mirabile thoracica. No nerves are obvious.

L - Lumen
TM - Tunica media

Fig. G to I. Test series. Rat tail artery processed with artery in Fig. J, K and L.

TM - Tunica media

Fig. J to L. Test series. Vessel of the rete arteriales mirabile thoracica. No nerves are obvious.

TA - Tunica adventitia
TM - Tunica media

Fig. M to O. Test series. Vessel (aorta caudalis) of the rete mirabile caudalis. Adrenergic nerves are indicated by arrows.

TA - Tunica adventitia
TM - Tunica media

Fig. A to C. Test series. Rat tail artery (A. caudalis) processed with the vessel in Fig. D, E and F. Arrow indicates nerve plexus.

**TM** - Tunica media

Fig. D to F. Test series. Vessel (aorta caudalis) of the rete mirabile caudalis. Note nerves (arrows) at the adventitia-media border and within the tunica media.

**TA** - Tunica adventitia  
**TM** - Tunica media

Fig. G to I. Test series. Vessel (aorta caudalis) of the rete mirabile caudalis. Arrow indicates nerve extending into the tunica media.

**TA** - Tunica adventitia  
**TM** - Tunica media
Plate 33. Retial innervation. Fluorescence technique. *Monodon monoceros*

Fig. A to C. Test series. Rat tail artery (A. caudalis) processed with the vessel in Fig. D, E, and F. Arrowheads indicate nerve plexus.

**TM - Tunica media**

Fig. D to F. Test series. Vessel of the rete mirabile caudalis. Nerves are indicated by arrows.

**TA - Tunica adventitia**

**TM - Tunica media**

Fig. G to I. Test series. Vessel of the rete arteriales mirabile spinalis (caudal portion). Nerve is indicated by the arrow.

**TA - Tunica adventitia**

**TM - Tunica media**

Fig. J and K. Test series (minus step 3). Vessel of the rete rete arteriales mirabile cervicalis ventralis. No nerves are obvious.

**TM - Tunica media**

Fig. L and M. Test series (minus step 3). Rat tail artery processed with vessel in Fig. N and M. Arrow indicates nerve plexus.

**TM - Tunica media**

Fig. N and O. Test series (minus step 3). Vessel of the rete arteriales mirabile cervicalis ventralis. No nerves are obvious.

**TA - Tunica adventitia**

**TM - Tunica media**
Plate 34. Retial innervation in *Monodon monoceros*. Ultrastructure.

Fig. A. Longitudinal section of a terminal axon(s) at the adventitia-media border in the aorta caudalis. Varicosities are indicated by the arrows.

Fig. B. Varicosities (arrows) and associated vascular smooth muscle cell (VSM) in the aorta caudalis (adventitia-media border).

Fig. C. Varicosity (arrow) at the adventitia-media border in the aorta caudalis.

Fig. D. Varicosity (arrow) in the tunica media of the aorta caudalis.

M - Mitochondria
NF - Neuro-filaments
VSM - Vascular smooth muscle cell

Fig. A. Terminal axons at the adventitia-media border of an artery from the rete arteriales mirabile spinalis (caudal portion). Arrow indicates a varicosity.

VSM - Vascular smooth muscle cell

Fig. B. As in Fig. A.

Fig. C. Terminal axons in the adventitia of a small artery in the rete mirabile caudalis. Arrows indicate varicosities.

Fig. D. Same nerve (arrow) as in Fig. C, but at a lower magnification to show its relationship with vascular smooth muscle cells of the tunica media.

EEL - External elastic lamina
VSM - Vascular smooth muscle cell

Fig. E. Terminal axon in the adventitia of a small artery in the rete mirabile caudalis. Arrow indicates a varicosity.

EEL - External elastic lamina
VSM - Vascular smooth muscle cell
Plate 36. Retial innervation in Monodon monoceros.

Ultrastructure.

Fig. A. Terminal axon (arrow) in outer layers of the adventitia in an artery of the rete arteriales mirabile thoracica. Note its distance from the tunica media.

EEL - External elastic lamina
TM - Tunica media

Fig. B. Axon in Fig. A. Arrow indicates varicosity.

Fig. C. Varicosity (arrow) in outer layers of the adventitia in an artery in the rete arteriales mirabile thoracica.

E - Elastin
Fib - Fibroblast

Fig. D. Nerve in outer layers of the adventitia in an artery of the rete arteriales mirabile thoracica. No varicosities are present.

NT - Neuro-tubules
NF - Neuro-filaments

Fig. E. Nerve in adventitia of an artery from the rete arteriales mirabile spinalis (cervical portion). No varicosities are present.
Plate 37. Ultrastructural localization of Glucose-6-phosphatase in liver and retial arteries of *Monodon monoceros*.

Fig. A. Hepatocyte. Enzyme specific lead deposition in the nuclear envelope (arrows) and endoplasmic reticulum (er).

N - Nucleus  
M - Mitochondria

Fig. B. Hepatocyte. Enzyme specific lead deposition in the endoplasmic reticulum.

M - Mitochondria

Fig. C to E. Vascular smooth muscle cell of artery from the rete arteriales mirabile thoracica. Enzyme specific lead deposition occurs in the nuclear envelope (arrows).

N - Nucleus

Fig. F and G. Vascular smooth muscle cell of artery from the rete arteriales mirabile thoracica. Enzyme specific lead deposition in the endoplasmic reticulum (arrows).

N - Nucleus  
M - Mitochondria
Plate 38. Electrophoretic profile of LDH isozymes in tissues of *Monodon monoceros*.

**Abscissa:**
- H - Heart (right ventricle)
- B - Brain (cerebral cortex)
- Li - Liver
- Lu - Lung
- R - Rete arteriales mirabile thoracica
- M - Muscle (epaxial muscle)

**Ordinate:**
- H - Heart type subunit
- M - Muscle type subunit

Numbers refer to the proportion of subunits in the isozyme.
Plate 39. Ultrastructural documentation of glycogen deposits in vessels other than those of the rete arteriales mirabile thoracica (*Monodon monoceros*)

Fig. A. Section of the aorta caudalis. Note the glycogen deposits (Gly) in the vascular smooth muscle cells.

Fig. B. Vascular smooth muscle cell in the tunica media of a small artery in the rete mirabile caudalis.

Gly - Glycogen
N - Nucleus

Fig. C. Section of the tunica media of an artery in the flipper (vessel counter current with veins).

Gly - Glycogen
N - Nucleus

Fig. D. Vascular smooth muscle cell in the tunica media of an artery from the rete mirabile spinalis (caudal part).

Gly - Glycogen
N - Nucleus

Fig. E. Portion of a vascular smooth muscle cell in the wall of a small vessel (vein) in the interstitial tissue of the rete arteriales mirabile thoracica.

Gly - Glycogen
Plate 40. Arcus aorta of *Monodon monoceros*. Note bulbous swelling distal to the origin of the coronary arteries.

AA - Arcus aorta
AC - A. coronaria
AT - Aorta thoracica


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APPENDIX 1

G-6-Phosphatase Assay
OUTLINE OF GENERAL PROCEDURE

Thaw samples in ice cold sucrose solution (.25 M pH 7)

Blot dry and dissect out retial vessels from surrounding tissues

Place in pre-weighed tube with sucrose (approximately 1-3 g tissue per 12-14 ml sucrose - note total volume)

Homogenize (Vortex blender - 1 min at 0°C and 600 rpm)

9 parts homogenate + 1 part 2% deoxycholate

Assay for activity

After Nordlie and Arion (1966)
### G-6-Pase Assay

<table>
<thead>
<tr>
<th></th>
<th>Cacodylate Buffer</th>
<th>G-6-P</th>
<th>Dummy G-6-P (H₂O)</th>
<th>H₂O</th>
<th>Enzyme</th>
<th>Dummy Enzyme (sucrose + H₂O + 2% Deoxycholate)</th>
<th>TCA</th>
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<tr>
<td>Sample</td>
<td>.6ml</td>
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<td>.6ml</td>
<td>.5ml</td>
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<td>Control 2a</td>
<td>.6ml</td>
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<td>.6ml</td>
<td>.5ml</td>
<td>100ul</td>
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<td>Control 2b</td>
<td>.6ml</td>
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<td>.6ml</td>
<td>.5ml</td>
<td>100ul</td>
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- Pre-incubate 5 min
- Incubate 10 min 31°C
- Centrifuge 5 min at 2000 rpm
- Zero Time Control

Phosphate Analysis: 1ml sample + 7.6ml H₂O + 1ml molybdate + .4ml reducing agent Read at 660 after exactly 10 min