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A. F. J. K. MAYER: ANATOMY OF THE EYE OF THE CETACEANS. AN ANNOTATED TRANSLATION

By Heiko L. Schoenfuss[1]

It is amazing that the paper presented here has remained almost unknown for the past 145 years, considering the fame of Dr. August Franz Joseph Karl Mayer during his lifetime. Dr. Mayer was recognized early on in his life as an outstanding anatomist. He was born on 2 November 1787 in the Southern German Kingdom of Württemberg and received his formal education through Franciscan monks at the local "Gymnasium" (high school). At the age of 24 he received his doctoral degree in medicine from the University of Tübingen. After a short stay at the Anatomical Institute in the Academy in Bern, Switzerland, he was appointed professor of anatomy and physiology in November 1815. He received a call to the newly formed University of Bonn, Germany and became, at the age of 29, the first director of the Anatomical Institute in Bonn. One of Mayer's priorities as director of the Anatomical Institute was to establish a large collection of anatomical specimens. In 1821 he was able to acquire Johann Abraham von Albers' anatomical collection, which included many of the specimens Mayer used for the paper translated here. He remained the director of the institute for 36 years and received numerous honors, including being knighted by the king of Prussia. Mayer was an active scientist to the very end of his life. Just a few days before his death he was still working on a publication regarding the egg of birds and reptiles. On 9 November 1865 he died at the age of 78 years.

Mayer's personal life was as active and apparently as successful as his academic one. After his first wife died young he remarried and became the

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father of three sons and one daughter. His second marriage lasted until his death and he appears to have been as devoted a father as he was as a researcher.

Mayer's academic drive is illustrated by his many publications, which number over 200 (for a complete account see Meyer, 1966). His publications cover, as was not unusual during his time, numerous scientific topics. Throughout his academic career he was a believer and strong supporter of the theories of the Naturphilosophen, who had one of their strongholds at the University of Bonn. Unfortunately, he never accepted evolutionary theories as valid, thus excluding himself from many of the biological discussions of his time. His fixation on the connection between body and soul and his rejection of any ideas of evolution alienated him later in his life from his students and colleagues. He was, however, a great observer and his papers, including the one translated here, are superb examples of descriptive and comparative anatomy.

After spending much time translating Mayer's publication on "The Eye of the Cetaceans," I feel a great admiration for his outstanding ability to observe and describe anatomical structures under conditions less sophisticated than those available today. Numerous times the author referred to the advancements in light microscopy, which allowed him to observe structures that authors before had missed. Nevertheless, Mayer's high-quality anatomical description, conducted without the help of imaging techniques, high power microscopes, and advanced surgical instruments, deserve special recognition. But this translation is more than a tribute to Mayer's work. It reveals information regarding the eye of cetaceans which has not been described elsewhere. Under these circumstances it is even more astonishing that this publication has remained forgotten for so long. Even a annotated bibliography of cetacean references (compiled in Germany!) (Bekierz, 1986), which contained almost 700 entries, missed Mayer's publication. Much research has been conducted on baleen whales in the last decade, and especially on the bowhead whale, *Balaena mysticetus* (for a review see Burns *et al.*, 1993), but much remains to be done. A recent dissertation re-evaluated the anatomical structures of the eye of the bowhead whale (Qian, 1996) and will certainly add much needed knowledge, but it was Dr. August Franz Joseph Karl Mayer who laid the foundation to the understanding of the eye of the cetaceans.

Information used to reconstruct Mayer's biography came from Schmiz (1920, 1943), Meyer (1966), and Steudel and Meyer (1992).

GUIDE TO THE TRANSLATION

Germany has had a turbulent history which is well reflected in its language. When Mayer's paper was published in 1852, Germany had not yet

approximately 70 kingdoms between the Atlantic and the Alps. Many of these countries spoke more or less different languages with a clear language break between the North and the South, a break which is still evident today. This diversity in the language, combined with a rather vivid style of writing in the 19th century complicated the translation greatly. A final linguistic hurdle is the uncertainty of the German language, which consists of far fewer words than the English language, but allows for more recombination of words to form new expressions. This ability to recombine words contributes to the often numerous meanings to one word.

The translation was further complicated by the limited biological knowledge at the time this paper was written. Charles Darwin had not yet published his ideas on evolution (and Mayer clearly struggled a number of times to explain phenomena, which could have been easily explained by evolutionary theories). The invention of the microscope and achievement of high magnifications, was still in early stages. Leeuwenhoeck (1632 - 1723), the inventor of the microscope, lived less than a century before Mayer. The histological knowledge had, therefore, to be rudimentary, which is indicated by some of his descriptions (e.g. "spheres" = nuclei; "organic fibers" = smooth muscle fibers; etc.). Mayer introduced microscopy at the University Bonn in 1829 as a means for physiological studies.

I did not attempt to interpret Mayer's publication any more than it was necessary to translate it in an orderly fashion. I will leave it up to the reader and his or her expertise to make sense out of some of the descriptions that did not appear very logical to me (e.g., the termination of vascular loops; etc.). I hope that the reader with a deeper knowledge of the anatomy of the eye, will be able to extract information where I was not.

I would like to add a few technical remarks to conclude this introduction:

- Any addition or annotation of mine to the text is bracketed by square parenthesis [ ]. Mayer's original parenthesis remain as round ( ) parenthesis in the text. All footnotes in the text are translations of Mayer's original footnotes.
- I followed as close as possible the *Nomina Anatomica Veterinaria*.
- Nomenclature not present in the *Nomina Anatomica Veterinaria* was altered as little as possible when transferred into English, but was placed in *italics* to signalize its status.
- The term "Ruminant" refers to *Bos taurus, Ovis aries,* and *Capra hircus*. The term "Artiodactyl" refers to *Sus scrofa domesticus* and the ruminants. The term "Perissodactyl" includes *Equus caballus*. The term "Ungulate" includes all of the above.
- Species names are current following Wilson and Reeder (1993).
- Mayer's use of references is sometimes less than perfect. All information given by Mayer is provided in parenthesis ( ) directly following the citation.
- The translation of the measurement units is as follow: 1 "Zoll" = 1

I give the units and measures as provided by Mayer in square parenthesis after their translation. "Zoll" frequently is indicated in Mayer's original with two apostrophes, "Linie" with three. Commas in the original are equivalent to a decimal point. So, [18''',6] means 18.6 Linien (or 18.6 x $^1/_{12}$ inch).

- A number of pages are not included in the translation. I excluded those paragraphs that dealt only with the anatomy of the eye of terrestrial animals. Those paragraphs do not provide any significant information, that has not already been published by other authors. The discussion of the human eye is also excluded since progress in ophthalmology and medicine has long surpassed the information provided by Mayer.
- Two new figures accompany the text. These are meant for the reader to gain a better understanding of the structures described by Mayer. In order to not disturb the organization of Mayer's figures the added figures are labeled "A" and "B", respectively.
- The alert reader will find some discrepancies with the original Roman numerals on Mayer's figures. Apparently, the artist included incorrect figure numbers on some of the original stone plates. The numbers referred to in the text correspond with the Roman numerals in the legends. The reader can, therefore, ignore any Roman numeral on the drawings proper.

I would encourage any reader that experiences difficulties with any part of the translation to contact me for further explanation. I will try my best to supply additional explanations.

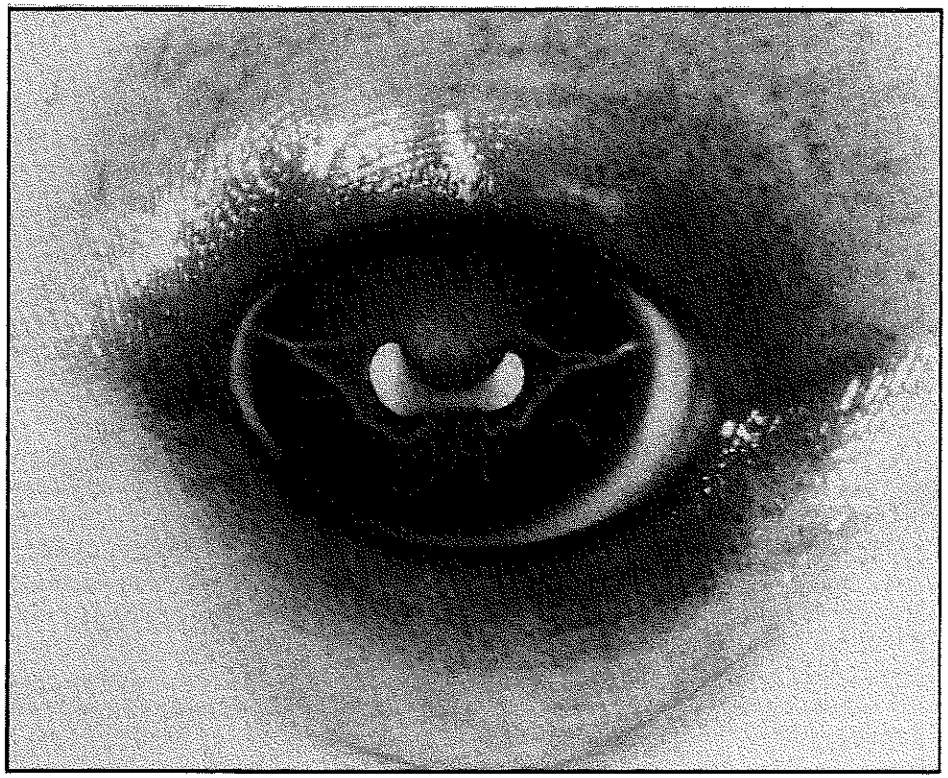

Figure A. Eye of a beluga whale, *Delphinapterus leucas*. The image depicts the horizontal oval pupillae with its dorsal indention. The extensive vascular network of the iris is clearly visible.

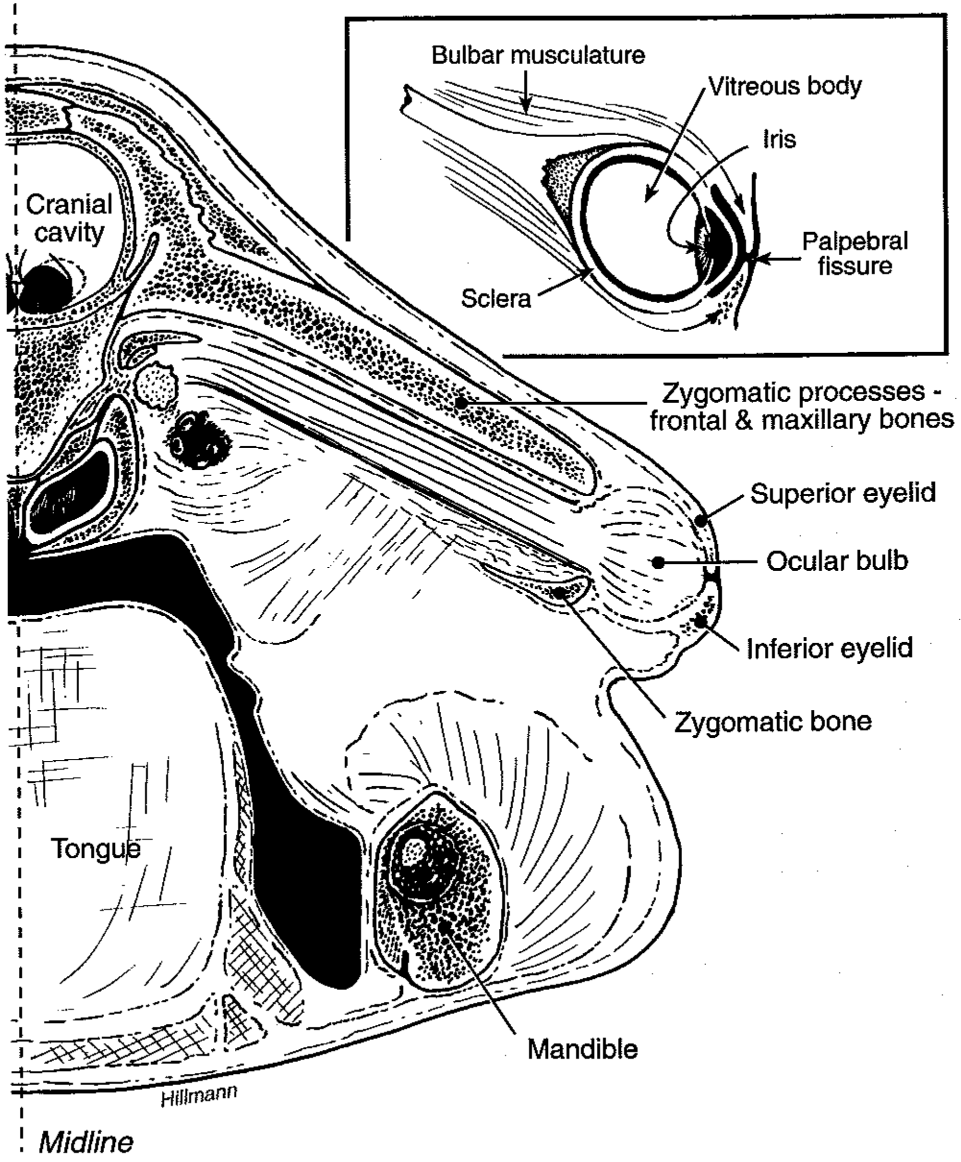

Figure B. Transverse section through the head of a fetal bowhead whale, *Balaena mysticetus*. Caudal surface of section. Inset: Sagittal section through ocular bulb and

THE TRANSLATION

The following is an abbreviated (see explanation above) translation of Dr. August Franz Joseph Karl Mayer's 1852 publication "Das Auge der Cetaceen."

PREFACE

The order Cetacea includes the most diverse, or most divergent body-forms of all mammals. Body-forms vary from the "phoca" [it is very unclear what Mayer meant by "phoca"; one possible interpretation is "seal," since Mayer referred to the seal as *Phoca vitulina*], so similar to the otter, through the plump walrus and manatee (pachyderms), to the shapeless bodies of the dolphins and baleen whales. In the latter we do not even find one of the main characteristics of mammals, the formation of teeth. The distance in body form from the mammal type is also documented in the anatomy of the eye, especially in the whales, and here especially in the mysticete whales. It is not surprising that the nictitating membrane of the eye, which is still present in the dugong [*Dugong dugon*] and the manatee [*Trichechus*], is missing in dolphins and baleen whales. Even though this membrane is present in lower vertebrates, in birds, and terrestrial amphibians it is missing in cetaceans because of their aquatic environment, which is one more analogy of whales and fish.

Even the size of the eye decreases in similar proportions from phocas to baleen whales. In the latter as well as in the manatees [*Trichechus*] and dugongs [*Dugong dugon*], and even in the dolphins we find next to the six muscles of the eye, the four recti and the two obliques, the musculus retractor bulbi, as we know it from ruminants and perissodactyls (see my paper "Beiträge zur Anatomie des Delphins" *in* Zeitschrift für Physiologie by Tiedemann und Treviranus [eds.]. 1834, pg. 124). In the baleen whales (*Balaena mysticetus*) the six regular eye muscles are completely missing and the only remaining muscle is the large, strong, and undivided musculus retractor bulbi [Mayer must have been overwhelmed by the amount of connective tissue surrounding the ocular bulb. All six ocular muscles are present, and there is currently debate over whether even more muscles are present in this area].

It is well known that the size of the eyeball is not proportional to the size of the mammal; this was recognized earlier by anatomists like von Rysch, Hunter, Cuvier, Schreger, W. Soemmerring, Treviranus, Albers, Rapp, and by other anatomists. Even so, the eye of the whale is nearly double the size of the eye of the biggest-eyed mammals, "mammalia macrophthalma," of the horse and deer family (the eye of a horse measures 39.4 mm [18''',6] in axial diameter, and 44.9 mm [21''',2] in horizontal diameter (after

diameter of 42.8 mm [20''',2], and a horizontal diameter of 61.5 mm [29''',0]), it still appears to be smaller than in other mammals compared to its great body size. The eye is also small in large pachyderm animals like the elephants, the rhinoceros, etc., but the eye is large in all ruminants, and in perissodactyls. We have to remember that the size of the eye of the whales is even further reduced if we subtract the thickness of the sclera, which constitutes the actual cavity of the eyeball, the camera vitrea bulbi, which is a third to one-half smaller than the external size of the eye. Therefore, the camera vitrea bulbi of the whale is actually smaller than that of the ox and the horse, with a volume ratio of 13:18, or close to 2:3 in favor of the horse. The camera vitrea bulbi of the whale is greatly compressed in cranio-caudal direction, thus limiting the extent of the corpus vitreum, which is, therefore, smaller than in the animals mentioned above. The lens itself is smaller in *B. mysticetus* than in other mammals. The largest vertical diameter of the lens in the whale is 5:19 the size of the diameter of the camera vitrea bulbi. The lens is somewhat too large in Soemmerring's drawings. We could add that the size of the eye has no proportional relationship to the size of the brain, as it is most prominently documented in the dolphins, which have a very large and extensively folded brain, while the eye is relatively even smaller than in the [baleen] whales. The smallness of the eye, however, does not affect the visual ability, the fire, and the intelligent looks of these animals, as we can see in the small eyes of the carnivores and the intelligent eye of the elephant. [Mayer searched throughout his life for the evidence to link the body to the "soul" of an organism, thus his emphasis on animal intelligence].

This rule can be followed regarding the size of the eye of mammals when no other physiological explanation for the size phenomenon can be found: "The size of the eye increases with the altitude at which the animal chooses its habitat, and with the latitude at which it searches for feeding grounds and food." Therefore, the eye is small in animals living close to the ground or beneath the ground in borrows, and in carnivorous animals (with the exception of nocturnal carnivores, which have to increase the size of the eye to accommodate for the small available quantum of light), especially badgers, moles, mice, and rodents in general. In contrast, the eye is large in ruminants, steer, sheep, the red deer family, which search for feeding grounds on high mountain slopes, and the horse. The eye of the deer and the gazelle is almost the ideal for poets. [Clearly, Mayer is struggling with a phenomenon for which natural selection would have provided a mechanism].

This rule is also consistent with the relationship between the eye of birds and their body size, with especially large and strong eyes in the high flying eagles, the owls (in which, as nocturnal carnivores, the eye is even more pronounced), the long-traveling snipe, the albatross, and other birds.

OF THE DIFFERENT STRUCTURES OF THE EYE

CORNEA AND SCLERA[1].--The connective tissue of the cornea is thick. Towards its periphery it is of a bluish color and contains, therefore, as in some animals, a conspicuous pigmented layer. The connective tissue is white above the cornea and at the sclera. Where the connective tissue reaches the edge of the cornea it forms a bluish-black circle, as in elephants, the rhinoceros, and the tapirs, which can be interpreted as the anulus conjunctivae. The bluish-black fibers of this area of the conjunctiva appear between the fibrous network of the sclera, which connect the sclera to the outer edge of the cornea. Even if the fibers of the conjunctiva are removed the *anulus niger anteriores* is still present. There is also a ring of folds apparent in this position, which can only be seen if the tissue has been dried out.

The cornea in whales is flat-convex, as it is well known for aquatic animals. Albinus states that the cornea consists of two lamellae [he probably refers to the lamina limitans anterior et posterior]. Albers counted more layers and subsequently criticized Albinus statement, but did not realize that Albinus counted the conjunctiva as one of the layers. "Cornea divisa manu" [literally translated: "The cornea was divided by hand"]. The division of the layers is artificial when Leeuwenhoeck (Epistolae phys. Ep. IV.) counted 22 layers of the cornea, while Rapp (Die Cetaceen 1837) only counted 12 layers. The thickness of the cornea is, by any count, substantial. Overall it is rounded and the sclera penetrates only marginally its posterior portion.

It is amazing, as Cuvier stated, and as I saw in earlier preparations in his museum, that the fibers of the sclera invade the cornea in its outer portions. This is the case in the eye of all specimens that I have studied, and not only in one as Albers stated. The fibers invade the layers of the cornea and attach to them, but they do not reach the center of the cornea. These fibers can easily be separated from the layers of the cornea and are visible to the naked eye as shiny white fibers. Under the microscope they appear very different from the fibrous network of the cornea. The layers of the cornea appear under 300 X magnification as delicately striped plates (see Fig. VIII. A.).

The fibers which invade the cornea from the sclera are, as the fibers of the sclera itself, very delicate, stiff, straight or radial fibers.

The sclera with its varying thickness, its fibers, and its canals for passing nerves and vessels is described in sufficient detail by von Rysch, Albers, and W. Soemmerring.

Above, we described the microscopic appearance of the fibrous connective tissue, and we illustrated its appearance internally as a more reticular substantia propria corneae, and externally as leaf-like substantia propria sclerae. Canals in the sclera, which were in the past believed to

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contain two muscles of the whale-eye, are described by Ransome (*In* Journal de Physique. Vol. 91 pg. 158) as leading from the sclera to the cornea, and being attached to the latter. Rapp does not mention these canals, as if he had not seen them. Albers and W. Soemmerring discovered that these canals do not contain muscles, which run through the sclera, but rather contain vessels. The origin of these vessels, their direction and nature, as well as the nerves that accompany them have not yet been investigated. These vessels are nothing else than ciliary vessels. They are regular arteries and veins. This is obvious even with the naked eye, especially in transverse sections in which arteries and veins are readily distinguishable. But these vessels are also accompanied by nerve branches (nervi ciliares). There are two origins for these groups of vessels. The lateral vascular branches, which pass through 2 large and 6 - 8 smaller canals through the sclera originate in the rete mirabile, which surrounds the optic nerve and will be describe later. These bundles of vessels are those arteries and veins which are called vasa ciliares anteriores in the eye of humans and other mammals. While these vessels run in all other mammals freely under the sclera, they are contained in their own canals within the sclera in the whale eye. Two of these *fasciculi vasorum ciliarium anteriorum* are thicker compared to the rest [Mayer refers to the complementary set of arteries and veins as "vasa"]. The two larger canals merge into the anterior group of vessels of the iris, as I will explain in more detail when I describe the structure of the iris.

There are two additional canals in the sclera, an upper and a lower canal. Both begin at the external, caudal end of the sclera and continue in anterior direction. These two canals split into two branches close to the border of cornea and sclera. These two canals contain the *nervi ciliares antices*.

All nerves of the sclera enter through its posterior end, but all lead forward mainly through openings in the iris and some through openings in the cornea into the conjunctiva. Their course can easily be seen as they run between the fibrous network of the sclera and as they leave the sclera rostrally to reach the iris. It is possible to observe some nerve branches leaving the canals forward to penetrate the cornea itself and to reach the conjunctiva.

But there are also posterior, internal bundles of vessels, which directly penetrate the choroidea and which could be described as arteriae et venae ciliares posteriores. There are five or six large bundles and the same number of smaller bundles present. These bundles penetrate the sclera more or less close to the optic nerve and leave it through 10 or 12 openings at its posterior inner surface to reach and penetrate the choroidea.

These perforations form a semi-circle of openings or slits on the internal surface of the sclera. This can be observed after the sclera has been cut in its posterior portion and after the retina and choroidea, to which the retina is tightly connected by vasa ciliares, have been removed. The larger semi-

contains the openings for the nervi ciliares, which also penetrate the sclera and run to the center together with the ciliary vessels (see Fig. VII.)

The entrance of the optic nerve can be found off-center between the first and second third of the frontal diameter of the eye towards the inside. The openings for the arteria et rami vena centralis retinae are visible in the opening but are also slightly off-set.

Four larger openings are visible in the structural center of the sclera, when the sclera is cut in transverse section, which is illustrated in Fig. VII. Two and two opposing each other, one to each side for the vasa ciliares anteriores, and one above and one beneath for the nervi ciliares, which immediately penetrate the iris; there are also two smaller openings present for the smaller nervi ciliares antices.

It becomes obvious in the sagittal section of the sclera, as it is shown in Fig. I., how these more lateral openings lead to larger canals, which are completely filled by the continuation of the rete mirabile.

The vasa ciliares anteriores, namely the two that were described above in their canals in the sclera, leave the sclera rostrally in a medial direction close to the border of the cornea, where they run in a groove on the medial aspect of the sclera. Once they have left the sclera they penetrate the choroidea laterally and immediately lead into the iris. In the iris they form the vascular networks at the periphery of the anulus iridis major, and create the *pupillary sinus*. These two vessels are illustrated in Fig. II., which documents how they merge with the vascular network of the vasa ciliares posteriores of the iris. In this illustration one vessel is especially prominent. I named this vessel, which runs oblique to the outside border of the anulus iridis minor, *circulus venosus pupillaris*.

I studied a larger bundle of the posterior ciliary vessels in a transverse section to gain more insight into the relationship of arteries and veins. We can observe 6 - 9 vessels cut in the transverse section, 2-3 of the smaller ones are arteries, while 4-6 are veins, which are each accompanied by a nerve. The other vascular networks of the iris, the vasa ciliares posteriores, penetrate, as mentioned earlier, the choroidea and then immediately lead to the iris. The nerves that accompany this vascular bundle are the *nervi ciliares posteriores*. They penetrate the choroidea more posteriorly through the sclera.

The *anulus niger* is prominent on the medial surface of the cornea, as is the *Canal of Fontana* between the *anulus niger* and the ciliary band.

ORBICULUS CILIARIS.--At the outer edge of the iris at its border towards the choroidea, a bulging layer of circular fibers is situated. This layer consists of 12-15 thick, wide fibers, which form a musculus sphincter pupillae. This structure is situated just posterior to the *anulus niger corneae*, where in humans and other animals the orbiculus ciliaris or the *ligamentum ciliare* can be found. The musculus sphincter pupillae is covered with a serous

considers this membrane to be of serous character], which covers the vascular network of the choroidea. Each fascicle of this muscle consists of some smaller bundles, as it can be seen under the microscope at 300 X magnification. Each bundle contains small spherical structures, which can be observed along the muscle fibers as well as perpendicular to them, and which gives the fascicle as well as each muscle fiber a striated appearance or an appearance of a *fibrae transversales* [Mayer is not aware of the intracellular structure of skeletal muscle]. This muscle is a type of circular muscle, which substitutes for the *ligamentum ciliare* (see Fig. II.). The musculus sphincter pupillae is covered externally by a thin sheath, which I believe is a continuation of the lamina fusca sclerae (see Fig. II. a.). It is well known that the orbiculus ciliaris is well developed in birds.

From the most medial bundles of this brown arrangement of circular fibers (musculus sphincter pupillae) or circular muscle originates a large number of thin threads which descend into the disk of the iris and form a delicate network between the vessels of the iris. This network can be observed continuously to the margo pupillaris. In many places they are not distinguishable from the capillary and nervous networks. These fibers form the analog of the fibrous layer that is present in most other mammals and man peripheral to the vascular layer of the iris.

I will describe next the ring of nerve ganglia, which is situated in birds in the *ligamentum ciliare* or in its muscle, and which I have already described for these animals in 1830 (*In* Bericht über das anat. Institute Bonn 1830. pg. 18. no. 14.). It is also well developed in the eye of the whale.

The orbiculus ciliaris of the human eye is generally considered to be of cellular-fibrous structure. Hyrtl distinguishes between two layers, a cellular layer, the *orbiculus ligamentosus*, and a layer consisting of the network of nerves and some ganglionic structures, the *orbiculus gangliosus*. But there is no cellular layer present in it and its fibers are very different and unusual in their structure. In humans and mammals it is not a real *musculus ciliaris*, as it was named by Todd and Bowman, or a constrictor muscle of the choroidea as it was named by Bruecke. It needs also to be remarked, that the direction and position of its fiber bundles is different in mammals than in man. We do not yet have a detailed description or illustration of the appearance or direction of the fibers of the orbiculus ciliaris in man or in mammals. The orbiculus ciliaris forms in man in some places a network of yellowish bundles, which appear to be similar to a plexus of "soft" nerves when observed at 2-6 X magnification. This would explain why Lieutaud (Essays p. 128) saw in it a plexus nervosus. Soemmerring (Abbildung des Auges p.75) also said: "It appears, therefore, that this ridge of the vascular layer is formed by a nerve node or ganglion, which is the result of fused nerves." This structure has indeed similar thick, straight, yellowish bundles, which at 10 X magnification, have the same appearance as the network of nerve branches of a ganglion. The bundles of the orbiculus ciliaris are, however, not branches of

of yellowish fibers. The nerves are too small to be seen clearly at 2 - 3 X magnification. The fibers of these parallel bundles in man appear at 240 X magnification as if they were formed by aligned spheres, which give them an appearance even more similar to the muscle fibers in the eye of the whale. These bundles frequently form some kind of yellowish colored network, comparable to the trabeculae carneae of the heart. These bundles are mainly of fibrous character in the orbiculus ciliaris of larger mammals, e.g. the ox, where they form thin light colored threads without spheres. In larger mammals these fibers and the whole bundle are not straight and parallel to the axis of the eye, but are rather circular and follow closely the circular ligament. The larger and thicker bundles in horses are somehow striated due to the spheres interspersed between them.

In birds the orbiculus ciliaris is definitely muscular and was described earlier by von Crampton as an independent muscle. This muscle of the bird eye that von Crampton (1815) discovered was first seen in our group as a muscle by Trevianus (1846). Trevianus believed, as did later Krohn (1837) and more recently Bruecke (1846), that the muscle, which was described by von Crampton as well as the muscle of the iris are both of striated nature. The iris itself, however, has even in birds no striated muscle fibers, but has smooth, light colored, organic fibers, which are lined by pigment. Only in the uvea [or tunica vasculosa bulbi] behind the iris do we find circular fibers towards the pupil, as in man, and only those are striated in birds and are real muscle fibers.

Bruecke (Müller's Archiv 1846) believes in another muscle, in addition to von Crampton's muscle, which acts as tensor of the choroidea, the *musculus tensor choroidea*. But what would be the use of a tensor of the choroidea? The orbicular-circular fiber ring is, in my observation muscular in birds and plated amphibians, while it consists of organic fibers in man and mammals. The orbiculus ciliaris consists in birds, the plated amphibians as well as some mammals, of longitudinal fiber bundles, while it consists of circular bundles in other mammals. By the latter is a function of this structure as tensor of the choroidea impossible [it is impossible from Mayers account to specify to which species he is referring]. I believe that it is the function of this muscular or fibrous ring to constrict the iris, to compress the corpus ciliare and the inserted zonula ciliaris, and to move the iris forward. This function would be consistent with the longitudinal and circular direction of the fibers of this ring.

The muscle discovered by von Crampton consists of two portions. The rostral portion is smaller and is located at the outer edge of the iris, while the medial aspect of the muscle is wider and attaches to the lamina fusca sclerae. In between the two portions is situated a large sinus, or *Canal of Fontana,* which is filled with cellular tissue. The latter, wider portion of the muscle was named *musculus tensor choroidea* by Bruecke. It has the two mentioned attachments and acts as a constrictor of the corpus ciliare, in front

of which the muscle is located. The smaller, rostral portion acts in focusing the iris and pulls it forward.

The fibers of the orbiculus ciliaris have a different direction in birds than they have in mammals. In birds the direction of the fibers is longitudinal from rostral to caudal, while in mammals these fibers have a circular direction and run from right to left or vice versa. The human eye displays, in this respect, a similarity to the bird eye as mentioned earlier. The striated muscle bundles of the orbiculus ciliaris as they are appear in the Lammergeyer [*Gypaetus barbatus*], *Meleagris gallopavo*, etc., at 240 X magnification has been illustrated in Fig. VIII. G. In *Gypaetus barbatus* the striation of the muscle clearly forms a spindle-shaped structure, which I believe is an optic illusion in muscle fibers as well as in nerve fibers. This is in contrast to Barry, who believes in the true nature of this structure.

Within the amphibians, such as *Caretta caretta*, the orbiculus ciliaris appears as a network of yellowish nerve fibers following a longitudinal course, similar to the condition in birds.

IRIS.--The iris forms an ellipsoid pupil with its long axis in a horizontal direction, in contrast to the illustration by Albin. Its inner edge is slightly serrated, not straight. The anterior surface of the iris is hardly covered by a fibrous layer, but immediately reveals the outer, considerably larger anulus iridis major, which consists of well developed, thick and serpentine loops of blood vessels with a delicate network of interconnecting vessels and accompanying nerve fibers. The much smaller inner anulus iridis minor reveals similar loops of blood vessels[2]. The inner ring illustrates more clearly than the outer ring a delicate fascia, which is the continuation of the *Membrana Demoursii*. This membrane is covered by a delicate, unique network of branches, which are actually a network of nerve fibers, as I will demonstrate later.

The vascular network of the iris deserves primary attention. These vessels have, as mentioned above, two origins. First, the vasa ciliares, which come from the choroidea and pass through or underneath the musculus sphincter pupillae. Its vessels are arteries as well as veins, which, upon arrival at the iris, split into blind loops that end at the edge of the *anulus externus*. Second, the two earlier described lateral vessels, vasa ciliares anteriores, which unite at the inner edge of the iris with the vessels of the vasa ciliares.

The large number as well as the thickness of the nerves of the iris is an unique and astonishing phenomena in the eye of the whale, as it was already emphasized by Albin and later by Treviranus. The array of nerves in the iris

2 A larger outer ring and a more delicate inner ring can be found not only in the iris of humans and animals, but also in the *ligamentum ciliare*, with a prominent anterior ring,

is accompanied by the thickness of the retina in the whale eye and finally with the large volume and the extensive convolution of the brain of these animals.

The nerves of the iris follow the same course as the blood vessels. Not only is their number impressive, but so is their thickness. I counted approximately 40 stems, which form a well developed nervous network with each other. From this nervous network originate the nervous branches, which travel through the *ligamentum ciliare* or the musculus sphincter pupillae, and into the iris (see Fig. II.). Within the iris a number of nerves, which have ganglia interspersed, are anastomosing.

At first sight, it appears as if every larger nervous branch contacts the surface of the arteries of the iris and then disappears, because of the white color of the lining of these vessels. Under the magnification of a microscope it becomes apparent that these nervous branches follow between the loops of the blood vessels, supply the loops with delicate branches, and form deep between them a nervous network with numerous ganglia. The nerves then form loops to approach the neighboring nervous branches and anastomose with them. From these nervous loops originate small branches, which pass over the vascular loops and penetrate to the inner ring, the anulus iridis minor, where they form a well developed network of small nerves. This network of small white threads, which can be seen with the naked eye on the smaller inner ring of the iris, especially in the corners of the horizontal-elliptic pupil, is formed by the nerves which lie between and under the vascular loops, which support the nerves. The nerves on top of the blood vessels are easily distinguishable from blood vessels due to their white color and their prominent folds.

In the whale eye the nerves of the iris are not only thicker, but also display many fibers, which are frequently swollen because of the presence of numerous ganglia, which form the well developed ganglionic networks, as illustrated in Fig. III. (60 X magnification) and in Fig. IV. (140 X magnification).

After the nerves of the iris have supplied the musculus sphincter pupillae, or the orbiculus ciliaris, and maybe even the longitudinal and circular fibers of the uvea below, as well as the arterial loops of the iris, these nervous fibers finally terminate towards the margo pupillaris. The termination of these nervous fibers, as is the case in other organs, occurs by means of terminal loops or networks, which are especially prominent in the strong anastomoses or thick nerve loops close to the margo pupillaris (see Fig. IV.). The nerves of the iris have, in my opinion, two different endings to them, as is the case in many other organs. Some nervous branches form strong, returning loops. Others penetrate the organ and terminate with their neurolemma in the fibrous fascia of muscle fibers while their neuroplasma terminates in the spheres of the muscle fibers.

The posterior surface of the iris, the so called uvea, consists of two

layers consists of wide, delicate, longitudinal fibers, which extend from the outer edge of the uvea, from the margin of the corpus ciliare, to the margo pupillaris. Underneath this layer of longitudinal fibers appears in anterior direction at the anulus iridis minor a layer of delicate circular fibers, which form a secondary, medial sphincter muscle, the musculus sphincter posterior pupillae. The longitudinal fibers, which could be interpreted as musculus dilatator pupillae, appeared under the microscope as flat longitudinal bundles, with interspersed pigmented fibers and pigments. The fibers do not display any striation[3]. The circular fibers of the musculus sphincter posterior pupillae, which I interpret as musculus contractor, are also without striation and are, therefore, organic [smooth] muscle fibers. Rapp had already stated that these fibers appeared to be muscular, but only the microscopic analysis could provide proof.

It becomes clear from the description of the iris that in the whale eye it is a wide-meshed structure, which is unique in its consistency and structure when compared to all other mammals. We find in the iris of baleen whales all the structural elements united as it is not found in the eye of man or any other mammal. It is well known that the nerves and fibers (muscular fibers) of the iris are still controversial among anatomists. The nerves of the iris of man, which, as I mentioned, are so clear and large in the whale eye that they can be seen with the naked eye, are still only recognized by a few anatomists, which were able to distinguish them from vessels, and here mainly the arteries of the iris.

The presence of nerves in the human iris has already been suggested by Zinn. Zinn probably confused them, however, with the arteries of the iris, since the nerves are only visible under at least 60 X magnification, which he probably did not use. Von Soemmerring, J. Weber, Eble, v. Ammon, and others considered nerves of the iris as either not present, or doubtful. A few good observers denied the existence of nerves of the iris altogether. F. Meckel stated that he saw the ganglia of the nerves of the iris in man (see his Anatomie IV. p. 86.). My statement with regard to Zinn might be true as well for Meckel. He did not study the iris at a magnification of 120 - 300 X, which is necessary to observe the ganglia and delicate terminal fibers. Arnold (Tab. anatomicae Fasc. II. Tab. II. Fig. 22) illustrates nerves of the iris of man at a magnification of 2.5 X. Nerves of the iris are not visible at this magnification and he must have observed blood vessels. Bruecke observed threads that lead to longitudinal and circular fibers. But those are missing in man and their nerve fibers are almost invisible. In general, anybody who claims to have seen thick nerve fibers on the anterior surface of the iris,

3 The longitudinal and radial fibers appear in the walrus, in other mammals, and in man as a ring of folds surrounding the uvea, as I will describe later. This ring of folds might

confused the nerves with arteries, as did the person who described them at 2.5 X magnification and even drew them.

These nerves are only visible at significant magnification and are very delicate, but are still formed by networks with some small nodes interspersed. In animals these nerves of the iris are much stronger, but often nearly invisible on the outer ring of the anterior surface of the iris due to the circular fiber bundles. In birds these nerves also are nearly invisible on the anterior and even posterior surface of the iris, due to the inner pigmented layer. In amphibians and fishes, however, the nerves are of considerable thickness. In *Caretta caretta* 6 - 8, thick nerves emerge from the choroidea and form an anastomosing network in the ligamentum ciliare, and then radiate into the iris where they end in terminal loops. In the ray (*Raja*), the nerves of the iris are visible with the naked eye. They extend in bundles across the iris and extend to the margo pupillaris.

This list illustrates the abundance of nerve fibers of the iris even in less developed taxa of the animal kingdom. The richness in nervous supply becomes even more prominent when we look at the ratio of nerves to muscle fibers in the iris. Even in man the presence of muscle fibers in the iris is still in dispute while the nerves and their nodes are clearly visible. How different in comparison is the heart, another involuntary muscle, when we look at the iris as a sphincter muscle. The heart has only a few nervous branches in man, some more in ruminants (I also found strong cardiac nerves in the narwhal. see S. Analecten I. p. 68.), and few in birds, amphibians and fishes. The heart of a large sturgeon, which is comparable in size to the heart of a newborn child, has only very delicate nervous branches.

In regard to the function of the orbiculus ciliaris, I have to add that its function must be different since the direction of its fiber bundles differs. When these muscle fibers are circular, as in baleen whales and most mammals, then they will act to constrict the pupil as a musculus sphincter pupillae. If they run, however, from posterior to anterior as in humans, primates, the birds, and amphibians, then they will be dilators of the pupil as a musculus dilatator pupillae. Maybe they could even be named a tensor of the iris, or *tensorem iris*, but not as Bruecke suggested a *tensorem choroidea*. I would like to add an observation I obtained when separating the orbiculus ciliaris from the sclera. A canal formed, due to the duplication of the lamina fusca sclerae, or *Membrana Demoursii*, which I did not mention earlier, because this canal, which is called the *Canal of Fontana*, is commonly found in all mammals.

All the "schoolbook-knowledge" of the muscle fibers of the iris, the contractor muscles, and the musculus dilatator pupillae, is largely hypothetical and unproven. In the human iris the presence of circular and longitudinal fibers on its anterior surface was suggested, but these were always confused with the veins and arteries of the iris. There are circular fibers present on the anterior surface of the iris, but not longitudinal fibers. In

anterior surface of the iris, but on the posterior surface, which is called the uvea. Here we find the described layers of non-striated circular and longitudinal fibers. The circular fibers form a sphincter muscle, while the longitudinal fibers form a musculus sphincter posterior pupillae. In man, who has a very sensitive eye, the iris forms on its posterior surface, around the pupil, the anulus iridis minor. A structure of weak, yellowish-reddish fibers, which are circular, very thin, and pigmented. This structure is the moveable, contractile element of the human iris. These fibers are only visible at 240 X magnification, and appear to be of delicate grain - not smooth and light colored.

It is assumed, especially in larger mammals, that there are on the anterior surface of the iris thicker circular fibers or circular bands, and folded circular bundles, which lay beneath the *Membrana Demoursii* and the pale or colored pigmented layer which is enwrapped by it. In ruminants, which have a horizontally elliptical pupil, these folded circular bundles insert on two lateral ligament-like strings [veins]. In wild cats, which have a vertically elliptical pupil, these bundles insert on a dorsal and a ventral string. The bundles are formed by rather dense, serpentine, clear, grain-less, non-striated and, therefore, organic [smooth] fibers. I will present more details in the following chapter on the description of the iris of animals.

CHOROIDEA.--The choroidea consists of four layers. The stratum vasculosum, or *choroidea vasculosa*, constitutes the outer thick layer, which connects to the sclera by means of the earlier described vasa ciliares posteriores. The lamina fusca sclerae is situated between the stratum vasculosum and the sclera. The lamina fusca sclerae becomes stronger in the anterior direction, as we have seen before at the transition to the *ligamentum ciliare*.

The tissue of the stratum vasculosum is, as it was mentioned earlier, only a continuation of the rete mirabile and consists of a network of arteries and veins with only two places at which the vasa vorticosa is prominent.

The blood vessels of the choroidea form networks, but are by no means as well developed as in the vascular loops and twists (vasa vorticosae) of the human eye, and other mammals [a vasa vorticosae as part of the plexus ophthalmicus is present in the carnivorous and ruminant mammals]. The blood vessels of the choroidea run straight in the anterior direction, similar to the straight vessels in the human eye, and form only slightly serpentine rows of vessels. Externally, these vessels are mainly veins, while the more medially arteries branch in a similar pattern as did the veins. This is also the case in the eye of the horse and the ox, etc., where there are no coiled veins present, but where the arteries run in serpentines between bundles of two to three veins in anterior direction. Some of these veins anastomose with the arteries, while others continue and flow into the circular sinus of the orbiculus ciliaris.

The second layer of the choroidea is the *Membrana Ruyschiana*, which can easily be separated from the former. It has a bluish-whitish opalescent color and shine and, therefore, resembles a tapetum [lucidum]. This membrane appears under 240 X magnification as a mainly fibrous tissue formed by delicate straight, bent, or C-shaped fibers, which are very similar to elastic fibers (which is similar to observations I made on the eye of other mammals, specifically the ox and the deer) [following Mayer's description this tapetum lucidum could be referred to as tapetum fibrosum, as in ruminant and equine species]. I call these fibers iridescent fibers (see later). Within the same tissue another tissue is apparent which consists of flexed cones with large, oval, granulated cells dispersed between them. On top of this layer a thin pigmented layer is situated. The pigment cells contain pentagonal or hexagonal pigments, which are delicately granulated and contain nuclei[4]. Therefore, the choroidea consists of four layers. First, the thick outer layer, which is formed by the vascular loops of the ciliary arteries and veins. Second, the cellular fiber layer. Third, the layer which contains the numerous oval cones, which appear hollow, or only filled with dust, and which radiate from oval central cylinders of the *Membrana Ruyschiana*. And fourth, the layer formed by the hexagonal, granulated pigment cells.

CORPUS CILIARE.--The corpus ciliare is well developed. It consists, as in humans and other mammals, of a double row of folds. The posterior row of folds is taller and thicker, while the anterior row of folds is lower and smaller and interdigitates with the posterior row. A total of 100 longer and shorter folds can be counted. Towards the end of the fold, proximal to the pupil, both folds increase, become tubular, and bear grayish colored nodes on their surface. These nodes, *flocculi*, appear under the microscope as well developed gyri of vascular loops, which are similar to those of the iris and are heavily pigmented [see Fig. V]. This condition is similar in humans, where the *flocculi* of the corpus ciliare consist of well developed vascular loops in which 9 - 10 vessels come together in one loop.

LENS CRYSTALLINA.--The crystal lens is round, as is well known. Albers accounted a ratio of axial diameter to longitudinal diameter of 13:15. The lens consists, as in other mammals, of two golden shining layers, which easily separate when immersed in spirit of wine [ethanol]. They become denser towards the center of the lens. The fibers of the lens consist of delicate, slightly oval shaped spheres in a pattern which makes the lens appear to be slightly indented, but not serrated. The capsule is fairly dense.

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4 Another pigment consisting of round spots, can be found in the parenchyma of the tapetum as round spots. I generally differentiate between two types of pigments: The first pigment is the inner, parenchymatic pigment, which appears as dots, spots, flames

The zonula, or *corona* ciliaris around the crystal lens is wide but thin. The folds of the zonula ciliaris are as long as those of the corpus ciliare. This ring of folds is attached to the capsule of the lens by a dense and strong fibrous ring.

The corpus vitreum is wide, but small in anterior-posterior direction, which gives it a lens-like appearance. The *Membrana Hyaloidea* is rather strong.

RETINA.--The retina forms a thick, bulging membrane. It was impossible to discriminate any structural components in the retina, since it was nearly coagulated, due to the long storage in spirit of wine [ethanol]. I was not able to find a distinct *Membrana Jacobi*.

It is possible with magnification to discriminate the mark, which contains spheres, delicate fibers, and additional ganglionic spheres with a diameter between 0.002 mm [0.001'''] and 0.064 mm [0.03''']. These ganglia are contained in wider band-like fibers and enclose nuclei and pigments. The cubical, small crystals, which can be seen on the retina as well as on all other structures of the eye, are artifacts from the spirit of wine in which the eyes were permanently stored.

RETE MIRABILE.--The fibrous tissues of the sclera are commonly referred to as a continuation of the fibers of the dura mater, which surrounds the optic nerve. This view, however, is wrong, as becomes especially apparent in the whale eye. The sclera begins independently and isolated with its network-like white fibrous tissue, while the dura mater or fibrous sheath of the optic nerve [vagina externa et interna nervus optici] ends where the optic nerve narrows. The sheath of the optic nerve also consists of strong circular fibers and not of a network of fibers. The sclera and the fibrous sheath of the optic nerve are further separated by the rete mirabile, which continues into the lamina vasculosa of the choroidea. Therefore, it is not possible to refer to the sclera as a continuation of the dura mater of the optic nerve. In addition, we also find a fibrous sheath, consisting of strong, white, serrated bundles (which will be described later), which surround the rete mirabile of the optic nerve. It has such an intimate connection with the sclera, that its fibers are immediately continuous with the outer fibrous layer of the sclera, which, at least peripherally, is also concentric. The optic nerve is in addition surrounded by yet another fibrous layer, which can be separated from the optic nerve, or more specifically from the mark of the optic nerve, which runs in a hollow canal. It could be thought that this inner, fibrous membrane would be continuous with the inner lamellae of the choroidea, the so called *Membrana Ruyschiana*, even though its penetration by the optic nerve through the so called foramen cribrosum [area cribrosa sclerae] is smooth and can easily be separated from the fibrous membrane.

Now is the time to mention the size and development of the large *rete*

is 63.6 mm [2 Zoll 6 Linien], its cross-sectional diameter measures 55.1 mm [2 Zoll 2 Linien] anteriorly, and posteriorly it measures just 12.7 mm [6 Linien], thus having a funnel-shaped appearance. It consists of a network of thick veins with numerous anastomoses and of less frequently anastomosing arteries. The transition of these bundles of vessels of the rete mirabile into the canals of the sclera or the choroidea was discussed earlier.

THE EYE OF OTHER CETACEANS

WALRUS, *ODOBENUS ROSMARUS*.--The above description of the eye of *Balaena mysticetus* is based on a specimen that belonged to the collection of Dr. Albers from Bremen, which I acquired in 1823, and on a specimen from the Anatomical Museum of the Botanical Gardens of Paris [France]. The numerous treasures of the Paris collection, which were mainly collected by Cuvier, the great comparative anatomist of our century and also my honorable mentor, were opened by him to myself and Oken with the greatest possible liberty. Dr. Albers described the gross anatomical features of the eye of the whale in his 1810 publication for the "Physikalisch-Medizinischen Gesellschaft zu Erlangen."

Within Alber's collection of whale eyes was also a glass container labeled "Augen von Trichechus Rosmarus, Penis, etc. desselben" ["Eye of *Odobenus rosmarus*, penis, etc. of it"]. When I studied the contents of this jar in greater detail I discovered that the eye in this container must have belonged to a baleen whale. I also discovered that the supposed penis of the walrus was only an inverted piece of whale intestine. The supposed eye of the walrus was slightly different in its appearance from the eye of *Balaena mysticetus* or *B. groenlandica* [*B. groenlandica* refers to the same species as *B. mysticetus*, the bowhead whale]. Its diameter in the ventral-dorsal axis measured only 50.9 mm [2 Zoll], 44.5 mm [1 Zoll 9 Linien] in its cross-sectional diameter, and only 21.2 mm [10 Linien] in its axial diameter, while the average eye of *B. mysticetus* measures 72.1 mm [2 Zoll 10 Linien] in the ventrodorsal axis, 63.6 mm [2 Zoll 6 Linien] in its cross-sectional diameter, and 21.2 mm [10 Linien] in its axial diameter. The pupil was oval with its long axis in a horizontal direction. The uvea reveals a ring of folds, which extend to the pupil, beneath the thick pigmented layer. All other features of the eye were similar to that of a baleen whale.

Another jar with the label "Auge etc. des Walross" ["Eye etc., of the walrus"] of Alber's collection had been transferred to the anatomical museum in Berlin at the time when I acquired the collection. I asked now Mr. Geh. Med.-Rath Müller to send me this eye to allow me further studies, which he did with his usual friendliness.

The latter eye was very different in size and structure from the eye of baleen whales. It measures 25.4 mm [1 Zoll] in its ventrodorsal diameter, and

compressed along its anterior-posterior axis. The sclera measures only 3.2 mm [1.5 Linien] at its central, thickest spot, and becomes even thinner anteriorly as well as posteriorly. Its fibrous tissue is only little developed, but the vascular canals are still barely visible in it. The cornea is flat. The optic nerve is thin and its fibrous sheaths are hard to detach. There is an obvious swelling at the location where the optic nerve penetrates the sclera. The vasa ciliares posteriores and *nervi ciliares posteriores* have their openings around the entrance of the optic nerve. The vasa ciliares anteriores and *nervi ciliares anteriores* exit the sclera in anterior direction through longitudinal rows of openings to both sides of the optic nerve and before entering the choroidea they come together as a complete circle. The choroidea is black. The *Membrana Ruyschii* of the choroidea has the reflection of a tapetum. The iris is brown, smooth, bulging, and has no visible nerves. The orbiculus ciliaris has circular bands and its ciliary nerves are delicate. The corpus ciliare is wide. The ring of folds of the uvea extends nearly to the margo pupillaris. Lens and corpus vitreum were missing. The retina is relatively thick.

The walrus, therefore, is positioned, judging from the structure of its eye, between the dolphins and the phocas.

NARWHAL, *MONODON MONOCEROS*.--The eye of the narwhal, *Monodon monoceros*, is built along the same line as the eye of the baleen whales. Albers has described it briefly and illustrated the eye of the narwhal in a paper of the Society of Erlangen [The "Physical-medical Society of Erlangen/Germany"]. Stanius found the ring-like tear gland in the eye of the narwhal. I believe I can add the following information:

The eyeball, which measures just 1/4 the size of the eyeball of the baleen whale, has a rete mirabile of comparable size around its optic nerve. The optic nerve forms at its entrance into the sclera a node as it is found in dolphins. The cavity of the eye is even more compressed in its anterior-posterior axis than it is in the case of the eye in baleen whales. The anterior-posterior diameter measures only 10.6 mm [5 Linien], the horizontal diameter measures 27.6 mm [13 Linien]. The sclera is very thin towards the cornea, in the middle and posterior aspect 3.2 mm [1 $^1/_2$ Linien] thick, and becomes again very thin around the optic nerve. The cornea is flat and exhibits the anulus niger externus et internus. The fibrous tissue is similar to that in baleen whales and its fibers also penetrate between the layers of the cornea. The canals of the sclera as well as the posterior ciliary vessels are little developed. The choroidea is brown, its tapetum is narrow and only extends to, but does not overlap, a 6.4 mm [3 Linien] wide ring anterior to the choroidea. The corpus ciliare with its posterior network-like ring of folds and its anterior folds is little developed. The vessels of the choroidea form parallel running longitudinal networks. The ciliary fibers of the orbiculus ciliaris are numerous and fragile. The pupil is oval with a horizontal long

thick vascular loops, which extend from the *appendix iridis* in the middle of the oval pupil to pass to the outer margo pupillaris. The inner ring is mainly smooth. Nerves are scarce and delicate. The ring of folds of the uvea is delicate. The pigment is black. The inner ring contains no well developed circular fibers. The vasa ciliares posteriores forms no fascicles as in the baleen whales.

DOLPHIN, *DELPHINUS DELPHIS*[5].--Its eye, even though much smaller, is overall built in the same way as in baleen whales. The pupil is also oval in shape with a horizontal long axis. The optic nerve, in contrast to the baleen whales, first narrows, then forms a node when it enters and passes through the sclera. The optic nerve is also surrounded by a well developed rete mirabile. The fibers of the sclera, which are thin anteriorly and posteriorly, but thicker in the middle, are also yellow and brittle. They appear to have relatively wider spaces in-between them. These fibers also disappear while radiating into the cornea. There are 2-3 posterior vascular bundles present, which are already covered with a blue coat while passing through the sclera. The two openings for the anterior ciliary nerves are also present, but are positioned more laterally. The tapetum is extensive. The *Membrana Ruyschiana* cannot be separated. The membrane has a porous appearance, which is caused by the presence of black pigmented nodes. The nerves of the iris are relatively as strong, well developed, and numerous as in the baleen whales. These nerves also exhibit many swellings. The *musculus externus iridis*, which I named as a substitute for the *ligamentum ciliare*, appears with strong circular bundles. The nervous bundles in its course are as well developed as in the baleen whales and also exhibit similar ganglionic swellings. The vena ciliares anteriores, which also exits the iris laterally and continues on the external surface of the sclera, forms a thick vascular loop at the upper and lower margo pupillaris. It appears as if the vena ciliaris anteriores communicates with the *Canal of Fontana*, even though I have never found any blood in it, neither in the dolphin, the other mammals, or man. The uvea possesses a prominent ring of folds to it. The fibrous rays of the retina are very prominent.

DUGONG, *DUGONG DUGON*.--I received a well preserved eyeball of an adult dugong due to the friendliness of Mr. G. R. Müller in Berlin. Rapp had already briefly described the eye of a fetal dugong. He described the pupil as round and did not find a tapetum. The circular tear gland was not mentioned by Rapp. He described the gap of the eyelids as small, but it appears to be not unusual relative to the size of the eyeball and measures a

5 Additional information about the structure of the eye in the dolphin can be found in my papers regarding the anatomy of the dolphin *in* "Tiedemann und Treviranus

width of over 25.4 mm [1 Zoll], while it is only 12.7 mm [6 Linien] wide in the dolphin. The eyeball itself is round and measures 21.2 mm [10 Linien] in diameter. Four rectus and two oblique eye muscles can be distinguished. The two oblique muscles of the eye are the musculus levator palpebrae superioris and the musculus depressor palpebrae inferioris, which disappears into the musculus orbicularis. No *musculus suspensorius* is present. A strong nictitating membrane is present and covered with small, brownish glands. A very strong ring of glands extends around both eyelids and is the attachment site for the musculus orbicularis. The musculus orbicularis exhibits on the internal surface of the eyelids many openings with similar brown glandular structures. The *Harderian Gland* [glandulae sebaceae], which is equipped with fibrous cartilage, is present with its excretory duct and its small slender muscle of the nictitating membrane. Finally, a flat tear gland [glandula lacrimalis] is present in the outer upper corner of the eye with its large ducts. Therefore, it becomes apparent that the circular gland could be seen as a large *Meibom's Gland* [glandulae tarsales], while the *Harderian Gland* could be seen as an inner tear gland. That the acini of the tear gland exit along the upper and lower edge of the eyelid further supports this view.

The eyeball is still somewhat flat and round in shape with a horizontal diameter of 21.2 mm [10 Linien] and an axial diameter of 18.0 mm [8.5 Linien]. The optic nerve is thin and enters the eyeball from the left side. Rather than a rete mirabile, the optic nerve is only surrounded by fat. The sclera is relatively uniform, thin, and without a network. The cornea is somewhat oval and accordingly thin. The anulus conjunctivae and the *anulus internus* are both very wide. The circular fibers of the orbiculus ciliaris are weak. The iris is covered with a heavy layer of brown pigment, which forms longitudinal and oblique folds. The longitudinal vascular loops are covered by this layer of folds. The pupil is round to oval with a slightly serrated edge. The outer ring of folds of the uvea is prominent, while the inner ring of folds is small. The pigmented layer is black. The corpus ciliare is normally developed. The choroidea is brownish-black. A trace of the tapetum is present, which develops from a 4.2 mm [2 Linien] wide central spot. The ciliary nerves are numerous and thin and are not visible outside the orbiculus in the iris. The lens is rather flat. The zonula ciliaris consists of three folds. The corpus vitreum is dense and the retina is thin.

It can be concluded from these observations that the eye of the dugong is more closely related to the eye of the pachyderm's, namely to that of the swine, than to the eye of the cetaceans.

Professor Bischoff was also very friendly and helpful in my studies. He sent me the eye of a fetal dugong that he had described earlier (Müllers Archiv 1847 p. 1.). The eye measured 1 meter [3 Pariser Fuss] in length. I found, in general, similar structures to those described above. The sclera appeared to be relatively denser. The iris and choroidea were brown. The ring of folds of the uvea was prominent. No traces of a tapetum or a

The ring of glands around the eyelids and the nictitating membrane was already well developed. The nictitating membrane formed at the outer corner of the eye an unusual swelling, which gave it the appearance of a capsule of the conjunctiva, as it is the case in typhlus [*Spalax microphthalmus*], some amphibians, and the snakes (see Mayer's Analekten I. S. 52.), but in this case the appearance was only caused by an unnatural swelling of the gland.

It still needs to be mentioned that Rapp has already given a short description of the eye of a 33.02 cm [13 Zoll] long fetal dugong (l. c. p. 97.). He did not find a tapetum. He described the pupil as round and did not mention a circular gland.

SEAL, *PHOCA VITULINA*.--There is no circular gland of the eyelid present, but the inner gland, or *Harderian Gland* is present. A smaller tear gland is also present, following the description by Eschricht. The nictitating membrane is extensive. On the nictitating membrane we can recognize a papilla [Mayers refers to a "Pupille" or pupil in his publication, but this is probably a spelling mistake on his part, since the German words "Pupille" and "Papille" are very similar] and next to it the opening of the duct of the *Harderian Gland*. The eyeball is 42.4 mm [1 Zoll 8 Linien] wide, and 38.2 mm [1 Zoll 6 Linien] deep. The sclera is rather thin, and even thinner in its center as it was first described by Blumanbach and later by Eschricht. Since this thinning of the sclera is not present in other diving mammals, it might be more similar to the thinning of the sclera in baleen whales. The anulus conjunctivae and the *anulus internus* is present. The orbiculus ciliaris exhibits circular fiber bundles beneath a thin layer of a wool-like fiber network. The iris is brown. The pupil is oval to round. The outer ring of the iris consists of thin, longitudinal vascular loops which reach to the margo pupillaris. There is no visible fibrous layer on the iris. Nerves appear commonly in the orbiculus but seldom in the iris. The uvea only exhibits the one ring of fold with rays that extend to the margo pupillaris. The corpus ciliare possesses only small flakes. The zonula ciliaris is weak. The tapetum is extensive and iridescent. The lens and the corpus vitreum are large. There are no fascicles of the vasa ciliares posteriores present.

Manatee, *Trichechus manatus*. The eyes are small and set far apart (J. A. Wagner). The orbit is small. The lacrimal bone is small and not perforated (Cuvier Rech. V. 1. tab. 19.).

Trichechus senegalensis. The eyes are round and small. The iris is dark blue, the pupil is black (Adanson. Senegal. p. 143.).

SPERM WHALE, *PHYSETER CATODON*.--The eyes are set far back on the head between and above the pectoral fins and the corner of the mouth. The openings of the eyes are only 50.9 mm [2" wide] and 25.4 mm [1" high]. The eyelids have neither eyelashes nor cartilage to them. The conjunctiva

of half-moon-shaped appearance and very similar to the third eyelid of the horse. (S. Dr. Bennet. Narrative of a Whaling Voyage *in* Andreas Wagner Säugethiere VII. Theil S. 252, Mammals 7th volume, page 252).

[Pages 29 through 48 of Mayer's original publication are not included in this translation. Pages 29 through 34 discuss the anatomy of the human eye and the interested reader is referred to the medical literature, which will provide a wealth of information regarding such topics. The remaining pages to page 48 of Mayer's original publication describe briefly the structures of the eye of a variety of different species, including the cat, dog, horse, and ostrich.]

APPENDIX

I would like to discuss now, as an aspect of the general osteology of the cetaceans, the presence and anatomy of the tear gland, since there is no detailed study of this structure available. This investigation will also shed light on the presence of the tear gland in cetaceans. Rapp still mentioned (l. c. page 69) that the lacrimal bone is missing in cetaceans, even though Cuvier, Meckel, and myself described a non-perforated lacrimal bone. I described it first in detail in the dolphin and mentioned the characteristic hook-like shape of this bone (S. l. c. p. 114). Stanius also said later (l. c. page 384) that: "The lacrimal bone is missing in the dolphins, the phocas, and the walrus. In whales and the herbivorous cetaceans, the lacrimal bone is small and non-perforated (after Cuvier and Meckel)." But all of these accounts are either false or not precise enough. There is a lacrimal bone present in all cetaceans, which usually fuses early in development with the facial bone, but which usually remains clear from the orbital bone, as I will explain in my further discussion.

The lacrimal bone is present in the dolphin. It is the bone that I declared to be the lacrimal bone in my earlier descriptions and not the zygomatic arch, which some researchers had accredited to be the lacrimal bone (s. l. c. p. 114). The hook of the lacrimal bone is long and closes the orbit in its ventral aspect. There is no opening in the lacrimal bone and a groove seems to run in posterior direction into the nasal cavity.

In the baleen whales a flat bone is situated between the frontal bone and the maxilla, which I believe is the lacrimal bone. Cuvier agrees that this bone (Ossemans fossiles Tom. V) is the analog of the lacrimal bone.

The hook of the lacrimal bone is very long and prominent in the narwhals, similar to that in the dolphins, and there is only a groove, not a closed canal present.

The lacrimal bone in *Odobenus rosmarus* is almost completely fused, but there are either a slit, or two small openings in it, which lead to a 50.8 mm [2

feather. This canal runs nearly straight into the nasal cavity. The hook of the lacrimal bone is very prominent.

The lacrimal bone with its hook is present in the dugong and the manatee, *Trichechus manatus*.

The facial part of the lacrimal bone is fused in the seal (*Phoca vitulina*), while the orbital part is still slightly separated. The hook of the lacrimal bone is not very prominent. There is no general clear opening to the lacrimal canal present. In *P. cristata* and *P. jubata* etc. the hook of the lacrimal bone is very prominent.

(Two openings lead to the lacrimal canal in *Lutra lutra* and a hook of the lacrimal bone is present).

[Pages 50 through 52 in Mayer's original publication are not included since they refer to his pages 29 through 48, which are also not included in this translation (see discussion above)]

I will repeat now, briefly, the mostly new observations that I made on the structure of the human eye and of the eyes of animals in general, as I described them earlier. These are:

1. The orbiculus ciliaris consists of parallel bundles of longitudinal fibers in man, the apes, the carnivorous animals, the birds, and the amphibians. The orbiculus ciliaris consists of circular fiber bundles in the cetaceans, most of the ruminants, the horse, and the other mammals.

2. The fibers of the orbiculus ciliaris are striated muscle fibers in birds and amphibians; they are smooth tendon-like fibers in the horse and the ruminants, etc.; they are intermediate with delicately grained fibers in man, apes, and the carnivorous animals, as well as in the whale eye.

3. A separated, grid-like seam (*ora cancellata seu reticulata*) is present between the choroidea and iris in man and many other mammals. This seam contains arteries, veins, and nerves, which are separated and not covered by any tissue.

4. A special layer of folds, covered with its flakes on the posterior surface of the iris, forms the outer ring of the uvea in man and the higher animals,.

5. I suggest the following circular anastomosis, arterial as well as venous, in the eye of man and animals: a) Arterial and venous circle in the corpus ciliare; b) in the orbiculus ciliaris (J. Weber); c) at the outer ring of the iris, with its venous portion known as *Sinus Hovii;* d) at the inner circle of the iris; e) at the margo pupillaris, especially well developed and strong is the venous circle in baleen whales and dolphins; f) at the free margo pupillaris membrane (seldom); g) in the zonula ciliaris. All of these originate from the *vasis ciliaribus choroidea*. The following anastomosing vessels originate from the artery and rami vena centralis retinae: h) at the posterior wall of the lens capsule; i) in the corpus vitreum; k) within the

the optic nerve into the eye outside the sclera originate from the *arteriis ciliaribus exterioribus* (Zinn).

These circular anastomosing vessels are characteristic of sphincter muscles, and can be found at the sphincter palpebrae, the sphincter oris, the sphincters of the stomach, the sphincters of the reproductive organs, etc. The eye qualifies, therefore, as a *sphincter lucis internus*.

6. The iris, the corpus ciliare, and the zonula ciliaris all exhibit an inner and an outer ring.

7. A fiber bundle tissue rests on top of the layer of vascular loops of the iris in many mammals and most humans. This tissue can be seen as some type of erectile fiber bundles and appears to be a continuation of the fiber bundles of the orbiculus ciliaris.

8. The iris in the horse exhibits a well developed true rete mirabile (especially well developed in pale horses). This rete is also found in *Lutra lutra* and *Ursus meles* [most likely Dr. Mayer referrs to *Ursus arctos* or, less likely, *Ursus thibetanus*].

9. Clearly striated muscle fibers can be found in the uvea of birds, especially well developed in all ostriches, but they are not present in the iris, which exhibits smooth fibers that extend all the way to the margo pupillaris.

10. Striated muscle fibers in the iris of amphibians (*Caretta*).

11. The fibers in the iris of fishes have a striated appearance.

12. The lacrimal bone is present in the dolphins, the narwhal, the walrus, and all other cetaceans.

13. The lacrimal bone and two openings for the two canaliculi lacrymales are present in the elephant.

14. Nerves can terminate in two ways in an organ. First, as free loops, which appears to assure the nerves the supply with energy and nutrients , as do the anastomosing vessels secure the replacement and circulation of the blood. And second, as terminating nerves, which appear to fade into fibrous and marrow layers of the organs which they innervate. A third type of endings can be found in sensory structures where the nerves end as cone-like papillae.

REMARKS

I was unsuccessful in my attempt to obtain another eye of *Trichechus rosmarus* and I have, therefore, to explain this organ, following the laws of development, as the eye of a whale instead of the eye of a walrus.

FIGURE LEGENDS

Note: For an unexplainable reason the figure numbers in Mayer's publication do not correspond with his figures and their descriptions. The reader can ignore the roman numerals on the figures and follow their order as they appear in the tex and in the legend to each figure.

Figure. I. Vertical section through the eye of Balaena mysticetus in actual size. (a) tendon of the eye muscle; (b) outer fibrous layer; (c) rete mirabile; (d) the nervus opticus and its sheath of dura mater; (e) the sclera, between which the rete mirabile inserts; (f) the tapetum of the choroidea. Lens, corpus vitreum, and retina are removed.

Figure. II. Choroidea and iris. One can see the ciliary nerves enter to the inside through the choroidea. These nerves form then on top of the musculus sphincter iridis numerous networks and swellings before they descend between vascular loops of the anulus iridis major. The musculus sphincter iridis has clearly visible circular bundles, except in the area in which the membrana humoris aquei has been left in place. The ciliary nerves reappear at the smaller ring, anulus internus seu minor iridis, and form a very delicate network. Between the anulus major et minor one can see the large lateral vein, in which the fragile veins of the iris flow. Magnification 2 X.

Figure. III. Nerves, their ganglia and networks in the anulus iridis major at a magnification of 60 X. Deep beneath appear the vascular loops.

Figure. IV. The nervous network of the anulus iridis internus together with two vascular loops at a magnification of 140 X. One can recognize the large terminal loops or anastomoses of several nerves situated at the slightly serrated margo pupillaris.

Figure. V. Posterior surface of the iris together with the corpus ciliare and the attached choroidea. One can see in the transverse section of the latter the larger (posterior) lumina of the veins and the smaller (anterior) lumina of the arteries. One can recognize the tassels or cones of the processus ciliares. At the uvea itself is the layer of longitudinal fibers of the anulus externus and the layer of circular fibers of the anulus internus visible. Magnification 2X.

Figure. VI. A ciliary-nerve (a) which runs through the fibrous tissue of the sclera and divides anteriorly at (b), with one branch extending towards the iris and the second branch extends through the cornea into the conjunctiva. Natural size.

Figure. VII. The posterior portion of the sclera; (a) circle of the openings for the vasa ciliaria posteriores and the nerves; (b) point of entrance for the optic nerve; (c) canals in the sclera for the vasa ciliaria anteriores.

Figure. VIII. Microscopic tissues; A. of the cornea; B. of the sclera; C. of the crystal lens; D. of the unique structure of the Membrana Ruyschiana; E. of fibers of the skin; F. of the pigmented cells of the choroidea; G. of striated muscle fibers of the orbiculus ciliaris from *Gypaetus barbatus*; H. of fibers of the orbiculus ciliaris of the whale.

[End of Translation]

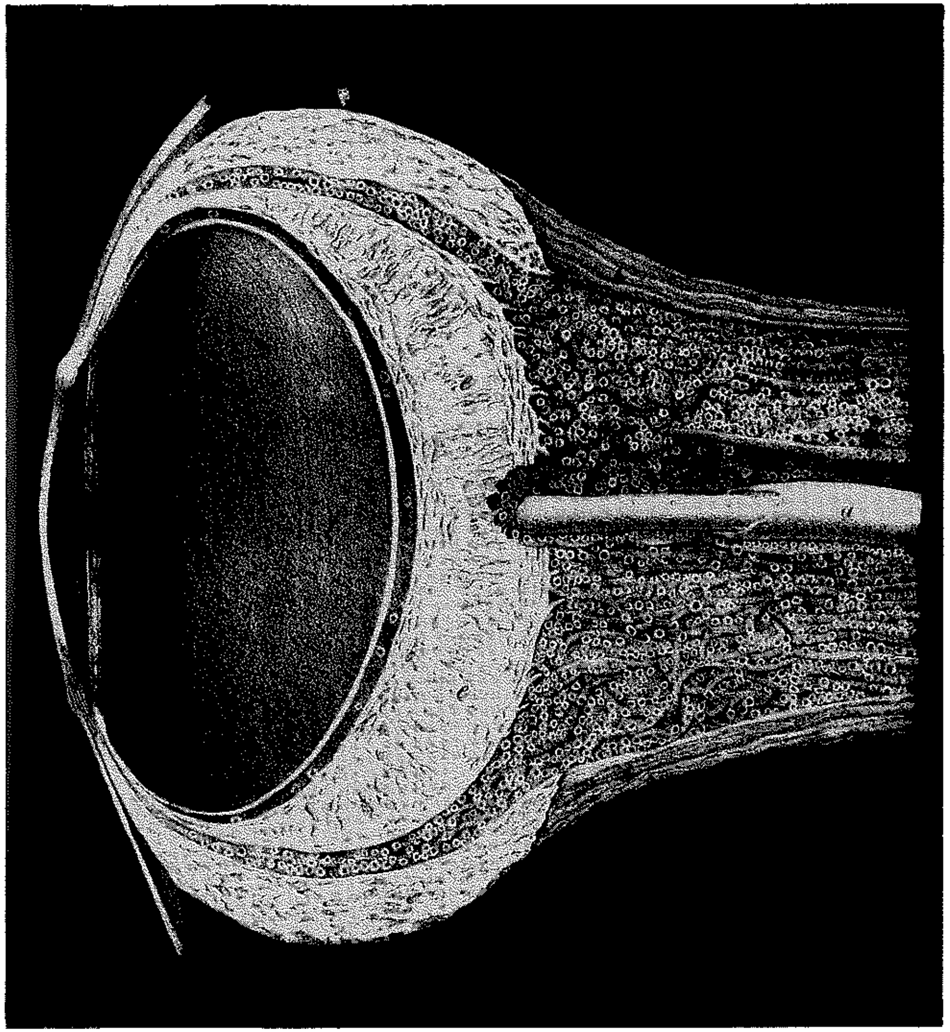


Figure I. Vertical section through the eye of *Balaena mysticetus*.

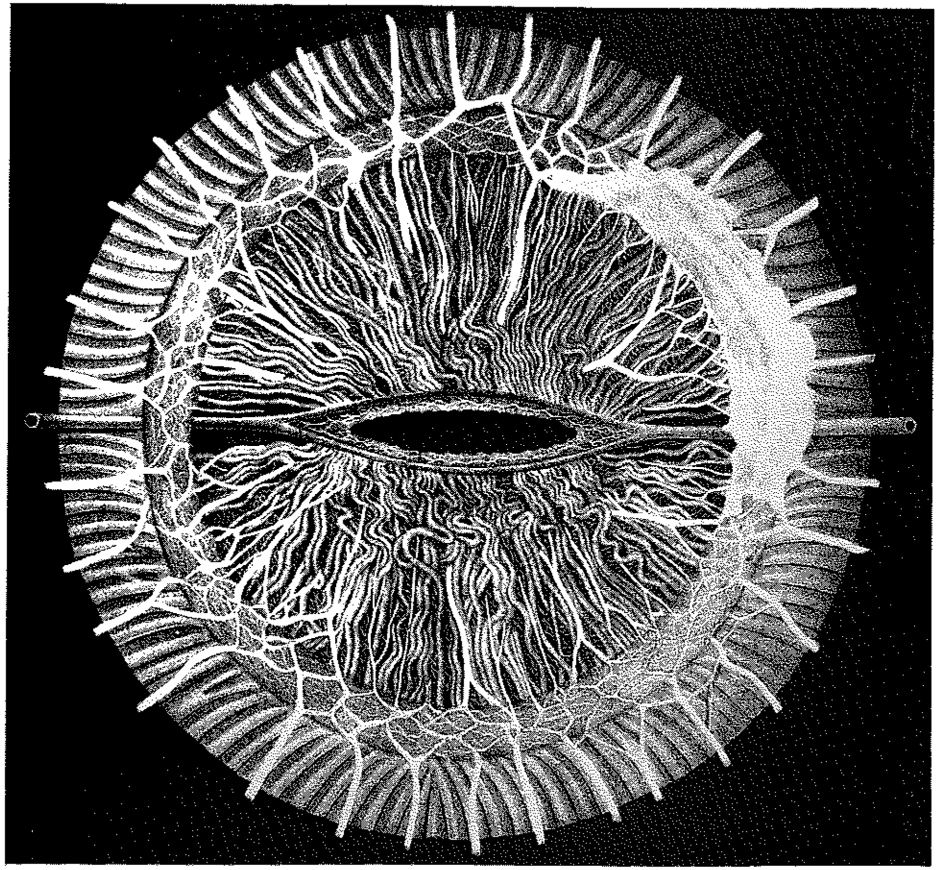
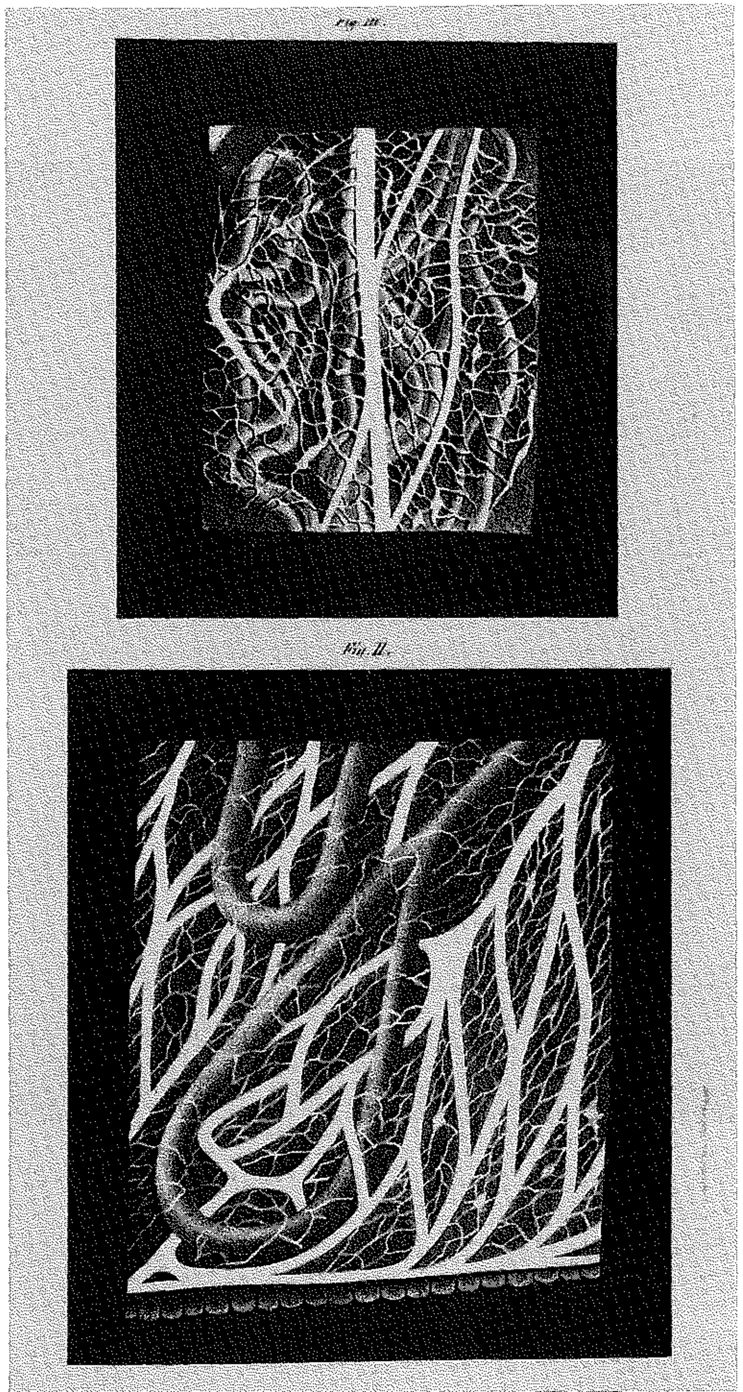


Figure II. Choroidea and iris.



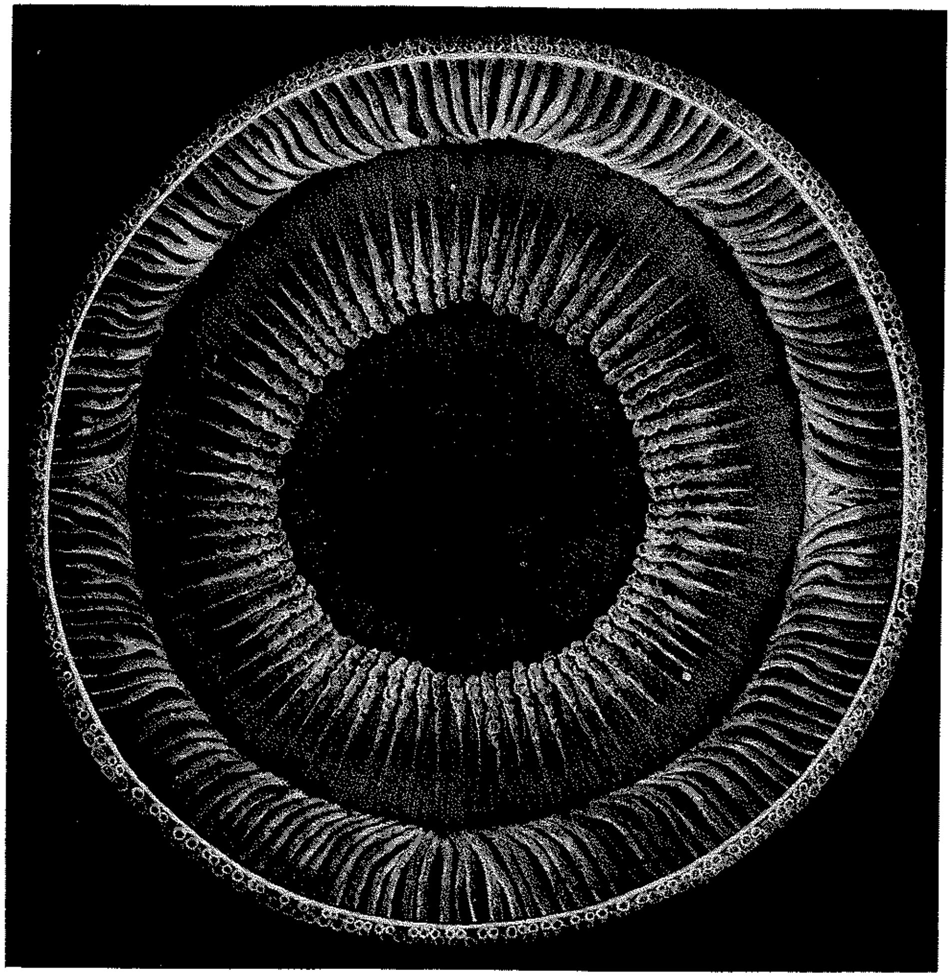
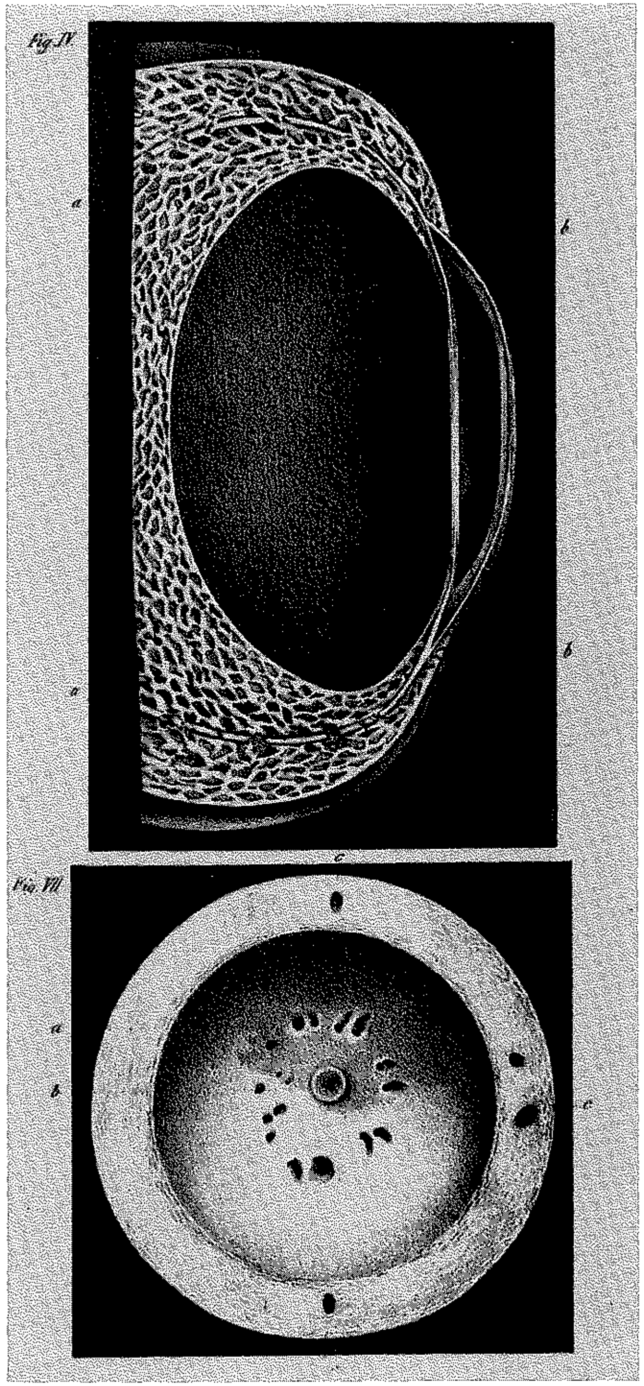


Figure V. Posterior surface of the iris together with the corpus ciliare and the attached choroidea.



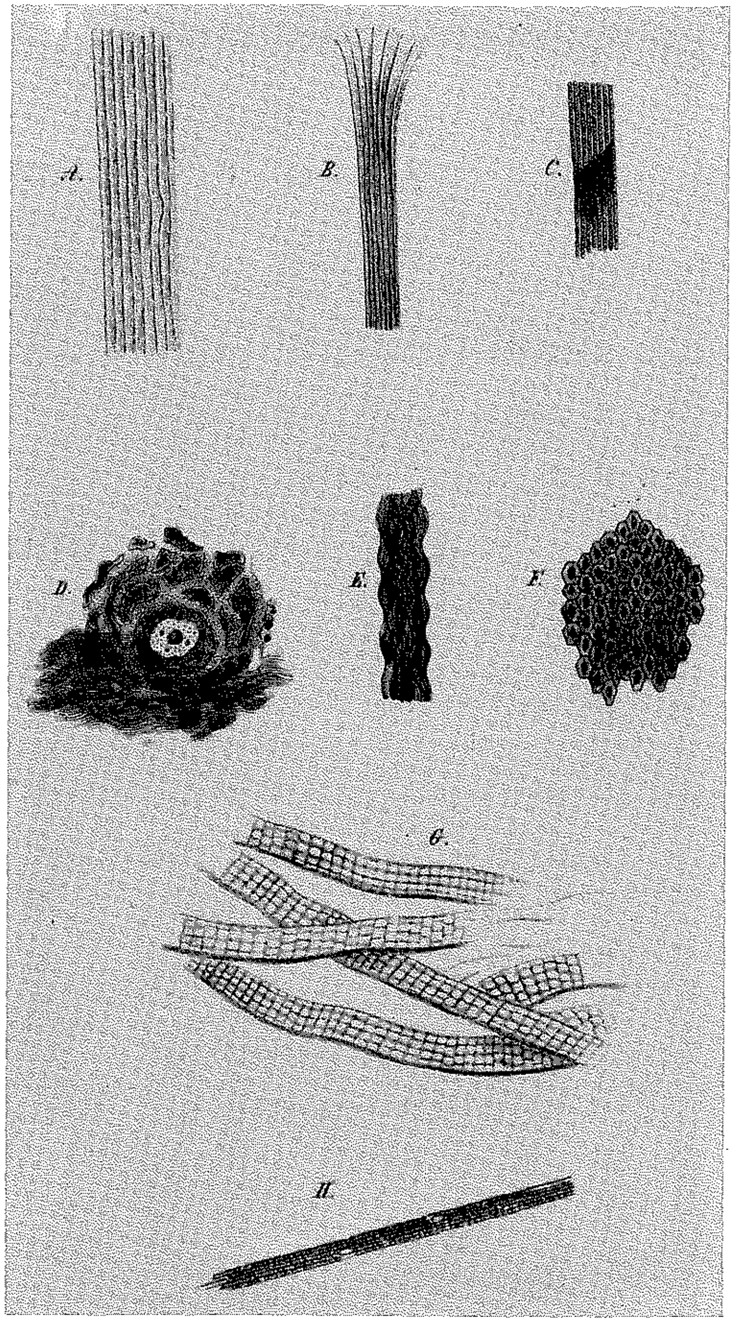


Figure VIII.

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