

2-1996

The Visceral *Retia Mirabilia* of Tuna and Sharks: An Annotated Translation and Discussion of the Eschricht and Müller 1835 Paper and Related Papers

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Recommended Citation

Fudge DS, and Stevens ED (1996) The visceral retia mirabilia of tuna and sharks: An annotated translation and discussion of the Eschricht and Müller 1835 paper and related papers. *Guelph Ichthyology Reviews*, No. 4, 92 pp.

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Comments

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GUELPH ICHTHYOLOGY REVIEWS

Number 4

February 1996

**The visceral *retia mirabilia* of tuna and sharks:
an annotated translation and discussion of the Eschricht & Müller 1835 paper
and related papers**

by

Douglas S. Fudge & E. Don Stevens



1996

Axelrod Institute of Ichthyology, University of Guelph,
Guelph, Ontario, Canada

A wonderful network

A wonderful network of people - tuna biologists, librarians, translators, photographers, historians, and publishers. A wonderful network of historical records, anatomical reconstruction, and new observations. A remarkable example of true scholarship seldom seen in current science.

It is with great pleasure that we publish this review by Don Stevens and his student Doug Fudge. Their painstaking attention to detail shows in every facet of the work, from accuracy of translation of the original German language articles, to verification of the first published citations, to exquisite photographs and illustrations of fresh preparations that reconstruct the key points of those first studies. This is a review in the true, scholarly sense of that term - and so of course it leads to new insights, new interpretations and increased understanding.

Almost every biology textbook states that tunas and some sharks have a limited ability to regulate the temperature of parts of their bodies above ambient. The concession usually appears to be grudging, perhaps in light of the thinly disguised dogma that only birds and mammals are "true" homeotherms - as befits their position on the pinnacle of the *scala natura*. Shades of Aristotle! With the notable exception of the most recent edition of a major ichthyological textbook, the true wonders of this property of tunas and some sharks has been sadly overlooked. At best it was a curiosity to trip up unwary students on comprehensive qualifying examinations.

In 1835 Charles Darwin was still voyaging on the Beagle, and Victoria was not yet Queen of England. In the United States Andrew Jackson was President and their Civil War was still 26 years in the future. Canada would not become a country for another 32 years. It would be 18 years before the American Admiral Perry and his Black Ships forced their way into Japan. Germany was a confederation of states under Austria.

But in 1835 the seminal papers on *retia mirabilia* in tunas and sharks were published. It is a testament to the standards of those papers that we can continue to learn from them - especially from the superb illustrations.

The saddest part of this review is the knowledge that it may be almost too late. Don and his co-workers required a special government permit to collect the four bluefin tuna used in their dissections. It is now an endangered species. Pursued since at least the time of the Phoenicians, the prized catch of trophy anglers, and eagerly purchased at astronomical prices for sashimi, the giant bluefin faces an uncertain future. Some might argue, however, that at prices as high as US \$50 000 for a single fish their fate is inevitable.

The large sharks may fare no better. They are even less well-known than the tunas, less likely to attract the attention directed towards large charismatic vertebrates such as whales, and subjected to largely unregulated harvest for fins, cartilage, and other trinkets.

With this issue of Guelph Ichthyology Reviews we continue our efforts to bring together in the Axelrod Institute of Ichthyology the full range of interests in scholarly activities in ichthyology. Those who would judge the worth of science often place a great deal of emphasis on the immediacy of its impact in citations. Here we see the value of excellent research that can be timeless and extend far beyond the technical and conceptual limits of the originators. We can also see that without an awareness and understanding of the history of our discipline we can be little more than technicians. How will our science be judged 160 years from now?

Guelph, 2 February 1996

David L.G. Noakes

The visceral *retia mirabilia* of tuna and sharks: an annotated translation and discussion of the Eschricht & Müller 1835 paper and related papers

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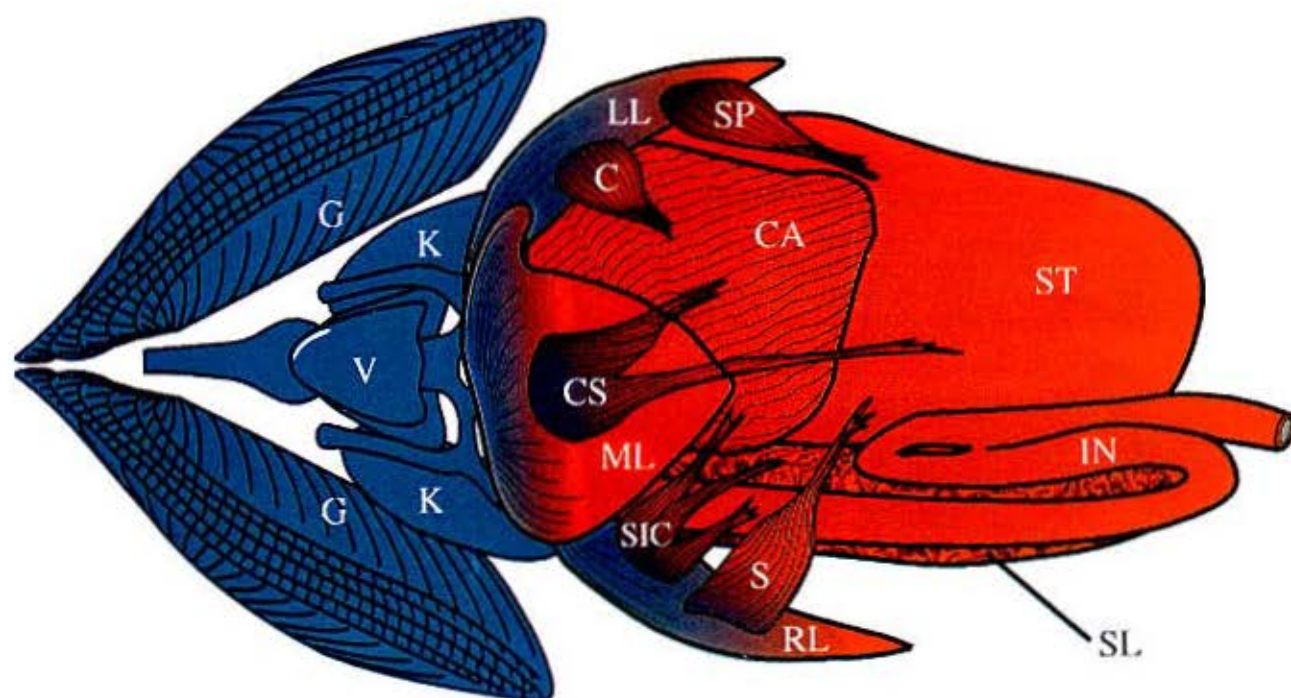


Fig. 1. Schematic of bluefin viscera and gills showing the five major *retia* and their connections to the liver and visceral organs. The two colors represent relative temperature, with blue denoting cold and red denoting warm. Not only do the *retia* thermally isolate the viscera from the relatively cold heart, kidneys and gills, the three liver lobes form a cap over the viscera. This arrangement most likely contributes further to the insulation of the viscera from the gills. Note that the diagram includes our hypothesis that the radiating liver vessels act as countercurrent heat exchangers, resulting in a temperature gradient along the liver. The locations of some of the organs have been distorted so that all of the *retia* and their connections can be seen. The middle liver lobe has been made semi-transparent so that the *rete* connected to it and the right liver lobe can be seen. For a more realistic view of the visceral anatomy, see Plate III, Fig. 1 from the original text and see Fig. 9 for a photograph of this region *in situ*. GI = gill, ST = stomach, K = kidney, CA = caecum, RL = right liver lobe, ML = middle liver lobe, LL = left liver lobe, V = ventricle, SL = spleen, IN = intestine, S = *rete* which serves right ventral portion of stomach, SIC = *rete* which serves the spleen, the intestine and part of the caecum, CS = *rete* which serves both the stomach and the caecum, C = *rete* which serves the caecum, SP = *rete* which serves the left ventral portion of the stomach and attaches near the pylorus.

Synopsis

The focus of this volume is an annotated translation of the classic work by J. Müller and D.F. Eschricht on the visceral anatomy of the bluefin tuna, *Thunnus thynnus*, published in 1835. This text, with its outstanding figures, is to this day the definitive work on the anatomy of the bluefin viscera and especially on the circulation to and from the viscera. In addition, the text is historically important in that it represents the first comprehensive description of visceral *retia mirabilia* in a fish. In this work, Eschricht & Müller meticulously elucidate the pattern of blood flow to, within, and from the viscera. In addition they describe and speculate about the function of such "peculiar" anatomical structures such as: the visceral *retia mirabilia*, the "radiating liver vessels" and the unusually large visceral nerves seen in this species. We have annotated the translation in order to connect the findings of Eschricht & Müller with our current understanding of warm fishes. Eschricht & Müller published a supplement to the tuna article in which they describe the visceral anatomy of the common thresher shark, *Alopias vulpinus*. We provide an annotated translation of this text as well. The main point of the supplement is that the vascular arrangement of the thresher viscera is completely analogous to that in *T. thynnus*, and distinct from that found in the other warm sharks, such as *Lamna nasus*, implying that endothermy has evolved independently at least twice within elasmobranchs. Finally, to round out the historical aspect of this volume, we include two papers and their abstracts by John Davy, who is credited with the first body temperature measurements of warm fishes. Eschricht & Müller were aware of Davy's measurements and discuss them briefly in their paper on tuna visceral anatomy. We also include plates from the 1923 paper by Kishinouye and some color photographs of the visceral *retia* from our dissections. The last two sections of this volume are facsimiles of the two texts by Eschricht & Müller as they appeared in their original form.

Key words:

Alopias, Bluefin, Endothermy, History, *Lamna*, *Rete*, *Rete mirabile*, *Retia mirabilia*, Shark, *Thunnus*, Tuna, Warm-blooded

Prelude

Preparing a translation of the Eschricht & Müller text for a modern audience required a lot of background and supporting research. Not surprisingly, by the end of the translation, we found that we were quite familiar with the authors and the scientific context in which they were working. We realized that this knowledge was not only helpful for an accurate translation, but it also put us in a good position to help document the very beginnings of the study of warm fishes. To this end, we have included other documents in this volume that are relevant to the origins of warm fish biology. The first of these documents is the supplement to the tuna article, which is primarily concerned with the vascular anatomy of the thresher shark. We also have included two papers and their abstracts by John Davy. The first article by Davy, entitled "On the temperature of some fishes of the genus *Thynnus*", includes the first mention in the scientific literature that tunas are warm-blooded. Of course the translation of the Eschricht & Müller work on the visceral anatomy of the bluefin tuna is the centrepiece of this volume. However, we hope that the inclusion of the supplementary texts will make this volume more than just a revival of a classic anatomical study. We hope it will shed some light on how the study of warm fishes got its start.

1. Introduction

The fact that some scombroids and sharks are warmer than the water they inhabit has been of considerable interest to comparative physiologists for many years. Research in this area could be classified as being guided by four questions.

- (1) How warm are warm fishes?¹
- (2) How do warm fishes generate and maintain an elevated temperature?²
- (3) What adaptive advantage accrue to fishes with high body temperatures?³
- (4) How did endothermy evolve in fishes?⁴

The articles selected for this volume are historically important because they represent the first attempts to answer the first two questions. The study of the biology of warm fishes got its start in 1835 in Europe when two important papers were published, one by an Englishman by the name of John Davy and the other by a pair of Germans, Johannes Müller and E.F. Eschricht. In the paper entitled "On the temperature of some fishes of the genus *Thunnus*," Davy presents the first measurements of body temperatures of warm fishes (in this case tunas). Because of these measurements, Davy is credited as being the first to describe endothermy in fishes. His work could be considered the first attempt to answer the first question in the above list. Shortly after the publication of Davy's work, Eschricht & Müller published an article entitled "On the arterial and venous *retia mirabilia* of the liver and a peculiar structure of that organ in the tuna, *Thynnus vulgaris*." In this work, Eschricht & Müller describe the visceral anatomy of the bluefin tuna, paying special attention to the vascular *retia* which we now know to be adaptations for endothermy. Although Eschricht & Müller were unaware of the significance of their findings, their work could be considered the first which contributed to answering the second question in the above list, the question of mechanism.

Although Eschricht & Müller never fully arrived at the connection between the presence of *retia* and endothermy, they certainly struggled over what the function of the visceral *retia* might be. The function we now ascribe to these structures (countercurrent heat exchange) would not be elucidated for more than a century, but it is rather clear from the text that Eschricht & Müller were very close to making a connection between the warm nature of these fish and their "peculiar" vascular anatomy. Müller says in section VII, "Perhaps the main reason for the peculiar (elevated) temperature of tunas... lies in the *retia*". Later in the same section, he reasons that if there is some functional

relationship between the possession of *retia* and elevated body temperature, then measurements of the body temperature of the porbeagle shark, *Lamna nasus* (which they knew also possess vascular *retia*) should help refute or support this hypothesis: "moreover, observations about the temperature of (the porbeagle) may become just as important". Unfortunately for them, there were no measurements of porbeagle body temperature available at that time.

Even almost 90 years later, in 1923, when R.H. Burne published his paper, "Some peculiarities of the blood-vascular system of the porbeagle shark", the function of visceral *retia* was still unknown. As we see in the following passage, Burne almost stumbles on a fruitful line of reasoning, but then abandons it, much like Eschricht & Müller, for a lack of basic information.

If the *retia* in *Lamna* are modifications for this purpose, as seems likely, one might hope to find indications of some special life habits to account for the need of them. Such, however, is apparently not the case, for this shark, so far as my information goes, presents no strongly marked peculiarities of habit. It is a pelagic shark of very powerful build and extremely active mode of life, though no more active than other genera in which no *retia* occur.

Burne is certainly not at a loss for hypotheses to explain the *rete* function, but never hits on the idea of heat transfer. Of course, it is understandable that this explanation would not be available to him considering the fact that no one knew at the time that porbeagles are endothermic. Not until Kamakichi Kishinouye published his "Comparative study of scombroid fish" in 1923, was the matter set on the right track. In this work, Kishinouye for the first time pronounces a firm connection between *retia* and elevated body temperatures:

The higher temperature of the body than the surrounding water, and consequently great activity of fishes of the Pleistocene is undoubtedly due to the peculiar circulatory systems above described.

Subsequent developments with regard to the elucidation of the mechanism and advantages of countercurrent heat exchange is another story all together.

Not only is this work by Eschricht & Müller historically interesting, but it also continues to have real scientific value. Of course the anatomical descriptions are useful and the plates are superb, but Eschricht & Müller also have unwittingly catalogued a fascinating example of convergent evolution in excellent detail. There are two structures which Eschricht & Müller find peculiar about the visceral vasculature of the bluefin tuna. The first is the visceral *retia* and the second is the "radiating structure of the liver vessels". Although they have no compelling hypotheses to explain the existence of either of the structures in question, they do what any good comparative anatomist would; they find similar structures in other animals. The rationale is that by comparing the physiology, lifestyle and behavior of the two species, the function of the structure in question may become clear. Unfortunately, their comparisons were fruitless at the time. Fortunately for us, Eschricht & Müller seem incapable of

¹ We refer the interested reader to the work of: Carey & Teal (1969a), Stevens & Fry (1974), Carey et al. (1981), Carey et al. (1984), Carey et al. (1985), Block & Carey (1985), Dickson (1994).

² See Bone & Chubb (1983), Carey (1982a), Carey & Gibson (1983), Carey & Teal (1966), Carey & Lawson (1973), Carey & Teal (1969b), Carey et al. (1985), Dewar et al. (1994), Graham & Dickson (1981), Holland & Sibert (1994), Linthicum & Carey (1972), Stevens et al. (1974), Wolf et al. (1988).

³ See Dickson (1988), Graham (1975), Stevens & Carey (1981), Stevens & McLeese (1984).

⁴ See Block & Finnerty (1994), Block et al. (1993).

omitting even the most seemingly insignificant detail, and they include these descriptions of analogous structures in spite of their apparent lack of utility in explaining their function.

In the case of the visceral *retia* they observe in the tuna, Eschricht & Müller are reminded of the peculiar vascular structures found in the viscera of the porbeagle. Armed with the benefits of 20/20 hindsight, we see the innocent wisdom in this comparison, because we know that the visceral *retia* of the porbeagle also act as countercurrent heat exchangers and help prevent heat loss through the gills. Although they are completely ignorant of the actual function of the visceral *retia* in both species, they go on to point out a distinction between the two systems that we can now see has important thermal consequences. The distinction is the position of the *retia* relative to the liver. In the tuna, the *retia* are located between the liver and the organs they serve, such as the stomach, caecum, spleen, and intestine. The consequence of this is that the liver does not enjoy the benefits of the *retia*, because it is outside the warm circuit isolated and defined by them. In the porbeagle, however, the *retia* are located on the other side of the liver, between the liver and the heart. The consequence of this arrangement is that the liver benefits from the presence of the *retia*, because it is included within the warm vascular circuit defined by them. Indeed, temperature measurements of various visceral organs in the tuna and porbeagle show that the liver of the tuna is cold relative to the other visceral organs served by the *retia* (Carey et al. 1984), whereas the liver of the porbeagle is about the same temperature as the other visceral organs (Carey et al. 1981).

In the case of the radiating structure of the liver vessels, Eschricht & Müller zero in on another excellent choice for comparison. In the original text, they claim that they could find this structure in only one other species. Unfortunately, at the time they don't know exactly which species that is, because the liver on which the radiating vessels were discovered was found in a jar separate from the rest of the body. Here the reader is subjected to a think-aloud session in which the authors try to figure out to whom the liver belongs. Fortunately, the issue is resolved in a supplement to the text which we also have translated and included. We are told (after more explanations of exactly how they reached their conclusion) that the liver in question belongs to the common thresher shark, *Alopias vulpinus*. What makes this text fascinating is the revelation that the thresher possesses not only a radiating structure of the liver, but visceral *retia* as well. Perhaps even more interesting is the fact that the visceral *retia* of the thresher are completely analogous to those in the bluefin in terms of their position relative to the liver. Without knowing it, through their fine descriptions of the vascular anatomy of the bluefin, the porbeagle, and the thresher, Eschricht & Müller present a rather detailed account of three convergent vascular systems that could support visceral endothermy. See Fig. 2 and 3 for a schematic comparison of the visceral circulation in these three species.

In their attempts to find analogous structures to the *retia* and the radiating liver vessels of the tuna, Eschricht & Müller illustrate three separate instances of visceral endothermy. Astute as their observations are, they fail to realize an important pattern

they uncover. The reason they examine a thresher shark at all is to find out if the liver in question (the one with the radiating liver vessels) belongs to it or to a hammerhead shark. It turns out that the liver belongs to the thresher, but it also turns out that the thresher possesses visceral *retia* (the opposite claim is made in the tuna paper). Not only does it have visceral *retia*, but they are located between the liver and the digestive organs, as in the bluefin, which we know also displays the radiating liver vessels. One might ask how the porbeagle fits into this story, being a warm fish with a warm liver. Eschricht & Müller mention that the porbeagle liver does not display the radiating vessels. It seems that the radiating vessels are present only when the liver is not served by the main heat exchangers.

These observations of the liver vasculature have led us into a whole new line of inquiry. We feel strongly that there must be some functional significance to a structure (the radiating liver vessels) which has evolved in two distantly-related lines (the tunas and the alopid sharks) that have converged on similar, high energy lifestyles. Our current hypothesis is that these peculiar vessels act as a crude *rete* which helps to conserve some of the metabolic heat produced in the liver. We are led to this hypothesis by the fact that this structure is shared by warm fishes whose livers are not kept warm by the main visceral *retia*. In addition, a close look at these vessels reveals that they are not all that different in structure from the main visceral *retia* (see Fig. 14). Our future research aims to determine the capacity for countercurrent heat exchange of these structures, as well as to find examples in other species which will either support our refute our hypothesis.

There is one other line of questioning for which this text has been invaluable. The question is whether bluefin tuna are capable of bypassing their visceral *retia*, which would presumably bestow them with greater thermoregulatory flexibility. In an anatomical study of the porbeagle viscera, Carey et al. (1981) showed that this shark possesses vessels which most likely act as bypasses of the visceral *retia*. In trying to determine whether bluefin possess analogous structures, we found the Eschricht & Müller text a good place to start. It is a testimony to the careful technique and powerful observational skills of both Eschricht & Müller that although neither of them made their observations with the bypass question in mind, we still found their descriptions useful to this end. We have indicated with endnotes those places in the text where their observations suggest that bluefin, unlike the porbeagle, are incapable of bypassing their visceral *retia*. We will explore the validity and implications of these findings in a subsequent publication.

Every time we revisit the Eschricht & Müller texts, we are surprised by how much relevance they hold for our current research. Although Eschricht & Müller operated in a pre-Darwinian framework, their assumptions about the connections between form and function led them to proceed much as modern comparative anatomists would. The result of their labours is an anatomical study of stunning relevance and it has been an honour to formally reintroduce them to the scientific community. We hope the reader will find these texts as compelling and useful as we have.

2. Reader's guide to the Eschricht & Müller translations

2.1 Brief notes on Eschricht and Müller

We could find very little biographical information about D.F. Eschricht. Although he almost certainly published more than the two papers we include in this volume, we could find no other references credited to him. We do know that Eschricht was an intimate friend of Müller's, and remained so until Müller's death in 1858. The life and work of Johannes Müller, on the other hand, is very well-documented. Müller was incredibly prolific, publishing 267 papers and texts while also working as a practicing physician and surgeon, university professor, and director of an anatomical museum. He published papers on a wide range of topics, from anatomy and physiology, to systematics and behavior. His choice of research animals was equally diverse, with the focus ranging from jellyfish to tunas. Perhaps at this point it comes as no surprise that Müller often drew his own illustrations which accompany his papers. In all, he is credited with 350 drawings (du Bois-Reymond 1859).

2.2 Miscellaneous notes on the translation

Because the Eschricht & Müller texts are so old, we feel that some advice to the reader is in order. We have done our best to make the language of the translation simple and easy to grasp. For many of the more cumbersome sentences, this was not an easy task. Indeed, many of these sentences were broken up into two, three, or even four separate sentences. We hope that we have remained true to the essence of the text in spite of our merciless editing. We realize that some sections are downright confusing. For whatever comfort it provides, take heart that those passages are equally confusing in German. In these instances, so as not to leave the reader completely dumbfounded, we have provided footnotes for supplementary information, commentary, and guidance. In general, the footnotes are there to help the reader get the most out of the text. We have tried to footnote generously, indicating instances where the authors are unclear or misled or where we can provide relevant commentary. With regard to the somewhat convoluted style, we urge the reader to be patient. Keep in mind that it was written over a century and a half ago, when the volume of scientific literature produced was infinitesimal compared to today's output. Indeed, it is quite apparent from the texts that the pressures to be concise were not as strong as they are for scientists today.

This may be an appropriate place to point out that the Latin term for one rete is *rete mirabile geminum* and the plural is *retia mirabilia geminia*. *Rete mirabile* (wonderful net) refers to a

splitting of a small artery (or vein) into a net of smaller arteries (or veins). *Geminum* (paired) implies that the net consists of a plexus of both arteries and veins together as opposed to a plexus of just arteries or just veins.

2.3 Taxonomic Guide

Because these articles were written over a century and a half ago, it is not surprising that many of the species names given are no longer in use. Below are two lists designed to help the reader decipher some of the generic and species names given in the texts. Species and genera for which both the name and the meaning of the name have not changed are not included in these lists.

Many of the genera mentioned in the text are no longer in use. For many of these names, it would be inappropriate to provide only one modern equivalent, since many of the genera have been split up in addition to being renamed. Here we provide a list of modern genera that correspond to each of the outdated genera mentioned in the text. These lists are not intended to be a reliable systematic reference, but rather a guide that will give the reader a rough idea of which species the authors are referring to. Most of the list was generated by looking up references to the genera in question in the appropriate FAO Species Catalogue and Eschmeyer (1990). If the genus name was listed as a synonym of a current species, the genus of that species was included in the list only if the date given was earlier than 1835. Any species given the name in question after that date would not have been known by Eschricht & Müller at the time of publication. In addition, any reference to the genus in question before 1835 that had subsequently been replaced by another name prior to 1835 was also not included in the above list. This type of search allowed us to be reasonably certain that the modern genera we list correspond to the species that Eschricht & Müller originally intended. As a rough guide, we assumed that the systematics laid out by Cuvier & Valenciennes in 1831 was consistent with the genera that Eschricht & Müller used. If you cannot find a particular genus name in the list, this means that the genus is still in use and has approximately the same meaning as it did in the original text. An * indicates that the valid name has not been confirmed. We have used the valid names in the translation except for a small section at the beginning of the supplement that concerns synonymy. We also have converted all units into metric.

Species in original text	Valid name	Common name
<i>Alopecias vulpes</i>	<i>Alopias vulpinus</i>	common thresher shark
<i>Auxis vulgaris</i>	<i>Auxis rochei</i>	bullet tuna
<i>Caranx trachurus</i>	<i>Trachurus trachurus</i>	scad
<i>Carcharias vulgaris</i>	unknown	unknown
<i>Carcharias vulpes</i>	<i>Alopias vulpinus</i>	common thresher shark
<i>Carcharias glaucus</i>	<i>Prionace glaucus*</i>	blue shark
<i>Lamna cornubica</i>	<i>Lamna nasus</i>	porbeagle shark
<i>Lamna cornubicus</i>	<i>Lamna nasus</i>	porbeagle shark
<i>Pelamis sarda</i>	<i>Sarda sarda</i>	Atlantic bonito
<i>Sciaena aquila</i>	<i>Argyrosomus regius</i>	meagre
<i>Sciaena hololepidota</i>	<i>Argyrosomus hololepidotus</i>	unknown
<i>Scomber colias</i>	<i>Scomber japonicus</i>	chub mackerel
<i>Squalus cornubicus</i>	<i>Lamna nasus</i>	porbeagle shark
<i>Squalus thalassinus</i>	<i>Prionace glaucus*</i>	blue shark
<i>Thynnus alalonga</i>	<i>Thunnus alalunga</i>	albacore tuna
<i>Thynnus brachypterus</i>	<i>Thunnus thynnus</i>	juvenile northern bluefin tuna
<i>Thynnus pelamis</i>	<i>Katsuwonus pelamis</i>	skipjack tuna
<i>Thynnus pelamys</i>	<i>Katsuwonus pelamis</i>	skipjack tuna
<i>Thynnus vulgaris</i>	<i>Thunnus thynnus</i>	northern bluefin tuna
<i>Zygaena malleus</i>	<i>Sphyrna lewini</i>	scalloped hammerhead
<i>Zygaena tiburo</i>	<i>Sphyrna tiburo*</i>	bonnethead
<i>Zygaena tudes</i>	<i>Sphyrna tudes</i>	smalleye hammerhead

Genus in text	Corresponding valid genus/genera
<i>Alopecias</i>	<i>Alopias</i>
<i>Anacanthus</i>	Most likely <i>Dasyatis</i> , but could also refer to <i>Anacanthus</i> or <i>Uromgymmus</i> .
<i>Carcharias</i>	<i>Carcharhinus</i>
<i>Centrina</i>	<i>Oxynotus</i>
<i>Cephaloptera</i>	<i>Mobula</i>
<i>Cestracion</i>	This genus most likely refers to the sharks of the family Heterodontidae, or the bullhead sharks. However, we could find no references to this name among the bullhead sharks until 1854. The only other alternative is that the name refers to the genus now known as <i>Sphyrna</i> . This is unlikely, however, as the authors refer to species from this genus as <i>Zygaena</i> .
<i>Galeus</i>	Most likely <i>Galeorhinus</i> , but might also refer to <i>Galeus</i> or <i>Mustelus</i> .
<i>Lamna</i>	<i>Lamna</i> , <i>Isurus</i>
<i>Lepidopus</i>	Although at the time of publication, many of the current species under the genus <i>Lepidopus</i> had not been discovered, all those that possessed this name at the time still possess this name.
<i>Myliobates</i>	Misspelling of <i>Myliobatis</i> .
<i>Notidamus</i>	<i>Hexanchus</i> , <i>Notorhynchus</i>
<i>Pelamis</i>	<i>Sarda</i>
<i>Propterygia</i>	This genus was based on a deformed specimen of <i>Raja batis</i> and is no longer in use.
<i>Rhina</i>	Most likely <i>Squatina</i> , but could refer to <i>Rhina</i> .
<i>Scomber</i>	<i>Scomber</i> , <i>Rastrelliger</i>
<i>Scyllium</i>	<i>Scyliorhinus</i>
<i>Scymnus</i>	<i>Dalatias</i>
<i>Selache</i>	<i>Cetorhinus</i>
<i>Spinax</i>	<i>Etmopterus</i>
<i>Stenops</i>	<i>Lorus</i>
<i>Thynnus</i>	<i>Thunnus</i>
<i>Thyrsites</i>	<i>Thyrsitops</i> , <i>Thyrsites</i>
<i>Trygon</i>	<i>Taeniura</i> , <i>Dasyatis</i>
<i>Zygaena</i>	<i>Sphyrna</i> , <i>Eusphyra</i>

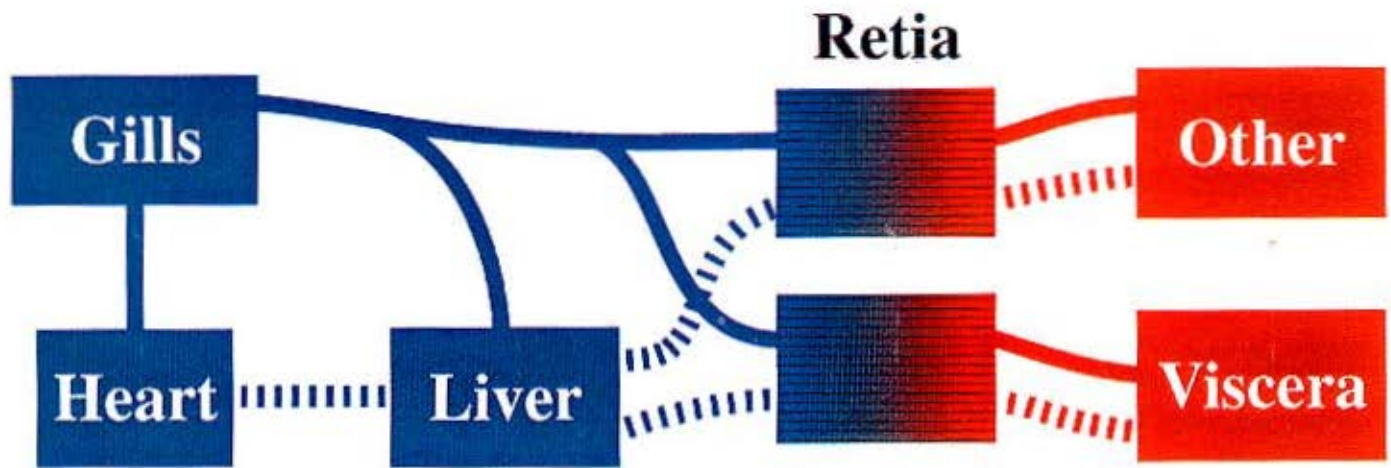


Fig. 2. Schematic of the visceral circulation in *Thunnus thynnus*. The two colors represent relative temperature, with blue denoting cold and red denoting warm. Solid lines represent arterial blood and dashed lines represent venous blood. Note that the liver is outside the warm vascular circuit defined by the visceral *retia*. The consequence of this arrangement is that the liver is cold relative to the digestive organs. According to Möller's descriptions, the visceral circulation in the elasmobranch, *Alopias vulpinus*, is completely analogous, with heat exchangers located between the liver and the digestive organs (such as the stomach and the spiral valve). The only difference between the two is that in *A. vulpinus*, the *retia* are closely associated with the organs they serve, as opposed to being right up against the liver as in *T. thynnus*.

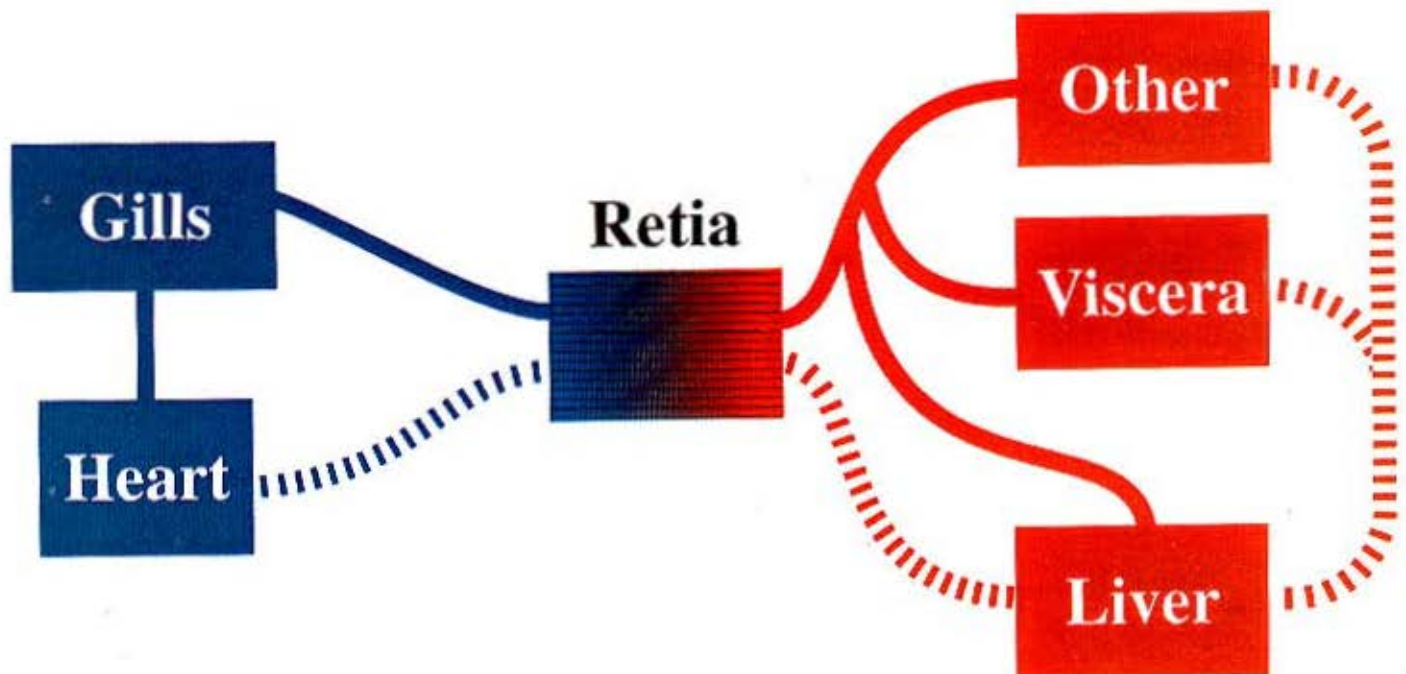


Fig. 3. Schematic of the visceral circulation in the elasmobranch *Lamna nasus* according to Möller's descriptions. Note that the liver is included within the warm vascular circuit defined by the suprahepatic *retia*, which lie between the liver and the heart. The consequence of this arrangement, in contrast to that seen in *T. thynnus* and *A. vulpinus*, is that the liver is as warm as the other viscera. Colors and symbols retain the same meaning as in Figure 2.

3. An annotated translation of D.F. Eschricht and J. Müller's "On the arterial and venous *retia mirabilia* of the liver and a peculiar structure of that organ in the tuna, *Thunnus thynnus*"

Translated with the assistance of Elisabeth Niimi.

Reported by J. Müller at the Academy of Sciences, 29 June 1835

With a few new additions

I. Purpose of the study

The tunas have been well known throughout the history of fisheries. However, with the exception of Cuvier's work, the natural history of these fishes has been poorly described. There has been a lot of confusion with regards to distinguishing species within the order of scombroids and many of their anatomical peculiarities have been for the most part undescribed until now.⁵ Aristotle⁶ examined animals of this family and discovered the unusually long and narrow gall bladder in *Sarda sarda*, which, according to Cuvier's observations⁷, is similar to the gall bladder of the tunas (*Thunnus thynnus*, *T. alalunga*). The shape and position of the viscera and the peculiarities of the skeleton are presently the only things we know about the anatomy of these animals. The physiological characteristics of this family are unusual in more than one respect. One need only consider their regular migrations, about which we know very little. Stranger still is the elevated body temperature of the tunas, which John Davy recently discovered⁸. According to J. Davy's observations, *Katsuwonus pelamis*, an Atlantic tuna⁹, had a body temperature of 37.2°C, in an ambient water temperature of 26.9°C, and there are other, less-reliable reports of elevated body temperatures in tunas. The observations we will report in this paper concern structural peculiarities of the viscera and their blood vessels, which are important in both anatomical and physiological respects. We have seen no traces of these structures in other animals. The other reason for the following examinations

involves a discovery of my dear friend Mr. Eschricht in Copenhagen. On November 1, 1833, Mr. Eschricht sent me a piece of liver from a tuna with a note that he had never seen such a peculiar liver structure. It consisted of numerous parallel vessels with small appendices. The whole mass could be torn only lengthwise and appeared fibrous. This sample sent by Mr. Eschricht interested me greatly. It seemed that the entire liver consisted of vessels with small lobes attached to them. In this preparation, the trunks of the vessels were no longer attached. I was therefore uncertain whether the structure belonged to the true glandular tissue of the liver or to the blood vessels. Fortunately, I found the liver and gut of a tuna at the Royal Anatomical Museum. Here I not only substantiated Mr. Eschricht's observations, but also determined that these partly parallel, but mainly radiating vessels were not part of the liver, but were blood vessels that originated from large blood reservoirs on the convex side of the liver¹⁰. The liver consisted of appendices attached to these channels which were quite visible with the naked eye. Such a blood reservoir was found in the convex part of each of the three liver lobes. The blood reservoir of the right lobe continued to the outside as a thick, short vessel trunk. The combined blood reservoirs of the left and middle liver lobes continued into one common vessel trunk. Both vessels trunks were severed close to the liver. When the reservoirs were inflated¹¹, all of the radiating vessels of the liver swelled as well. The gall ducts, on the other hand, did not possess this partly parallel, mainly radiating structure. I could not inflate the liver tissue at all by blowing into

⁵ Müller refers to the scombroids here as an order and in the next sentence as a family. Today they are classified as a suborder (Scombroidei) within the order Perciformes.

⁶ *Hist. anim. ed. Schneid.* Lib. II, 11. vulg. 15. (footnote of the authors, not the translators).

⁷ *Hist. nat. des poissons.* T. VIII, p. 66. 125. (footnote of the authors, not the translators).

⁸ The two papers by Davy are included in section 7 of this issue.

⁹ *K. pelamis* is in fact found in tropical waters worldwide.

¹⁰ The authors often indicate different parts of the liver by using the terms concave and convex. A quick glance at Plate III, Fig. 1 will make it clear why this terminology is convenient. Note that the three lobes of the liver essentially form a cap over the rest of the viscera. The surface of the liver that for the most part faces anteriorly is usually referred to the convex or outer surface of the liver. The surface that faces posteriorly is referred to as the concave or underside of the liver.

¹¹ The authors used the technique of inflating blood vessels with air to elucidate the pathways of the circulatory system.

the *ductus hepaticus*, nor any of the vessels. We then had to determine which of the blood vessels -- the arteries, veins, or portal vein branches create this vascular structure. It was unfortunate that the trunks of all the blood vessels were severed on the concave side of the liver and that the liver was not connected by any blood vessels to the digestive tract or the spleen. However, the end of the sinus on the convex area of the liver proved that it, as well as the vessels originating from the sinus, belong to the liver veins, because that side is positioned toward the heart¹². I could not inflate the entire liver from its main stem on the concave side, and although many vessels lead from there into the liver, the structure was very different from that of the liver veins on the other side, where the whole radiating distribution could be inflated from the sinus.

It became clear from our specimen that the radiating structure of the tuna liver was due to the liver veins¹³. I informed my friend Eschricht of this and requested that he examine his specimen further, but nothing more could be found from the isolated parts of the liver. Mr. Eschricht commented that he supposed that the channels were mainly a continuation of the vessels, and that he would welcome an opportunity to find out if this really were the case. He also felt that too little consideration had been given to the role of blood vessels in the glands, especially the liver. Although it is clear that in embryos the intestine is most prominent in the gut cavity, in adults it is the liver that is most prominent. This was clearly demonstrated in the well-injected specimens from Mr. Ibsen in Copenhagen, where the three vessel systems and the gall ducts were injected with four differently colored substances. With this preparation, the whole liver appears extremely, intricately corridor-like in spite of the fact that the capillaries and the blind endings of the gall ducts were not filled with the colored substance. He suggested examining the livers of dolphin embryos, which he believes possess the same characteristics.

I saw something peculiar on the tuna liver at the local anatomical museum, as well as on the piece of liver sent from Mr. Eschricht, which could not be explained without further investigation. They were 5 cm long, over 2-5 cm thick, tight bunches of reddish-grey vessels without any attached liver tissue. They were distinct from the true liver, and attached to the concave side of it, where the vessels are found. These lobes contained no sign of any liver tissue in their interior; I could

inflate the lobes by blowing into any of the larger vessels at the beginning of the vascular bundle or at the cross-section¹⁴. The tassel-like lobes were much tougher than the main liver tissue, but at the same time, more porous, because of the vessels within the structure. From our preparations, we could not determine what these structures associated with the liver were. Although it was clear that the innumerable vessels, which are held together by connective tissue, suddenly converge into larger vessels at the end pointing away from the liver, these vessels were severed, and I could not make out whether this vessel-like mass attached to the liver was a gland unique to the tuna or part of the vascular system. These lobes could not be confused with the incredible number of pyloric caeca. There was some similarity between a cross-section of the lobes and the cross-section of the testes of some fishes. The testes of the tuna can be inflated as well, but the aforementioned lobes clearly are not reproductive organs. Having observed so many peculiarities, we had to try to find a better-preserved gut of a tuna. I obtained one as a favor from Mr. Lichtenstein, who is the Prussian King's Consul in Montpellier. Although the viscera of this 90 cm long animal were already starting to deteriorate, we could still answer our main questions. I found that the attached mass which branched out on the concave side of the liver is a *rete mirabile* between the portal vein and the veins of the gut¹⁵, spleen, and stomach¹⁶. Therefore all veins of the digestive system are first dissolved¹⁷ into this vessel mass and the blood gets distributed throughout the liver via the *retia mirabilia*¹⁸. This structure is unique in the animal world and is

¹⁴ Müller refers to the gut *retia* as "lobes" here, which is confusing because he refers to liver lobes as well. Fortunately, his use of this term is limited to Section I.

¹⁵ Müller uses the term "Darm" which literally refers to that part of the alimentary canal from the pylorus to the anus, plus the pyloric caeca. There is no corresponding word for this in English. We use the term "gut" to denote this word.

¹⁶ It is true that the *retia* to which he refers form a connection between the veins of the viscera and the liver. There is some confusion over what exactly is meant by the term portal vein. The visceral portal vein connects the viscera to the *retia* and the hepatic portal vein connects the *retia* to the liver. Müller neglects to mention that these venous vessels represent only half of the vessels within the *rete*. The venous vessels are intertwined with arterial vessels formed from branches of the coeliac artery. This point is set straight in the contributions by Mr. Eschricht.

¹⁷ The authors use this term often to describe the incredible branching of relatively large vessels into the nearly microscopic ones which ultimately make up the *rete*. The authors clearly do not mean that the veins dissolve in the chemical sense.

¹⁸ This is the first of a series of comments which imply that there is no physical means for blood of the digestive system to bypass the gut *retia*. If it is indeed true that all blood from the digestive organs must first pass through a *rete*, this has important implications for speculation about the thermoregulatory capabilities of these fish. It has been suggested that a *retial* bypass could allow warm fishes to make dramatic changes in the effective thermal conductance of their gut, thereby affording them better thermoregulatory control of this region (Carey 1981). The complete absence of a vascular bypass of the *retia* would represent a significant stumbling block to this hypothesis.

¹² Although the evidence presented is not all that convincing, the assertion is correct. These vessels on the concave side of the liver are venous vessels leading blood from the liver to the heart.

¹³ These so-called radiating liver veins are actually arteries and veins, as is later stated. They are apparent in Plate I from the original, as well as in Fig. 4, 7, and 14.

stranger still because it seems to conflict with current ideas about the function of *retia mirabilia*. The *retia* on the liver in tuna are more complex than any *retia* observed in ruminants, sloths¹⁹, *Lorus*, dolphins and others. Indeed, one of the several larger *retia* on the liver of the tuna consists of hundreds of vessels²⁰.

Before I continue to describe in detail the *retia mirabilia* of the liver in tuna, I must first give a short description of the digestive system of this animal.

II. General description of the digestive system in *T. thynnus*

The digestive system in tunas and other scombroids was described by Cuvier in his *Histoire des poissons*, Volume VIII; he describes the long, intestinal shape of the gallbladder in *Thunnus thynnus*, *T. alalunga*, *Sarda sarda* and the same long gallbladder in *Scomber*, *Auxis*, *Thyrssites*, and *Lepidopus*. In his *System of Comparative Anatomy*, Meckel neglected the scombroids, probably for a lack of proper sample material. In Meckel's *Archiv 1826*, Rathke also neglected the scombroids in his article on the portal system in fishes.

The stomach of the tuna (Plate III, Fig. 1. *K*) is a long, conical, blind sac with fleshy walls that extends to the posterior end of the gut cavity. It is a direct continuation of the pharynx. The blind, blunt end of the stomach points posteriorly. The *pylorus* is positioned on the dorsal side of the sac. The *pars pylorica* of the gut, into which the trunks of the pyloric caeca (*M*) lead, are anterior to the stomach, with the pyloric caeca (*M*) positioned partly anterior to the stomach, partly to the left of it. The intestine first ascends from the *pars pylorica* anteriorly starting under the liver, turns and ascends posteriorly along the length of the stomach, then turns again anteriorly under the first dorsal bend, and again posteriorly, along the last ascending part to the anus. Its diameter remains constant throughout. The spleen (*S*) is long and narrow and is positioned between the first descending and the first ascending parts of the intestine. With regard to the numerous bunches of pyloric caeca and their structure, I refer to the figure and description which I gave in the paper *de glandularum structura penitiori* p. 64, Plate VII, Fig. 4.5.

As previously stated by Cuvier, the liver consists of three flat main lobes: one in the middle (*G*) and two off to the side (*F*, *H*). Generally triangular in shape, they possess further cleavages which result in secondary lobes; these secondary lobes, however, vary from individual to individual and the number of them is not

constant. The three main lobes of the liver are connected through thin, lobular strips of liver tissue; moreover, the middle lobe and the left lobe converge completely at the base and consequently, these two lobes share the same liver vein stem.

The gall bladder (*I*) is a very long, narrow channel with a blind end, which even in small tuna can be about 30 cm long. Its length is equivalent to the length of the first descending part of the intestine on which it lies, and its blind end reaches close to the anus. In two cases, it was slightly widened near the origin where it receives the liver ducts. The entrance of the gall duct into the gut is found in the region where the last of the five stems of the pyloric caeca enter the gut. The positions of and connections between the organs of the digestive system are shown in Plate III, Fig. 1.

III. Radiating structure of the liver veins. *Retia mirabilia* of the portal vein system

On the convex side of the liver, one can see where both liver vein stems originate (Plate I). The smaller stem (about 8.5 mm wide)²¹ leads blood out of the right liver lobe, whereas the second, thicker one leads blood out of the left and middle lobes. Both stems of the liver vein penetrate the diaphragm and descend into the *sinus venosus*, where they join the left and right body veins²². The *sinus venosus* leads into the atrium. The part of the liver vein stem that is connected to the liver spreads sinuously throughout the upper portion of the liver. The sinuous expansion of the right liver vein stem inside the right liver lobe is about five cm long; in the left and right liver lobe where the expansion is shared, it is about 10 cm long. Both expansions are about 17 to 25 mm wide. The inner walls of these cavities possess many indentations from which the radiating branches of the liver veins originate. These diverge to various regions of the liver, some ascending and others descending in a more or less radiating fashion. Each radiating branch of the liver vein soon branches into more branches, which continue in the same direction along the edge of the liver and continue to the lower surface of the liver. The largest of the radiating vessels have a diameter of 1 to 2 mm, and the smallest have a diameter of 0.5 mm or less. On macerated portions, flecks of liver tissue can be seen attached to the finest vessels. In spite of the peculiar radiating distribution of the liver vein branches, this arrangement of the liver in tuna is probably the same as in humans and mammals. According to Kernan's excellent examinations, the liver veins in mammals are

¹⁹ Müller uses the term "Tardigraden" here (literally, "slow-moving ones") which most likely refers to the sloths. Although the term is used today to refer to the group of invertebrates commonly known as "water bears", it is clear that these are not the organisms to which he is referring.

²⁰ In fact, each *rete* is made up of thousands of vessels.

²¹ Many of the measurements provided by the authors are in lines, which are 1/12 of an inch. We have converted to metric.

²² Fishes obviously do not possess a diaphragm as we know it. The structure to which Müller refers as the "diaphragma" is most likely a fusion of the peritoneal and pericardial membranes (Farrell, personal communication). See Fig. 8 for a photograph of this structure in *T. thynnus*.

packed with tiny *acini* and they receive the *venulae centrales* of the *acini* through innumerable small openings.

On the underside of the liver, one sees the *retia mirabilia* of the portal vein system. The *retia* are various 5 cm long, 13 to 51 mm thick tassels of fine, straight, occasionally-converging blood vessels that are held together with dense tissue. Each vein of the visceral portal system becomes either its own *rete* or, in most cases, part of a *rete* before entering the liver²³. At the base of each *rete*, the blood collects in large vessels which branch into the liver as visceral portal veins. Some of the *retia* are pear-shaped, with the tip pointing away from the liver and accepting the vein; the base sits on the liver and the attached part is smaller than the body of the *rete*²⁴. Other *retia* (namely the small ones) are spindle-shaped. The part facing the liver is always thicker than the stem. One of the largest *retia* is flat and is nearly as wide as it is long. This form is due to a greater number of side-by-side veins entering the *rete*. In such a *rete*, one can discern the small tufts of vessels which correspond to individual veins. As those small tufts can be either pear-shaped or spindle-shaped, the point at which the whole structure is attached to the liver is somewhat bunched together. The narrow base of this *rete* is composed of the smaller bases of the individual tufts. The vessel stem of the *rete* separates immediately into numerous branches, which again separate into smaller branches, so that the main structure of the *rete* consists of many hundreds of side-by-side, mostly straight vessels between 0.5 to 0.7 mm in diameter, which occasionally converge and continue toward the liver. If one inflates a stem, the parts of the *rete* which consist of vessels originating from that stem, swell up. The vessels are also attached at the base and collect into larger ones in various ways.

Three vessels lead from the stomach to the *retia*: one from the right side of the stomach, one from the left, and a third from the ventral surface. A large vessel stem originating from the spleen enters a separate *rete*. Many blood vessels originating from the pyloric caeca and the intestine enter individually into the largest of all the *retia*. All of the above form a row of *retia* over the *pars pylorica* of the intestine.

The right liver lobe possesses two large, separate *retia*. They are attached at their bases to the wide part of the concave area of this lobe; one is pear-shaped, the other is more spindle-shaped. The spindle-shaped *rete* receives a vessel from the right side of the stomach. In the middle and frontal section of the bunch, many small vessels enter from the frontal part of the stomach's ventral surface. The pear-shaped *rete* receives the large vein from the spleen. At the thinner part of that *rete*, smaller intestinal vein

stems enter as well.

The middle lobe of the liver has a very wide, flat *rete* which does not have a simple stem, but separates into many points on the free side²⁵. This *rete* is 5 cm long, has the same width and is 25 mm thick. Many small individual vein stems enter into the points from the *pars pylorica* of the intestine and from the pyloric caeca. Each point contains one or a few small stems. A stomach vessel which runs behind the gall bladder and spleen enters this *rete* as well.

There are several *retia* attached to the left liver lobe: two large, and three small ones. One of the large ones receives blood from the left ventral side of the stomach, the other from the pyloric caeca. This *rete* receives blood from a few small veins as well. On the concave side of the liver, there is a large, thick-walled vessel which partly branches within the liver and partly at the base of the *rete*. This is illustrated in Plate II, Y²⁶. This vessel splits into two branches, but its origin could not be determined in the last specimen because it was severed when the gut was taken out and cut away from the trunk. One branch runs along the concave side of the right lobe, while the other runs along the concave side of the joined middle and left liver lobes. If those vessel stems are inflated, the *retia* swell up as well. Because many of the branches exit the *rete* and spread out into the liver, and because the aforementioned vessel stems branch in the liver as well as in the *retia*, these vessels became even more puzzling. Is this stem an artery or vein? Is it a stem of the portal vein which forms out of the *retia* and connects all of them? If so, where does the main severed vessel originate? Perhaps it receives the veins of the trunk or the reproductive organs, which are not associated with the *retia* but still empty their blood into the portal vein²⁷? However, the fact that the walls of this vessel stem and its branches are quite thick challenges the idea that this vessel is a vein. The most extraordinary size of the nerves accompanying this vessel is also puzzling²⁸. In order to get a clear picture, a new tuna and its vessels had to be examined *in situ*.

The previous observations of the tuna liver and *retia* were presented in Plates I and II and in the last section of the article

²⁵ By "free side", he means the end of the *rete* pointing away from the liver toward the digestive organs.

²⁶ The vessel to which he is referring is the coeliac artery, which supplies the viscera with oxygenated blood from the gills.

²⁷ Blood returning from the trunk indeed does not pass through the gut *retia*. However, tunas do possess a large, sheet-like *rete mirabile* on either sides of their body through which both venous blood from the muscles and arterial blood to the muscles must pass. See Carey (1982) for more on the structure and function of the muscle *rete* in tunas.

²⁸ Indeed, the visceral nerves of the bluefin are gigantic. John Davy comments on the unusual size of the branchial nerves found in this species as well (see Section 7 of this issue). The significance of such large nerves in this species remain a mystery to this day. See Fig. 10 for a photograph of some of these large visceral nerves *in situ*.

²³ More evidence against the possibility of a physical retial bypass. See footnotes 47 and 48 for more information on this issue.

²⁴ See Fig. 13 for photographs of a complete set of bluefin visceral *retia in situ*.

presented on 29 June 1835 at the Royal Academy of Sciences. New materials which were obtained here²⁹ as well as in Copenhagen have yielded greater insight than our previous combined efforts could. New and important findings by Mr. Eschricht as well as the results of the examination of a second tuna here are contained in the next two sections. After personal communication with my friend in the fall of 1835 in Copenhagen about the *retia* of the portal vein, the questions at hand became more pressing to both of us. A rich source of information suddenly became available in Copenhagen. Soon after my departure from Copenhagen, they received a very large, fresh tuna caught in the strait³⁰. Mr. Eschricht not only confirmed the *retia* of the veins of the digestive system, but made a new and important discovery. He found that some of the vessels of the *retia* were arterial and that the artery of the digestive system, the aforementioned one which was puzzling to me³¹, branches partly into the liver and partly to the base of the *retia* where it dissolves into innumerable vessels which make up some of the *retia* and combine on the free end of the *retia* into a single vessel leading to the gut. Certain vessels of the *retia* which lead to the liver receive blood from the veins of the intestine, stomach, pancreas, and spleen. The other vessels of the *rete*, which run in between the venous vessels, receive arterial blood and lead to the digestive system: the spleen, pancreas, stomach, and intestines. In contrast, the arterial vessels of the liver do not form *retia* before entering the liver³². The *retia* therefore possess a double connection; they connect to the liver via the hepatic portal vein and to all the other parts of the digestive system via the arteries³³. Although they are connected with the liver, they are of equal importance to all the other organs of the digestive system.

I now present word for word the results of Mr. Eschricht's examination of the aforementioned tuna.

IV. *Retia* of the arteries of the digestive system. Relationship of these to the *retia* of the portal vein and to the liver veins

(Contribution to the anatomy of the tuna liver by Mr. Eschricht.)

The tuna whose liver was used for the following examinations arrived in Copenhagen on 29 September 1835. It was alleged to

²⁹ Berlin.

³⁰ The strait to which he is most likely referring is the Oresund, which is the strait which separates northeastern Denmark from Sweden.

³¹ The coeliac artery.

³² The physiological consequence of this arrangement is that the temperature of the liver is not as elevated as that of the other viscera, which are more thermally isolated from the cold arterial blood via the gut *retia*. The difference in temperature between the liver and organs such as the stomach and caecum can be 6 °C in this species (Carey et al., 1984).

³³ See Fig. 2 for a schematic of the visceral circulation in the bluefin tuna.

have been caught on the 27th near Helsingør in a large net, which the fish partly destroyed. Its weight was estimated to be around 180 kg. Its length from snout to tail was 270 cm, from snout to the edge of the operculum it was 67 cm and its girth at the widest part was 128 cm. It was a male (as was later determined).

The body cavity was widely cut open to the pericardium. Because the liver tissue was so soft that it tore easily when touched, we approached the main branches of the vessels, which were the easiest to get to, with great care. Mr. Ibsen injected the two large liver vein stems which were severed close to the pericardium with a green substance; some arterial stems which were positioned on the right side of the liver, beside several portal vein branches, with red, and several portal vein branches with a yellow substance. The gall ducts were injected (with very little success) with a white substance from the *ductus cysticus*. The injection substances all consisted of colored glue. The work on that colossal animal took from one o'clock in the afternoon until evening and because the liver continued to disintegrate more and more, it was removed and kept in a strong ethanol solution. A few days later, Mr. Ibsen tried (again with limited success) to inject several branches. The liver remained in ethanol for several weeks and was only examined long after the skin of the fish was stuffed and the flesh distributed for consumption. The width of the liver was 70 cm and from front to back it was 28 cm.

On the convex, anterior side, and on the posterior, slightly concave side, the tuna liver possesses several cleavages which give it its lobed structure. One can distinguish six lobes on the convex edge, each of these possessing four lobes. These lobules are separated to different degrees and are themselves further cleaved (though less deeply) or possess small appendages.

The outer surface of the liver is generally convex; the inner surface is somewhat concave. On the underside a few cone-shaped³⁴ masses stand out. There are eight of them.³⁵ The largest six exist in pairs and can be classified as the right, middle, and left pairs. Each of these pairs consists of a frontal and a back cone which are connected more or less at their base. In addition, there are two unpaired, smaller cones between the left and middle pair.

At the location where the base of the cone attaches to the underside, one can place a spatula partly between the cones and the actual liver if a small amount of tissue is removed. Only part of the base of the cone continues into the liver. The rest of the base is therefore contiguous but not continuous with the liver.

At the cone's point of connection, the liver itself is extremely

³⁴ Eschricht refers to the *retia* as "cones".

³⁵ Our examinations have led us to classify the *retia* into five main groups. This way of classifying the *retia* is for the most part in agreement with the authors' findings. The only difference lies in the way small associated *retia* are classified. Fig 1. clearly defines the five *retia* we consider to be discrete and indicates which organs they serve as well as to which liver lobe they attach.

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At the location where the base of the cone attaches to the underside, one can place a spatula partly between the cones and the actual liver if a small amount of tissue is removed. Only part of the base of the cone continues into the liver. The rest of the base is therefore contiguous but not continuous with the liver.

At the cone's point of connection, the liver itself is extremely thin; in my colossal specimen it was 6 mm thick at most. These thin areas of the liver cannot be seen on the convex side of the liver. On the concave side they appear as an indentation that surrounds all the cones. Here they are connected to each other by means of smaller vessels. These form the portal system of the liver.

In the hepatic portal area one can find (1) the gall ducts, (2) some nerve stems and (3) a large artery, which we will call "thick-walled" because of its nearly cartilaginous walls³⁶. The visceral portal vein enters into the tips of the cones whereas the liver arteries exit from the convex surface of the liver, not far from the back edge. On the tip of the cone, one finds beside the entering veins a few arterial stems whose walls are not nearly as thick as the walls of the aforementioned artery. On the right frontal cone (which was especially well-injected and therefore could be examined precisely), we found a nerve stem the thickness of a feather shaft. A similar, even thicker nerve stem could be seen on the base of the same cone or on the cone paired with it.

Among the gall ducts the *ductus choledochus* is quite narrow. Although it empties into an enormous gallbladder (84 cm long in the desiccated state), the *d. cysticus* is even narrower. The gall bladder lies along the midline of the whole body cavity and it was very difficult not to damage it while cutting open the body cavity. The *d. hepaticus* decreased in width several times, and continued across the lower liver surface, branching within the portal area to each of the liver lobes. The path of one of its branches was especially conspicuous. It passed between the two central cones, where it was covered in a bridgelike fashion by the tissue connecting the two.

Within the liver, the liver ducts seem mainly to follow the *tractus* of the arterial branches; deeper down, however, their exact path was difficult to determine because of their thin walls,

and because the injection was only partially successful.

The portal vein is formed by a large number of small branches which enter into the tip of the cones. These branches come mainly from the digestive system and possibly from other parts of the posterior half of the body (I agree with this speculation, but the findings from the last tuna do not substantiate it). The three paired frontal cones appear primarily to receive the veins of the gut, while the ones further to the back receive the veins of the gut as well as veins from the surrounding area. The blood enters the aforementioned cones through many stems. For example there are 14-16 stems which enter the middle cones in the back; each of the stems soon after turns into a flat mass which appears to be part of the liver tissue.

Prior to injection, most of the liver surface, namely the cones and the convex surface, appeared striped, as I noticed a long time ago on a tuna liver preserved in alcohol, which, incidentally, was the observation that originally instigated this study. After injection, everything became clear. The arteries were red, the portal veins yellow, the liver veins green, and the gall ducts were (very incompletely) white.

After injection, different parts of the liver were distinctly colored, with most of the parts appearing striped in alternate colors. The cones were striped throughout with red and yellow, without any trace of green and without any evidence of other tissue in between. The convex surface of the liver appeared striped in a fan-shaped manner. The stripes were mainly green in color with fewer red, far fewer yellow, and very few individual white stripes. The lower liver surface was striped with the same color pattern in the portal area; the area closer to the frontal edge was not striped, but was grey-brown with isolated darker round spots each with a diameter of about 2 mm.

After some incisions were made and many tests performed in order to follow the individual stems, the following results were obtained.

Structure of the cones. They are truly *corpora spongiosa*, in that they consist only of vessel bunches of the portal vein and the arteries. The two blood vessel types are completely isolated so that nowhere did the injected material mix³⁷. The vessel bundles consist entirely of many long vessels of nearly the same diameter (about 0.7 mm wide - all measurements were done with the naked eye), which are fairly straight and parallel to the axis of the cone and which continue along its entire length. This can be seen on the surface of the cones, as well as by cutting into them. The cut surface of a cross-section appears sieve-like because of the

organs they serve as well as to which liver lobe they attach.

³⁶ Here again is a reference to the coeliac artery described previously by Müller (see footnotes 26 and 31).

³⁷ This remark is significant in that it implies that there is no mixing of arterial and venous blood within the *rete*.

numerous, nearly similar diameter holes of the severed vessels³⁸. At various locations, the vessels deviate from this straight path. This occurs in particular around the aforementioned large nerve stem, which branches slightly within the cone and continues within it approximately along the cone axis. Within the *rete*, the nerve stem is enclosed by a cellular sheath, similar to the *commisura anterior* of the brain. Around this sheath the vessels are not straight, but instead form a kind of mesh. At the base of the cone the vessels deviate completely from their previously parallel, lengthwise direction. First, they turn toward the centre, and when they reach it, they then turn toward the base. They turn a final time, radiating out, and soon after appear as true vessel stems.

The vessels of the cone are therefore connected at their tip as well as at their base with the vessel stems, and this applies to both the vessels of the arterial system as well as those of the portal vein system. The vessels within the cones are generally analogous to *retia mirabilia*, especially those found in the extremities of sluggish mammals. If these cones did not belong to the true liver, but instead were a diverticulum of the digestive vasculature, the tunas could be called "liver sloths"³⁹.

The question at hand is whether the blood in each cone flows from the tip to the base or vice versa, a question which must be resolved by examining the parts in relation to one another, but also through the examination of the isolated liver.

At the base of the *rete*, the vessel stems with which the *rete* vessels are connected are found in the portal area. These vessels then become the portal vein stems which lead only into the lobes of the liver; there therefore must be a subsequent or second branching. For the portal blood vessels, the question of the blood's path is easily answered; the blood enters from the digestive system into the tip of the cone, diverges into numerous vessels and converges in the portal area. Thereafter it branches in the usual way in the liver lobes.

If the direction of blood flow for the arteries in the cone is the same as that of the portal vessels (as described above), this would be consistent with other animals, in which the arterial and portal blood flow in the same direction. However, the situation is seemingly the opposite. First of all, the portal vein branches come from the digestive system and the arterial blood can not come from there, but instead must go there. Secondly, the arterial stems in the tips of the cones are quite thin-walled, whereas the ones in the portal area are very thick-walled, so that by cutting

into the previously-mentioned thin liver areas, the tissue seems slightly cartilaginous. There are branches of the thick-walled artery in the portal area which branch again, accompanying the secondary or true portal vein branches into the lobes of the liver. This view is supported by the fact that the large nerve stem, the vagus, of the right frontal cone, only passes through in such a way that it enters at the base and exits at the tip. Inside the cone it only branches a few times, with all of the branches directed towards the tip, except for the last branch which runs back into the tip of the cone⁴⁰.

The path of the arterial blood is as follows. The thick-walled artery is the common stem of the liver arteries and the arteries of the digestive system. In the portal area, it branches out partly as the true liver artery, entering the lobes of the liver with its branches following the path of the hepatic portal veins, and it partly transforms into innumerable thin vessels, which originate from the main branches at rather shallow angles. Thereafter (along with the similar *rete* vessels of the portal vein stems), the branches form the spongy cones. At the tips of the cones, they reconverge at very sharp angles into branches according to their destinations into the digestive system⁴¹.

Now we will describe the lobes of the liver. As previously described, the liver veins originate from the convex liver area close to its back edge; these areas appeared with thick, green stripes after injection (the color of the injected liver veins). The stripes radiate in a fan-shaped manner over the entire surface toward the frontal edge, and in this case, a few branches of the portal vein, the liver arteries, and some of the bile ducts run parallel to these stripes. It was also observed that on the underside, at least in those parts closest to the portal area, a similar fan-shaped distribution exists, otherwise in that area the liver surface appears more evenly grey-brown, with isolated darker spots.

The stripes, which can be seen on the surface of the liver lobes, are mainly due to straight vessel branches of similar thickness of all three vessel types⁴² (especially the liver veins), and as far as I know, the bile ducts as well. These vessels have a completely different significance from the vessels in the cones. They are not *retia*⁴³. Their linear form can be attributed to the

³⁸ See Fig. 12 for close-ups of all the major visceral *retia* in cross-section.

³⁹ By naming these tuna "Leberfaulthiere", Eschricht is making a (somewhat bizarre) connection between the structure of the *retia mirabilia* found in the tuna gut and those found in the extremities of the sloth.

⁴⁰ This passage is extremely confusing. As odd as it may sound, Eschricht seems to be saying that the nerve actually exits the tip of the *rete*, turns around and re-enters it. More importantly, the passage suggests that the nerve branches within the *rete*. The implication is that the vessels that make up the *rete* are innervated.

⁴¹ This and the previous paragraph are the first clear statements indicating that arterial blood flow is countercurrent to venous blood flow.

⁴² The three vessel types are hepatic arteries, hepatic veins, and hepatic portal veins.

⁴³ We believe that these vessels make up a crude *rete* which helps conserve metabolic heat produced in the liver.

fact that the liver separates regularly from the portal area out into subsections in approximately the following manner:

Adjacent to the portal area, the liver tissue is tube-like. At this point, all of the branches diverge slightly, spreading first toward the frontal edge, then turning towards the lower surface. Along this path, more and more granular tissue appears between the vessels, and beginning with the lower surface and the frontal edge, this tissue makes up a great part of the whole. If one tears the liver tissue, especially the somewhat macerated pieces, it always tears parallel to the given direction and doesn't appear cellular like the cones. Instead it is granular due to the tissue surrounding the vessels. Because of this, the vessels appear to quite often have blind sacs attached to them. However, I could not find any injected material from any of the vessels entering into these sacs.

If one could explain the nature of the granular tissue, the tuna liver would be the first liver whose structure was sufficiently understood. As is usually the case, one small, but important bridge remains to be crossed.

If we take a detour around this bridge, and follow the returning liver veins, then we see that they converge into two large reservoirs which are found transversely on the convex surface of the liver, not far from the back edge. From there the reservoirs discharge into two very large vessel stems which soon after lead into the venous sinuses⁴⁴.

This is the conclusion of Mr. Eschricht's observations.

V. Characteristics of the other visceral organs and vessels

The main goals of the entire investigation were reached. However, the relationship of the veins of the reproductive organs and the urinary system to the rest of the veins remained to be explained. A 90 cm long tuna which had been sent in the fall of 1835 from Montpellier reached us in Berlin in April, which was early enough to shed some light onto this matter before the conclusion of our work. We are thankful for the consideration of Mr. Lichtenstein in Montpellier, who arranged the sending of the specimen to us. At the same time, Mr. Eschricht was nice enough to send the injected liver described previously from the tuna acquired in Copenhagen for comparison, even though he had sent the results of his examinations much earlier by letter. After examining the injected liver, I have nothing to add to Mr. Eschricht's findings.

One observation that I made on the second tuna from Montpellier concerns a strange peculiarity of the structure of the

kidneys. After the side walls of the body were removed, the gut of this animal was prepared *in situ*. The drawings of Plate III, Fig. 6 were made thereafter.

The kidneys of the tuna are not positioned along the upper body wall, as they are in most fishes. Instead they are positioned only over the anterior part of the body cavity. Indeed, the majority of the tissue can be found in the space between the pectoral girdle and both sides of the beginning of the aorta, at the point where the aorta originates out of the convergence of the gill veins, dorsal to the esophagus, and dorsal and posterior to the gills. See Plate III, Fig. 5. Its anterior end reaches up to the anterior gill veins, and nearly to the posterior part of the skull; at this point the two posterior gill veins of each side are covered by the kidney from above. From the beginning of the aorta to the point where large arteries branch off to both sides of the trunk, the kidneys are separated and between them the largest part of the aorta is found. Prior to the continuation of the aorta as the *arteria caudalis*, the kidneys exist as a common mass, continuing unpaired⁴⁵ and narrow for a stretch in the middle of the upper body wall, without reaching the halfway mark of the length of the body cavity. The anterior, paired part of the kidney is very thick and wide and its outer and upper surface is adjacent to the outermost and uppermost part of the inner trunk walls and the pectoral girdle; in contrast, the smaller posterior part is very thin. The kidney clearly consists of small flat lobes; this is especially evident on the upper and small posterior parts. Just before the posterior end, the unpaired kidney separates again into two short terminal lobes, with a branch of the ureter originating from each lobe. Both branches combine immediately at a steep angle to form an unpaired channel, which continues in the midline of the body wall as a thick-walled tube. Only the beginning of the ureter of the tuna is paired and the stem which passes through the largest part of the body cavity is unpaired, a formation which is not known in any other fish. Upon opening the body cavity, neither the kidneys nor the ureter are immediately visible. They are separated from the body cavity by a fibrous tissue, which must be removed in order to see them. This tissue is very strong and firm where it descends prior to the unpaired ureter. The 2.5 mm long body of the urinary bladder is connected to the lower wall of the most posterior end of the ureter. The urethra continues behind the rectum and enters into the common urogenital opening which is positioned posterior to the anus, as it is in other fish.

The beginning of the aorta originates from the first two pairs

⁴⁴ See Fig. 4 for a photograph of these vessels which lead blood out of the liver toward the heart.

⁴⁵ In this section, Müller often uses the terms "paired" and "unpaired" to describe organs and vessels. When he uses the term "paired", he means that there are two separate, discrete structures. "Unpaired" is used to refer to a singular mass or vessel that in some nearby location is paired.

of the gill veins. At first, the first two gill veins combine on each side into a common stem. Both common stems, the *venae branchiales communes*, converge at a steep, posteriorly pointing angle. This is why the start of the aorta is unpaired between the anterior ends of the paired parts of the kidneys. The beginning of the aorta receives them as well as the two posterior gill veins from each side. From the beginning of the aorta to the branching off of the arteries of the trunk, the *arteriae axillares*, the aorta is very thick⁴⁶. From that part of the aorta, some kidney arteries branch off laterally and the only large artery of the digestive system branches off in a ventral and posterior direction. The *arteriae axillares* and the *venae axillares* penetrate the posterior area of the lateral main portion of the kidney in such a way that they obliquely lead to the muscles of the trunk. Within the kidney, the *arteriae axillares* send off branches to the kidney. After the exit of the *arteriae axillares*, the dorsal aorta suddenly decreases in diameter by more than half. This part of the aorta continues for only a short distance above the posterior, unpaired part of the kidney, which still contains branches at this point, and then enters into the channel of the lower spinal processes, until it ends as the *arteria caudalis*. The channel of the lower spinal processes begins in tuna at the ninth vertebra in the anterior part of the body cavity. At this point, the posterior ribs are affixed to the lower processes. The tail does not start until the 19th vertebra. For its whole length, the aorta is positioned in the channel of the lower spinal processes.

The *arteria systematis chylopoetici* descends with the large nerves of the digestive organs between the pharynx and kidney, comes from the right of the pharynx to the concave area of the liver, and separates at this point into two branches, sending small branches to the diaphragm and the surrounding area. One branch follows the concave surface of the right liver lobe; the other follows the same area of the middle and left liver lobe. At the point where the branches run along the base of the *retia*, they send many branches, the *arteriae hepatica*, into the concave surface of the liver. The remaining branches get distributed completely into the bases of the *retia* and form the arterial part of them⁴⁷. Leaving the *retia*, the arterial branches converge again into the formerly described stems which have much thinner walls than the arterial branches entering the *rete*. The arterial vessels originating from the *retia* branch out everywhere accompanied by

the veins to the stomach, intestine, spleen, and the pyloric caeca. All arteries of the digestive system, including those of the liver, originate from that artery. All branches of this artery intended for the stomach, gut, spleen and pancreas first transform into *retia*⁴⁸. I could not find the arteries of the reproductive organs without injection.

The sinus for all the body veins, which is connected to the atrium, has a pointed appendix on the left side. At the posterior end, the sinus receives the two liver vein stems after they penetrate the diaphragm; ventrally and anteriorly, it receives a vein from the ventral wall of the throat area (the *vena jugularis inferior*). From the left and right, it receives the *venae cavae communes*, with each vein consisting of an anterior and ventral branch. The anterior branch is positioned on the ventral side of the paired portion of the kidney between the kidney and the pericardium. The posterior portion of the *vena jugularis* penetrates the lower part of the paired, main portion of the kidney on each side, receiving kidney veins as well as the veins of the prostate along the way, and ending as the posterior main vein of the trunk muscles, the *vena axillaris* or *vena lateralis posterior*. No vein exits at the point where the continuations of the aorta enter the channel of the lower spinal processes. One can see that the positioning of the main venous vessels differs slightly from that in other fishes⁴⁹.

VI. *Retia* in other fishes

The *retia* of the tuna are not the only *retia* of their kind in this class of fishes. First of all, this structure seems to be shared by all species of the genus *Thunnus*⁵⁰. In addition to having the opportunity to examine *T. thynnus*, we have also examined juvenile *Thunnus thynnus*⁵¹. Dr. Grube was nice enough to send us the gut of a tuna from Cette⁵² that I recognized as a juvenile *T. thynnus* because of its small, silvery swimbladder, which

⁴⁶ The arterial supply to the musculature of bluefin tuna is via lateral arteries, *arteriae axillares*, and not via the dorsal aorta.

⁴⁷ Müller previously implies (see footnote 23) that all venous blood from the digestive system must first pass through a *rete* before reaching the liver. Here he implies that the same is true for the arterial blood en route to the digestive organs. If both of these implications are true, it seems highly unlikely that a macroscopic physical bypass of the gut *retia* exists. Of course, this kind of evidence does not rule out the possibility of some other kind of functional bypass.

⁴⁸ More evidence against the possibility of a physical bypass of the gut *retia*. See footnotes 23 and 47 for more on this issue.

⁴⁹ *T. thynnus* is one of the only fish known (along with *Lamna nasus*) to lack completely a posterior cardinal vein. Lateral subcutaneous veins return blood to the heart in these fish. It is actually somewhat surprising that Müller doesn't mention the prominence of the lateral circulation displayed by this species. See Carey & Teal (1966) for more information on the unique circulatory modifications of tunas and how they relate to their endothermic lifestyle.

⁵⁰ Not all species of the genus *Thunnus* possess visceral *retia mirabilia*.

⁵¹ *Thunnus brachypterus*, the name used by the authors, is most likely the name (mis)assigned to small individuals of the species *Thunnus thynnus* (Bruce Collette, personal communication). With this in mind, the striking similarity between the viscera of *T. thynnus* and that of this "species" is not surprising.

⁵² We are at a complete loss as to the meaning of the this word. There is no geographical place in the modern world named Cette. It is possible that Cette was a museum or the name of a private collection.

Cuvier describes. The *retia* behave the same way as in mature *Thunnus thynnus*; the kidneys are found in the same location and the ureter is unpaired as well. The *retia* receive the blood from the same areas as in mature *T. thynnus*, except that the blood from the small swimbladder is received by the portal vein via the back *rete* of the right side⁵³; this small vein receives the blood from the surface of the swimbladder and the posterior portion of the peritoneum that lies atop the swimbladder; veins not belonging to the digestive system do not enter the *rete* at this location. I have not yet been able to examine *Sarda* and *Thyrssites*. I found no *retia* in *Scomber scombrus*. I did observe a similar structure in the elasmobranch⁵⁴, *Lamna nasus*. Not long ago, the Royal Anatomical Museum received a very large specimen of *L. nasus*, which was captured near Copenhagen and preserved in salt. Mr. Eschricht acquired this large female shark for us in exchange for another specimen and sent it fresh. Although it took a long time to get here, the viscera were preserved well enough that we could examine them. Upon removal of the gut, I became aware of two adjacent masses composed entirely of blood vessels which lay on the dorsal side of the body cavity to either side of the pharynx and partly over the liver. They were shaped like a flat, compressed pyramid with the base of the pyramid pointing posteriorly. Both their form and structure resemble the *retia* of the tuna. They consisted of anastomosed blood vessels which ran lengthwise, and could be completely inflated from the top as well as from the bottom of the mass. On the upper and lower part of the vessel bodies, the vessels formed a far-reaching network and converged into larger vessels. In addition, I could differentiate arterial and venous vessels within these bodies. The severed vessels started from the upper part of the mass in a bunched form. Here they entered on each side of the pharynx into the *retia*. We could not determine where the stems originated due to the manner in which the gut had been removed. The arterial part of the *retia* seemed to be braided throughout with a venous mesh. On the base of the *retia*, many (arterial?) vessels collected into stems, which spread out to the organs of the digestive system but also into the liver itself. The arrangement of the *retia* described above was not the same as that in the tuna. The venous part of the *rete* behaved quite differently. It did not originate from the portal vein. Instead, the portal vein ran completely and directly to the portal area, where it spread out into both of the long, flat lobes of the liver. The liver vein stems on the other hand, instead of immediately

reaching the sinus of the body veins, continued along the base of the *retia* and supplied them with a great number of vessel bundles⁵⁵, while on the upper part of the *retia*, these vessels collected again into large reservoirs. Because these reservoirs were severed when the gut was separated from the upper body wall, we could not determine how the vessels continued. Overall, only the general structure could be determined because of the decomposing condition of the gut; how far we can expand and supplement these aforementioned findings will depend on further examinations. The kidneys of *L. nasus* do not lie in the anterior-most part of the body cavity as they do in the tuna, but rather in the posterior region of the body cavity, as is usually the case in sharks. The separation of the spleen into a large number of little lobes caught our attention, as well as the unusual thickness of the *ductus choledochus*, which is a result of its thick walls. Completely surrounded by a muscular tissue characterized by distinct longitudinal strands, it descends into the beginning of the gut where the spiral valve is found. After dissecting out the eye, one finds on the bottom of the eye socket a tissue composed of twisted vessels, whose connection could not be determined any further⁵⁶. I have searched for *retia* in the body cavity of various sharks of the family Scyliorhinidae or in the genera *Galeorhinus*, *Squatina*, *Mustelus*, *Etmopterus*, *Oxynotus*, *Sphyrna* (*tiburo*), but I have not found any analogous structures in any of them. The individual genera within the shark family possess so many anatomical peculiarities that we should not be surprised by these differences. In addition, the rays of the genera *Myliobatis*, *Raja*, *Taeniura*, *Torpedo*, and *Rhinobatus* which I examined also showed no analogous structures. The liver of *L. nasus* does not possess the exquisite radiating structure of the liver veins as seen in the tuna, although the vessels do diverge slightly over long stretches.

VII. Significance of the *retia*

⁵⁵ Müller's description of the gut vasculature in *L. nasus* implies a different style of heat exchange than occurs in the tunas. Based on Müller's descriptions, the gut *retia* in *L. nasus* serve all of the visceral organs including the liver. In the tuna gut, the *retia* are positioned between the liver and the other visceral organs. The result of this arrangement is that the liver in *T. thynnus* is cold in relation to the digestive organs. In *L. nasus*, the *retia* occur on the other side of the liver. All arterial blood en route to the viscera must first pass through a heat exchanger. Similarly, all blood leaving the viscera, including blood of both portal and liver vein origin, must also pass through an exchanger. In this way, all of the visceral organs, including the liver, are thermally isolated from the cold gills. See Carey et al. (1981) for more information on this issue. See also Fig. 3 for a schematic of the visceral circulation in *L. nasus*.

⁵⁶ These twisted vessels to which he is referring make up the orbital *rete*, which is a countercurrent heat exchanger which allows the temperature of the eye, brain and ocular muscles to remain elevated above ambient. See Block & Carey (1985) for more on the cranial *retia* found in warm sharks.

⁵³ The implication here is that in mature *T. thynnus*, the blood from the swimbladder does not pass through a *rete*.

⁵⁴ The authors use the term plagiostome here, which, has been replaced by the term elasmobranch.

The different vessels which make up the hepatic portal vein enter the liver individually, which is a common arrangement in fishes. Rathke has reported a few examples. However, the unusual *retia* that occur at this transitional location represent a structure that has not been observed until now. Likewise, no case has been reported which could, even to a small extent, be considered analogous to the *retia* of the arteries of the digestive system. The idea that the arteries of the digestive system of all animals form anastomosing arches of the first, second, and third order⁵⁷ is not supported in this case. The network of vessels within the *rete* converges into one or a few stems which continue from the *rete*. A mesh-like distribution of an artery without the development of a new stem may have some characteristics of a true *rete*, yet such a structure is more similar to the usual anastomosing behavior of the small arteries, which often form net-like structures long before diverging into capillary networks. The dissolution of an artery stem into a plexus that is not designed to make distribution of blood easier, but rather collects the blood into a new stem, points to an undiscovered function for the particular arrangement of these structures⁵⁸. If one were to compare the visceral *retia* of the tuna with similar structures in other animals, one would realize that they not only represent some of the few true *retia* known, they are the most elaborate structures of this kind known to date. Without a doubt, an explanation of the function of the *retia* lies within the *retia* themselves.

Retia are known currently to be found in the following locations: in the extremities of *Lorus*, *Tarsius*, the sloth, and the anteater, in the tail of the latter, on the *carotis cerebralis* of the ruminants, on the *arteria ophthalmica* of some mammals and birds, on the penis of the bird⁵⁹, on the *venae iliacae* and the intercostal arteries of the dolphin, and on the so-called carotid gland of the frog⁶⁰. The existence of such a formation can be

attributed partly to a mechanical cause, as can be recognized by the increase in surface area and the small size of the vessels which result in a local slowing of the blood flow relative to the speed in the other parts, due to the effects of friction and capillary action, which increase within these formations⁶¹. The *rete* of the *carotis cerebralis* is a good example of the above phenomenon. It is strange that the animals which possess true *retia* in their extremities, such as the sloth and *Lorus*, stand out due to their sluggishness. On the other hand it is possible that the arterial *retia* in the extremities and tail assist blood flow by essentially bypassing obstacles to flow presented by the continuously contracting climbing muscles. The latter hypothesis cannot be used to explain the existence of *retia* which are not exposed to muscle pressure, such as the *retia* of the *carotis cerebralis* of the ruminants, the *carotis* in frogs, and the arterial and venous *retia* of the tuna and *L. nasus*. According to Rapp's observations, in animals with a *rete* of the *carotis cerebralis*, the *arteria vertebralis* does not supply the brain with blood. This shows quite clearly that in these cases, more of a retardation of the blood flow is intended⁶². This explanation has the advantage that it can be applied to all *retia*, although the reason for the local retardation of the blood flow relative to other areas remains a mystery. For the arterial and venous *retia* of the tuna and *L. nasus*, one could apply this explanation in the following way. The usual arrangements of the portal vein system in all animals will most likely be the reason for a local slowing of the blood flow in the capillaries of the gut, spleen, and liver. Because the blood coming from the gut, spleen, and pancreas must pass through a second capillary vessel system, namely that of the portal system of the liver, the blood flow in the vessels of the whole digestive system must be a little slower than in the other parts of the body, where the blood, after it overcomes the resistance of friction and capillary action of a simple capillary system, immediately reaches the general circulation. The *retia* of

⁵⁷ What Müller is trying to convey is that the presence of the visceral *retia* in this species is inconsistent with the concept that arterial vessels originate as a large vessel (i.e. the aorta) and branch into ever-smaller vessels, eventually forming the capillaries. The *retia* represent a violation of this rule, because the arterial vessels at the warm end of the rete actually converge and increase in diameter before proceeding to the viscera and diverging into capillaries.

⁵⁸ The undiscovered function to which he alludes we now know to be countercurrent heat exchange.

⁵⁹ Most birds do not possess a penis. Müller is most likely referring to waterfowl, most of which do possess a penis.

⁶⁰ We refer here to the papers of Carlisle, Vrolik, Rapp, Huschke, Barkow, v. Baer, and Breschet:

Carlisle. Philos. Transact. 1800. Account of a peculiarity in the distribution of the arteries sent to the limbs in slow-moving-animals. *Continuation Philos. Transact.* 1804.

Vrolik. *Disquisitio anatomico-physiologica de peculiari arteriarum extremitatum in non-nullis animalibus dispositione*. Amstelod. 1826.

Rapp. "Über das Wundernetz (der Carotis)". Meckel's *Archiv für Anat. und Physiol.* 1827.

Huschke. "Über die Carotidendrüse einiger Amphibien. Tiedemann's *Zeitschr. f. Phys.* IV 1.

Barkow. "Anatom. physiol. Beobachtungen." Meckel's *Archiv für Anat. und Physiol.* 1829.

v. Baer. "Über das Gefäßsystem des Braunfisches." *Nov. Act. Nat. Cur. XVII*. Breschet. *Hist. anat. et physiol. d'un organede nature vasculaire de couvert dans les cetacés*. Paris. 1836.

(footnote of the authors, not the translators)

⁶¹ Müller's analysis is flawed here. The relative rate of flow of the blood is inversely proportional to the total cross-sectional area of the vessels in parallel. Compared to this phenomenon, the effect of drag from the vessel walls is negligible.

⁶² The implication is that the *rete* must serve some important function if in those species which possess a carotid *rete*, blood flow through the *rete* is obligatory. Müller believes the important function to be a slowing of the blood flow, which we now know is not false, but is incomplete as an explanation. See the next footnote for more musings on this issue.

the portal vein in tuna will slow the blood flow even more than it does in the portal veins of other animals. The thousands of fine vessels through which all blood of the visceral portal veins must flow before reaching the liver represent additional resistance and because of that, the blood flows even more slowly than in the capillaries of the gut and portal vein branches of other animals. The *retia* of the arteries of the digestive system in tuna represent yet another obstacle which affects all of those areas downstream of the *retia*. For this reason, the passage of blood through the vessels of the gut, spleen, and liver is slowed even more. In the tuna, one might conclude that the *retia* of the portal vein have something to do with the liver. However, the same could not be said about the *retia* in *L. nasus*, in which the portal vein takes no part. The above reasoning also is consistent with the two visceral *retia* found in *L. nasus*. The blood flow is slowed to the same degree in the same areas. The origin of the arterial part of the *rete* could not be found in *L. nasus*; with regards to the resistance to flow resulting from the venous *retia*, it is the same for the entire digestive system, regardless of whether the slowdown occurs before the blood enters the liver or after. In both cases blood flow in the entire digestive system is slowed⁶³.

Given what we know, it cannot be determined whether this explanation is correct. The difference between the arrangements of the venous parts of the *retia* in the tuna and *L. nasus* supports this theory. Because the visceral portal blood must pass through *retia* en route to its union with the rest of the venous blood, the flow of blood throughout the entire digestive system is affected, but the quality of the blood is unchanged for its passage through the liver. The last assumption is only possible in tuna, where the venous *retia* are found before the blood enters the liver.

We cannot conclude with certainty whether a quantitative

change of the blood takes place in the *retia* of tuna and *retia* in general. However, there are several reasons for not abandoning this idea.

The lymphatic plexus and its transition into lymph glands, which mainly are made up of fine branches of lymph vessels, offer a good parallel to the blood vessel formation mentioned here. What are the lymph gland vessels other than *retia* of the lymphatic vessels between the *vasa adferentia* and *efferentia*? With regard to the lymphatic *retia*, the key to their function lies in their increased surface area, the qualitative changes that occur there and the chemical influences exerted there. Exactly the same could be concluded about the analogous vascular *retia* of the digestive system.

Perhaps the main reason for the peculiar temperature of tunas, first reported by J. Davy⁶⁴, lies in the *rete*⁶⁵ and the chemical action of the vessel walls and the blood. He observed a few years ago that *Katsuwonus pelamis* had a temperature of 37.2 °C in water that was 26.9 °C. According to reports from fishermen, the common tuna, *Thunnus thynnus*, is alleged to be warm-blooded and according to the same reports, other species of this genus have an elevated temperature as well. J. Davy suspects that the high position of the kidneys near the gills is related to heat production in tuna, in that the gill nerves are so extraordinarily large and furnished with large ganglia. It is unlikely that this hypothesis is correct. One can hardly conclude something about the function of an organ merely by its position. For example, the *corpora suprarenalia*⁶⁶, which lie close to the kidneys, have no physiological relationship to them; they could just as well be positioned in the pelvic region or the thorax, and often *corpora suprarenalia* and kidneys are completely separated from one another. Attempting to infer the physiological significance of a structure merely from its position in the body is shown to be inappropriate by the examples of: the Wolffian bodies⁶⁷, the kidney, the *corpora suprarenalia*, and the testes.

From *Katsuwonus pelamis*, which J. Davy examined exclusively, while observations of the common tuna were done by fisherman, we have no knowledge of the presence of *retia*⁶⁸. On

⁶³ Müller's reasoning about blood flow velocity in this paragraph is sound. Indeed, one of the effects of the *retia* must be a slowing of blood velocity within the *rete*. As Müller points out, the increased surface area encountered by the blood in the *retia* results in greater friction drag. Müller never argues the other side of the coin; if the *rete* has a function other than slowing flow, then the animal must compensate for the increase in resistance imposed by the *rete*. That is, the animal must do more work to pump the blood through this extra vascular bed.

A point that Müller overlooks is the fact that relative flow velocity must necessarily decrease within the *rete* itself as a result of the fact that the total cross-sectional areas of the retial vessels are greater than the total areas of the vessels that feed them. One consequence of this localized slowing of the blood is a facilitation of heat transfer between the arterial and venous blood via an increase in the contact time between the two. It is interesting to note that there are two distinct ways of increasing the contact time. One way is to increase the cross-sectional area of the retial vessels relative to input vessels. The other way is to lengthen the *rete* itself so that arterial and venous vessels are in contact over a greater distance, and therefore for a greater time. Assuming that *rete* morphology has been fine-tuned by natural selection so that efficient heat exchange is accomplished with the minimum anatomical and physiological cost to the animal, it is interesting to note that the former design has been at least partly chosen over the latter (if the latter design were the best, *retia* would be longer and the intraretial cross-sectional area would be the same (or less) than that of the input vessels.

⁶⁴ *L'institut. Journal general des societes et travaux scientifiques*. No. 108. (Footnote of the authors, not the translators). We have not been able to locate this article.

⁶⁵ Although Kishinouye (1923) is traditionally credited with the first publication in which the elevated body temperature of tunas is attributed to their vascular *retia mirabilia*, it is apparent here that Müller considered this possibility 88 years earlier.

⁶⁶ The adrenal glands.

⁶⁷ The *mesonephros*, the excretory organ of the embryo.

⁶⁸ Indeed, the skipjack tuna, *Katsuwonus pelamis* possesses no visceral *retia mirabilia*.

the other hand, one can not doubt that such an exquisite structure might be shared by the various species of the genus *Thunnus*. Because the extraordinarily large intestinal nerves observed by Mr. Eschricht not only pass through the *retia*, but branch there as well, it is more or less probable that unusual chemical processes take place there. With respect to the temperature of various body parts of living tuna, namely the *retia* and their associated organs, the validity or invalidity of this theory will soon be discovered⁶⁹. Moreover, observations about the temperature of *Lamna nasus* may become just as important⁷⁰.

VIII. Analogs of the peculiar structure of the liver vessels

Once the overall essence of the aforementioned structure was understood, I began a search for analogs in other fishes. We could not find anything similar in our freshwater fishes. Meanwhile, I was especially eager to examine other scombroids. In *Caranx trachurus* I was unsuccessful in finding analogous blood vessels. The specimens of *Scomber colias* that I was able to examine had no gut; meanwhile I found that the mackerel, *Scomber scombrus*, possesses a liver structure far different from the tuna and it possesses no *retia*. On the other hand, in *Auxis rochei* from the Mediterranean, I found the beginning of a radiating formation of the liver veins without a sinus. While examining many other Mediterranean fishes which were sent to the anatomical museum from Doctor C.W. Schultz (now in Naples), I found only one example of a radiating formation of the liver vessels. While identifying and classifying the fishes of the Schultz collection, I found in one container two large, separate liver lobes along with (but not attached to) the digestive tract of a large elasmobranch, which I identified as such because of its dense pancreas and spiral valve. The completely flat liver lobes with parallel side edges and rounded ends obviously belonged together; the first is 30 cm and the other is 20 cm long. Both are 9 cm wide. All vessels enter and exit on the side edge of one end of the liver lobes, from which the entire liver lobes can be inflated. These vessel stems run superficially and lengthwise along the flat area of the lobes, without creating a sinus. They send many oblique, partly parallel, partly (on the end of the liver)

radiating branches to the periphery in such a way that the vessels resemble a feather. Upon inflation, this radiating distribution appeared only on the flat side of the liver. All of the vessels entering into the bluntly cut end of the liver also displayed this behavior. Judging from the size of the liver, it could only have come from one of the largest bony fish or an impressive cartilaginous fish from the Mediterranean.

The Schultz collection did not include any tunas. In addition, none of Cuvier's descriptions of livers in other tunas are consistent with this liver. I examined juvenile *Thunnus thynnus* myself; the liver lobes are three-sided. The description of the two-lobed liver of *Thunnus alalunga*, where one of the lobes is the shape of a playing-card-heart and the other three-sided, also does not match the liver in question. It resembles the liver of *Sarda sarda* more closely, but this fish is only supposed to reach a maximum of 65 cm in length. Cuvier says that the liver of *S. sarda* is separated into two lobes in which the left lobe occupies about a third of the width and length of the body cavity, whereas the right lobe is a little narrower. The liver lobes in question are of uneven length, have the same width and are longer than they are wide. *Xiphius gladius*, *Argyrosomus regius* and *Coryphaena hippurus* also belong to the large bony fishes of the Mediterranean. The liver of the latter is completely different from the one in question according to Cuvier's description of it. Cuvier did not report anything about the liver of *Argyrosomus regius*, and unfortunately, the large specimen which was caught and sent to us from the North Sea had already been gutted. However, Cuvier's remarks about the liver of *Argyrosomus hololepidotus* from the Cape⁷¹ suggest that the liver from this fish also does not match the one in question. I received the gut from a large, fresh swordfish which was caught in Swinemünde during my stay there and was able to determine that the liver of this fish also is not a match.

Thereafter it became more likely that the liver lobes with the radiating vessel structure and the gut of a large elasmobranch, which were found together in the same specimen jar, did indeed belong together. Certainly the well-preserved rays and sharks of the Schultz collection did not possess any such radiating liver vessels, even though the shape of the liver in question suggests that it is from a shark. For the most part, the rays and sharks of the Schultz collection of the family Scyliorhinidae, and the genera *Etmopterus*, *Mustelus*, *Galeorhinus*, *Squatina*, *Oxymotus*, *Raja*, *Rhinobatus*, *Taeniura* and *Myliobatis* possessed well-preserved viscera and could be examined. One specimen of *Alopias vulpinus* from the Schultz collection was gutted. The head of a large hammerhead shark, *Sphyrna malleus* was also found. The

⁶⁹ Unfortunately, "soon" came along almost 90 years later, when Kamakichi Kishinouye published his "Comparative study of the so-called scombroid fishes" in which he matter-of-factly states what Müller only hinted at: "The higher temperature of the body than the surrounding water, and consequently great activity of fishes of the *Pleistoei* is undoubtedly due to the peculiar circulatory systems above described."

⁷⁰ Indeed, the porbeagle shark, *Lamna nasus* is one of the few shark species that maintains an elevated body temperature. It is evident from Mr. Müller's musings that if he had been aware of the endothermic nature of *L. nasus*, he would undoubtedly have made the connection between the possession of visceral *retia* and endothermy.

⁷¹ Müller is most-likely referring to the Cape of Good Hope.

gut and liver could belong to either one of them. I could only compare the gut of a small specimen of *Sphyrna tiburo*⁷², which was brought by Mr. Erman from Brazil. This comparison showed that the shape of the liver is for the most part similar. Both liver lobes were very long, narrow and flat, but they were of the same length. The position of the vessel stems was similar, but the radiating or feather-like distribution of the branches was missing. The other digestive organs seemed to match. Dr. Schultz answered by mail that the liver might belong to *Sphyrna malleus*⁷³. I'm very sorry that this point can't be made absolutely clear and beg natural scientists who have the opportunity to examine the species of the genus *Sphyrna*, to determine whether or not this species indeed possesses this liver structure, in contrast to *Sphyrna tiburo*⁷⁴.

The radiating structure of the liver vessels and the *retia* of the portal vein and gut arteries are seemingly unrelated⁷⁵. The liver

of *Auxis rochei*, which shows a hint of the radiating liver structure, and the unidentified liver described above possess no *retia*⁷⁶. The fact that the radiating structure of the liver veins is unrelated to the *retia* was mentioned earlier. The reason for such a structure of the liver is completely unknown⁷⁷.

⁷² *Sphyrna tiburo* is another species of hammerhead shark. Müller examines this species because he suspects that the liver in question belongs to *Sphyrna malleus*, but unfortunately he has no viscera from *S. malleus* to examine. The best he can do is examine the viscera of the closest available relative, which is *S. tiburo*.

⁷³ Other than the gut of this animal, Dr. Schultz only had the gut from a large shark. The latter was packed in his absence from Palermo and sent to Berlin, and everything rotted en route, except for the liver which he had enclosed in a specimen jar. The livers of the various sharks that I examined showed only the usual arrangement of blood vessels. *Lamna nasus* barely showed a hint of the diverging distribution of the liver vein branches. If the liver lobes in question and the gut are from a large shark, they most certainly are not from *Lamna nasus*. The spleen doesn't match at all either (footnote of the authors, not the translators).

⁷⁴ The issue of to whom these mysterious viscera belong is resolved in the supplement to this article. They are from *Alopias vulpinus*, the common thresher shark.

⁷⁵ Actually, there does seem to be a relationship between the presence of the kind of visceral *retia* seen in *T. thynnus* and the presence of the aforementioned radiating structure of the liver vessels. In the supplement to this article, we discover that *Alopias vulpinus* was the rightful owner of the viscera in question (the ones with the peculiar radiating structure of the liver vessels). We also learn that *A. vulpinus* possesses visceral *retia* much like those seen in *T. thynnus*. One might argue that this so-called relationship between the presence of visceral *retia* and radiating liver vessels is refuted by the fact that *Lamna nasus* possesses visceral *retia*, but does not display the radiating liver vessels. However, it is interesting to note that a major difference exists between these two visceral heat exchange systems. The visceral *retia* found in *T. thynnus* and *A. vulpinus* are located between the liver and the digestive organs. In contrast, the two visceral *retia* found in *L. nasus* are located on the other side of the liver, between the liver and the heart. The consequence of this difference, simply stated, is that the livers of *T. thynnus* and *A. vulpinus* are cold, whereas the liver of *L. nasus* is warm. We believe that it is not a coincidence that *T. thynnus* and *A. vulpinus*, which both possess the same relative position of the visceral *retia*, also display a radiating structure of the liver vessels. *Auxis*, which has a hint of the radiating structure on the liver, does not have visceral *retia*, but does have lateral *retia* serving the musculature. It is not known if these structures on the liver in *Auxis* consist of both arteries and veins, or if they could act as a countercurrent heat exchanger.

⁷⁶ *Auxis* does have a hint of the radiating structure on the liver but does not have visceral *retia*, whereas *Alopias vulpinus* (the owner of the unidentified liver) does possess visceral *retia mirabilia*, which for all intents and purposes are completely analogous to those in *T. thynnus*. Müller assumes that this animal lacks visceral *retia* because there are none attached to the liver, which is where they are located in *T. thynnus*. However, in the supplement to this article, we learn that the visceral *retia* of *A. vulpinus* are located close to the organs they serve, instead of adjacent to the liver.

⁷⁷ There has been no literature on this point since Eschricht & Müller brought it up in 1837. We believe that these peculiar liver vessels probably act as a crude *rete* designed to conserve some of the metabolic heat generated in the liver. We find it interesting (and important) that it is only endothermic fishes which have been shown to possess the radiating structure of the liver vessels. In addition, the structure is only seen in warm fishes whose livers do not enjoy the benefits of the visceral *retia*. In other words, it is only seen in fishes whose livers are on the "cold" side of the *retia*. In contrast, the heat exchange system in *L. nasus* is such that the liver is served by the visceral *retia* and is therefore kept "warm". In this species, no radiating liver vessels are seen. One of our future research objectives is to determine the potential for countercurrent heat exchange in these liver vessels.

4. An annotated translation of D.F. Eschricht and J. Müller's supplement to the article on the *retia mirabilia* on the liver of the tuna. "On the *retia mirabilia* of the digestive system of *Squalus vulpes* L., *Alopecias vulpes* Nob."

Translated with the assistance of Elisabeth Niimi.

The viscera of the shark described in the last section of the tuna article, which was believed to belong to either *Zygaena malleus* or *Carcharias vulpes* Cuv., is now known to belong to *Carcharias vulpes* Cuv., *Squalus vulpes* L.⁷⁸ Mr. Duvernoy recently showed (*Annales des sciences naturelles*, May, 1835), that the spiral valve of *Zygaena tudes* differs from that in other sharks. Among the elasmobranchs, this valve is typically helical, i.e. its insertion into the gut wall as well as the free edge form a screw-like spiral. In *Squalus thalassinus* Val., which is the type species of a new genus closely related to *Galeus*, and in *Zygaena tudes*, Mr. Duvernoy found a sail-like valve which is attached longitudinally, and which is only rolled up in a spiral-like fashion. He also described a large branch of the portal vein which runs along the free edge of the valve. Because the same structure was found in *Zygaena tiburo*, it seemed most probable that the previously mentioned viscera from the Schultz collection with the *structura pinnatifida* of the liver vessels did not belong to *Zygaena malleus*. Because the spiral valve in those viscera was screw-like, it was most probable that the viscera belonged to *Squalus vulpes*, which, aside from *Zygaena malleus*, was the only other shark in the entire Schultz collection whose viscera had been removed. Mr. Lichtenstein allowed us to examine another specimen of *Squalus vulpes* in the zoological museum and it helped to confirm that the viscera in question were indeed from *Squalus vulpes*. Although the fish had been sent from the Cape⁷⁹, its anatomy was virtually identical to the specimen of *Squalus vulpes* from the Mediterranean. While examining this fish, I found not only the *Structura pinnatifida* of the liver vessels, the same shape of the liver, spleen, and pancreas, but I also convinced myself that the place in which Cuvier put *Squalus vulpes* L. is not correct. It indeed belongs with the genera *Carcharias* and *Lamna*, to the taxon of sharks which lack spiracles and possess an anal fin, but it can not be included in the

genus *Carcharias*. *Squalus vulpes* has a screw-like spiral valve. As I've found in *Carcharias vulgaris* and *Carcharias glaucus*, the true *Carcharias* possess the same sail-like spiral valve as those within the genus *Zygaena* and *Squalus thalassinus* Val. The specimen of *Squalus glaucus* brought by Mr. Meyen was found to possess a longitudinal flap. But because *Carcharias glaucus* Cuv. and *Squalus glaucus* Bloch both have the same coloration of *Squalus thalassinus* Val., more definite proof was necessary. I obtained this by examining *Carcharias vulgaris* and *Carcharias glaucus* at the zoological museum. The latter is the specimen described and illustrated by Bloch. Therefore, the true *Carcharias* possess a longitudinal sail-like gut valve, whereas *Squalus vulpes* possesses a screw-like valve, as do those of the genus *Lamna* of the same family. The teeth of *Carcharias* do not differ greatly from those of *Squalus vulpes*; in both they are triangular and flat, but only in *Carcharias* are they serrated. The lack of an anal and second dorsal fin and the unusual length of the upper lobe of the caudal fin are unique to *Squalus vulpes*. I therefore, along with Rafinesque, place *Squalus vulpes* L. and *Carcharias vulpes* Cuv. into the new genera, *Alopecias* Nobis and *Alopias* Rafinesque. At this time there is only one species, *Alopecias vulpes*. The family of sharks that possess anal fins and lack spiracles therefore includes the genera *Carcharias*, *Alopecias*, and *Lamna*. The name *Alopecias* has been used in ichthyology for a long time. *Artemi synonymia piscium* ed. *Schneider*. Lips. 1789. 134.138. With regard to the distribution of the sail-like valves, I could not find them in other genera of sharks or rays. We examined the genera: *Lamna*, *Scyllium*, *Galeus*, *Mustelus*, *Spinax*, *Centrina*, *Squatina*, *Rhinobatus*, *Torpedo*, *Narcine*, *Raja*, *Myliobates*. They all have the screw-like spiral valve. The sail-like longitudinal valve is therefore only presently known in *Carcharias*, *Zygaena* and *Squalus thalassinus* Val. The viscera of the genera *Notidanus*, *Selache*, *Cestracion*, *Scymnus*, *Pristis*, *Rhina*, *Anacanthus*, *Propterygia*, *Rhinoptera*, *Cephaloptera* have not been examined.

⁷⁸ In this first part of the supplement we do not use valid species names because the focus of the discussion concerns synonymy and validity of species names. In the second part of the supplement concerning *retia* we use valid names.

⁷⁹ Once again, it is unclear to which cape he is referring, although it is most likely that he means the Cape of Good Hope at the southern tip of Africa.

The second part⁸⁰ of the supplement concerns the *retia mirabilia* observed on the gut of *Alopias vulpinus*, which I could not find on the viscera found in the Schultz collection which had been separated from the liver⁸¹. A large tassel-like *rete* consisting of many hundreds of ray-like vessels which converge from all sides and whose blood enters the stem of the portal vein at a common area, still some distance away from the liver, is located on the side of the stomach. They proceed in a somewhat parallel, bunched manner from the walls of the stomach and have a thickness between 0.5 and 1.0 mm. The vessels anastomose between one another. Shortly before the entrance of the portal vein into the liver, the portal vein receives yet another small *rete* from the uppermost part of the stomach or from the pharynx. The stem of the portal vein which ascends from the gut receives small bundles of veins from the spleen, pancreas and a very large *rete* from the spiral valve, long before it receives the large *rete* of the stomach. The *rete* associated with the spiral valve is of the same size of that associated with the stomach. As is the case in all other elasmobranchs, a large gut vein, the beginning of the visceral portal vein, ascends in a screw-like fashion from the lowest part of the gut, closely positioned along the surface of the gut. In *Alopias vulpinus*, one finds at this position a swelling as

far as the vein stem follows this part of the gut, where the spiral valve is found. The swelling is created by the *rete*. All of the vessels which originate from that part of the gut create many fine, parallel vessels which now and then anastomose between one another and are packed together in the tightest possible way, so that the walls of the gut in this area are not visible because the vessels are so tightly packed. The vessels enter the stem from both sides, either in a straight line or at a slight angle, so that the whole structure strongly resembles the shape of a feather fan. The *rete* stops where the spiral valve ends. Here on the rectum, the blood vessels have the usual tree-like branching formation.

This type of *rete* is different from those on the liver of the tuna and the *retia* of *Lamna nasus*, in that the tassel-like vessels going in one direction don't collect into new stems. It is more similar to the *rete* found in the extremities of the sloths, in which the convergence of the *rete* vessels is also not complete. Within the *retia* of *A. vulpinus*, the visceral arteries behave in a manner similar to that of the veins. I have searched many rays and sharks for this structure, but could find it nowhere else. Thus far, the fish in which *retia* have been described are the bony fish, *Thunnus thynnus* and the cartilaginous fishes *Lamna nasus* and *Alopias vulpinus*. Given the opportunity, I will illustrate the *retia* of the latter. I must also mention the very long, channel-like gall bladder of *A. vulpinus* which is wound in a snake-like fashion and which is for the most part covered by the tissue of the larger liver lobe. I will include an illustration of this structure in a subsequent publication⁸².

⁸⁰ We use the valid names in this section because it should not create any confusion.

⁸¹ Interestingly, this is the first and last mention in the literature of the visceral *retia* of *Alopias vulpinus*. Not only has the subject been ignored, the retial endowment of the thresher viscera has been misrepresented if what Eschricht & Müller claim is true. In a summary table of the different kinds of *retia* seen in pelagic fishes, Carey (1982) claims that the thresher possesses eye and brain *retia*, most likely possesses muscle *retia*, but does not possess visceral *retia*. It has since been confirmed that the thresher possesses significant muscle *retia* (Bone & Chubb 1983). Clearly more work needs to be done on the visceral vasculature of *A. vulpinus*.

⁸² Regrettably, there are no subsequent publications by Eschricht or Müller on any of these subjects.

5. Plates from the Eschricht & Müller paper and a supplementary figure

Plate I. Convex side of the tuna liver from the anatomical museum.

A. Sinus of the liver veins on the convex side of the right liver lobe. a. Stem which originates in the sinus and exits the surface of the liver.

B. Sinus of the liver vein from the middle and left liver lobes. b. Stem which originates in the sinus.

C. Radiating liver vein branches.

Fig. 4. Whole liver from a 250 kg bluefin showing the three main liver lobes, anterior view. This photograph is analogous to Plate I in the original text. The tips of the hemostats indicate the two large branches of the hepatic vein which exit the liver and proceed toward the heart. Note also the prominent radiating pattern on the liver lobes which is due to the antiparallel arrangement of liver arterioles and venules. We propose that this arrangement helps conserve metabolic heat produced in the liver and is responsible for the proximal/distal temperature gradient which occurs along the liver lobes as reported by Carey et al. (1984).



See Green's Bericht aus. Weidmanns Bild u. d. Hauptach. - Phys. Bd. 1830.

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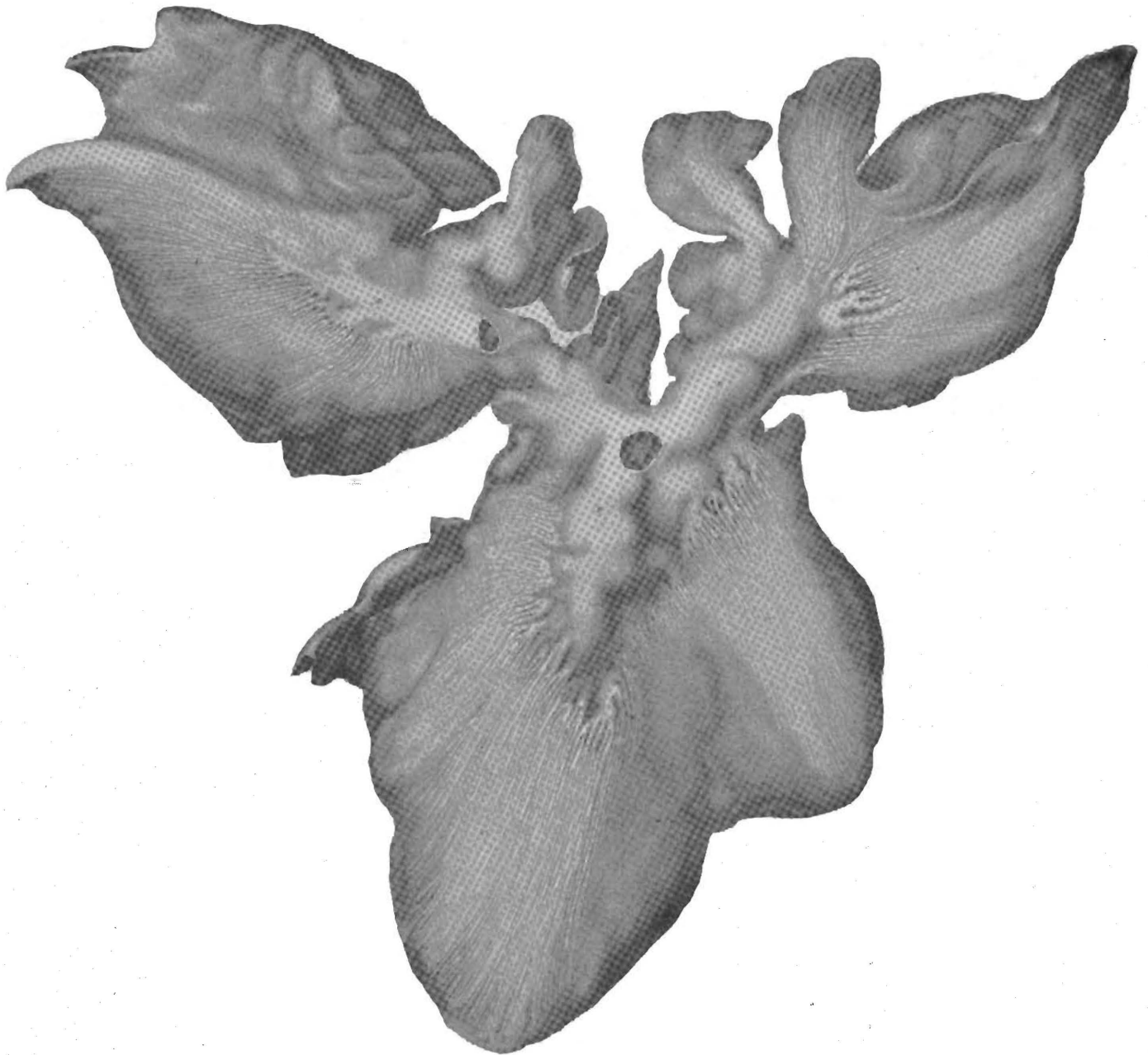


Plate II. The *retia* of the tuna liver *in situ*, from the first specimen of *Thunnus thynnus* from Montpellier. The liver lobes have been lifted and the digestive organs shifted from their natural positions so as to improve the view. For the natural arrangement, see Plate III.

- D. Right liver vein stem.
- E. Left liver vein stem from the middle and left liver lobes.
- F. Right liver lobe.
- G. Middle liver lobe.
- H. Left liver lobe.
- I. Gall bladder. I'. Swelling of its exiting duct.
- I". Common bile duct appearing behind the *rete* V. of the middle liver lobe, positioned between the blood vessels of the pyloric caeca and descending into the *pars pylorica* of the gut.
- K. Stomach, pulled to the right.
- K'. Side branch of the stomach, *pars pylorica* of the same.
- L. *Pars pylorica* of the intestine.
- M. Pyloric caeca.
- N. Oblique ascending part of the intestine.
- O. First descending part of the intestine.
- P. Second ascending part of the intestine.
- Q. Second descending part of the intestine.
- R. Rectum.
- S. Spleen.
- T. Spindle-like *rete* of the right liver lobe.
- T'. Stomach vein which receives it.
- T". Small venous branches from the stomach.
- U. Pear-shaped *rete* of the right liver lobe.
- U'. Spleen vein which receives it.
- U". Small venous branches of the intestine.
- V. Flat *rete* of the middle liver lobe.
- V'. Veins from the intestine and the pyloric caeca which enter the tip of the *rete* .
- V". Stomach vein which enters into this *rete*.
- X. Small *retia* of the left liver lobe.
- X'. Veins of the pyloric caeca which enter it.
- Y. Artery of the digestive system.
- Y', Y". Both branches thereof.
- Y'. The branch that enters at the base of the *retia* T. and U., branching partly into the right liver lobe, and partly dissolving into the *retia*. At the tips of the *retia*, the retial vessels converge into the arteries, which accompany the corresponding veins to the stomach Z and the spleen Z'.

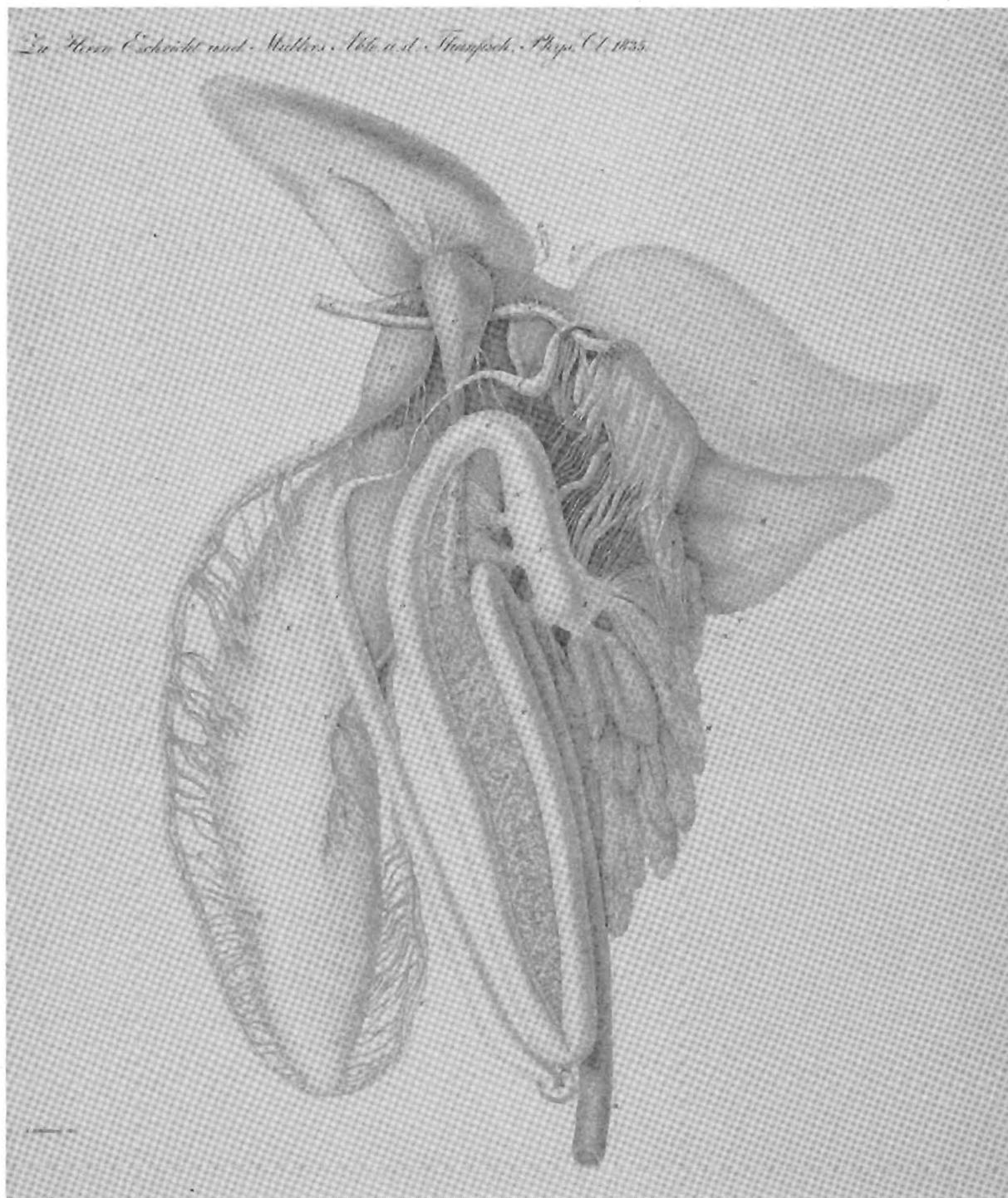


Plate III.

Fig 1. Diagram of the viscera of the tuna *in situ* from the second specimen (*Thunnus thynnus*) from Montpellier (reduced in size). The stomach is pulled a bit to the left.

- A. Ventricle.
- B. *Bulbus aortae*.
- C. Atrium.
- D. Sinus of the body veins. D'. Tip of the sinus.
- a,a. Liver veins.
- b,b. Lateral vein stems. c. *Vena jugularis*. d. *Vena lateralis posterior*. The latter passes through the kidneys E. and receives veins from the kidneys and the reproductive organs and enters into the muscles of the trunk.
- F. Right liver lobe.
- G. Middle liver lobe.
- H. Left liver lobe.
- I. Gall bladder. I'. Widening at the beginning of the gall bladder. At this point a few liver ducts enter from the right lobe. I'' *Ductus choledochus*.
- K. Stomach. K'. Pars pylorica of the stomach.
- L. Pars pylorica of the intestine.
- M. pyloric caeca.
- N. O. P. Q. R. S. as in Plate II.
- T,U *Retia* of the right liver lobe.
- V. *Retia* of the middle liver lobe.
- X. *Retia* of the left liver lobe.

Fig. 2. Piece of the right liver lobe.

- a. Branch of the visceral artery which spreads into the liver as well as the *rete*.
- b. *Rete*.
- c. Branches of the hepatic portal vein which lead from the *rete*.
- d. Branch of the visceral portal vein which leads to the *rete*.
- e. Artery which leads from the *rete*.

Fig. 3. Connection of a branch of the visceral artery to the liver and its *rete*, cut open.

- a. Artery.
- b,b. *Rete*.
- c. Connection of the artery to the *rete*.

Fig. 4. A branch of the visceral artery with its associated *retia*; from the injected liver sent from Copenhagen.

- a.. Artery.
- b,b. Hepatic branches of the artery.
- c,c. Branches of the artery into the *retia*.
- d,d. *Retia*.
- e. Portal vein branches which come from the organs of the digestive system and enter the *retia*.
- f. Arteries which leave the *retia* and lead to the organs of the digestive system.
- g. This entry absent in original text. Possibly nerve stems associated with the visceral artery branches and the *retia*.

Fig. 5. Cross-section of a liver *rete*.

Fig 6. Main artery stems and kidneys of the tuna from the dorsal side.

- A,A. Upper, paired part of the kidneys, over the most anterior part of the body cavity, just behind and above the gills.
- B. Commissure of the paired parts of the kidneys.
- C. Lower, unpaired, flatter and narrower part of the kidneys.
- C',C'. Downward pointing separation of the same.
- D. Unpaired ureter. D'. Paired origin of the ureter. D''. Bladder.
- D''. Urethra.
- E. Sperm ducts. E'. Common sperm duct, positioned in front of the urethra and separated from it up to the common urogenital opening.
- F. Rectum.
- a,a. Anterior roots of the aorta from the first two efferent gill arteries a',a'.
- b,b. Posterior root of the aorta from the two posterior gill efferent arteries.
- c. Stem of the aorta between the paired parts of the kidneys.
- d,d,d. Kidney arteries. d',d''. Posterior kidney arteries from the aorta.
- e. Common artery stem of the digestive system *arteria coelomesenterica* (Plate II, Y).
- e',e'. Both of its branches (Plate II, Y',Y'').
- f. *Arteria axillaris* penetrating the kidneys with the *vena lateralis posterior*.
- g. Thinner continuation of the aorta toward the midline, entering the channel formed by the lower spinal processes.
- h. *Vena lateralis posterior*. h'. *Vena lateralis anterior, jugularis*.

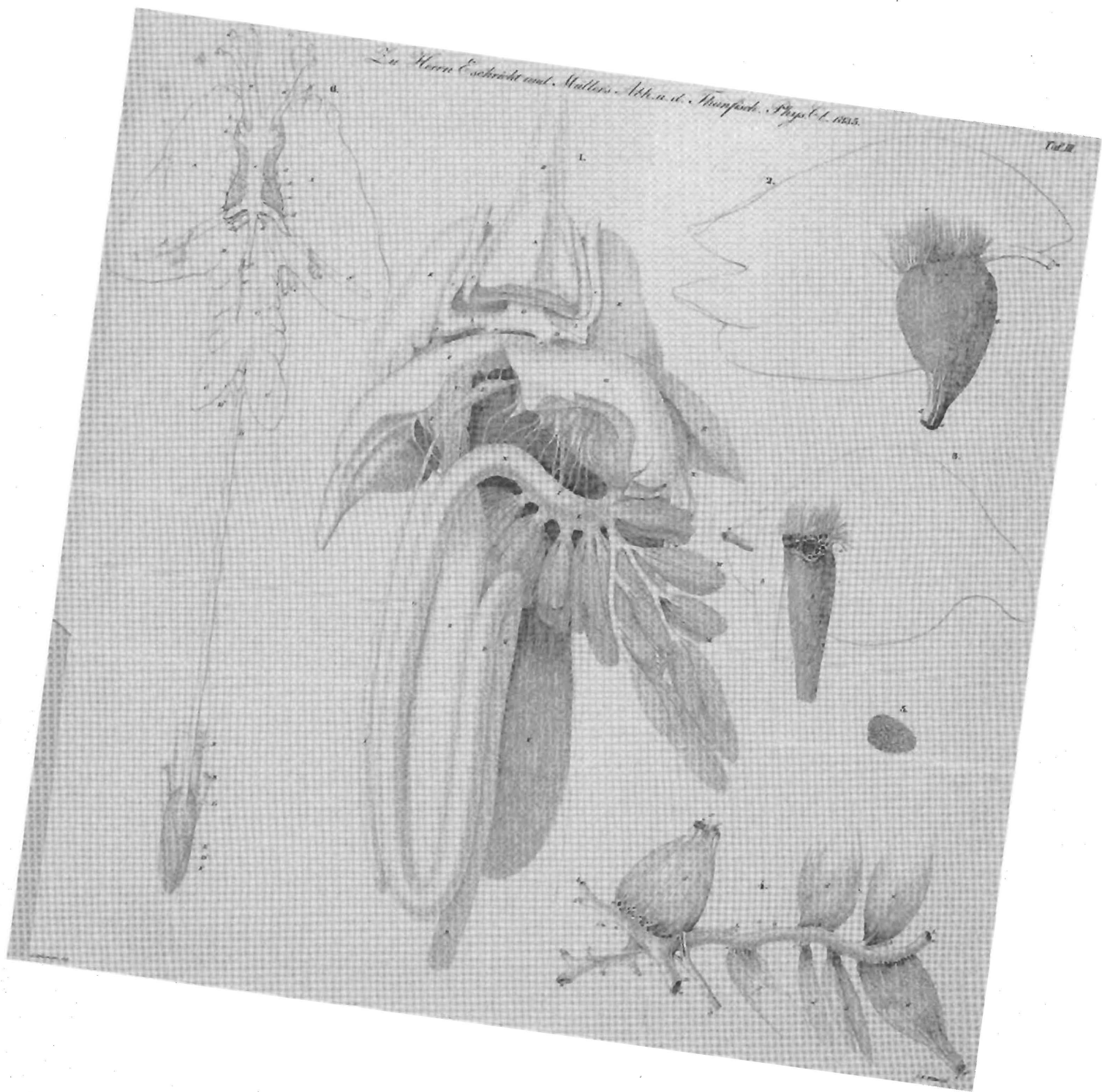


Fig. 5. Visceral arterial systems of four tunas from Kishinouye (1923): d - *Thunnus alalunga*, e - *Thunnus thynnus*, i - *Katsuwonus pelamis*, j - *Euthynnus affinis*. Note that *T. thynnus* and *T. alalunga* possess visceral *retia*, whereas *K. pelamis* and *E. affinis* do not. Note also that Kishinouye portrays *T. thynnus* as having five major visceral *retia* in this diagram, which is consistent with Eshricht & Müller's and our own observations, but inconsistent with Fig. 6, in which Kishinouye implies that *T. thynnus* possesses only four major visceral *retia*.

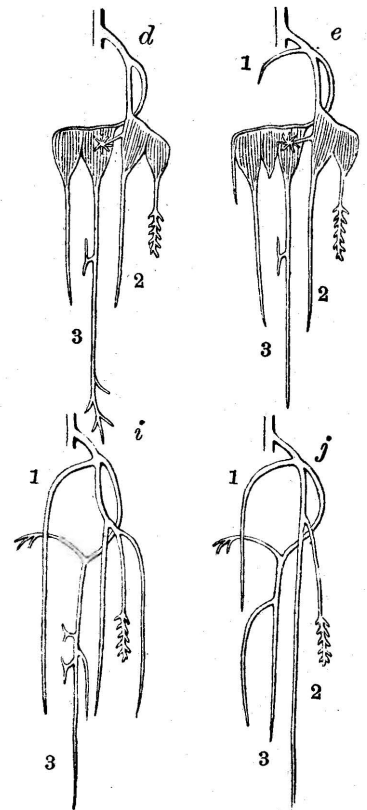
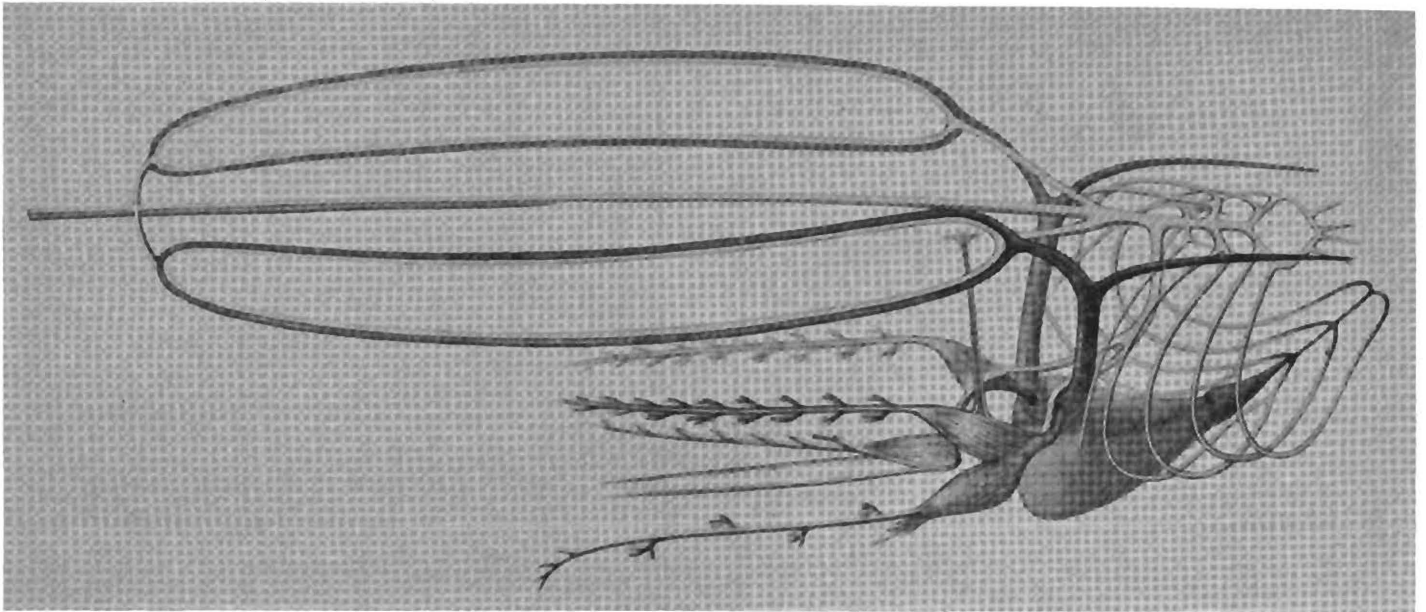


Fig. 6. Diagrammatic representation of the vascular system of *T. thynnus* from Kishinouye (1923). Dark vessels are veins and light ones are arteries.



6. Supplementary figures

Fig. 7. Right and middle liver lobes in a 155 cm (fork length) fixed specimen of *T. thynnus*. Note the prominent radiating liver vessels on both lobes.





Fig. 8. Ventral view of the same fish described in Fig. 7. The ventricle is pulled anteriorly to expose the membrane that separates the heart from the liver, referred to by Müller as the 'diaphragm'.

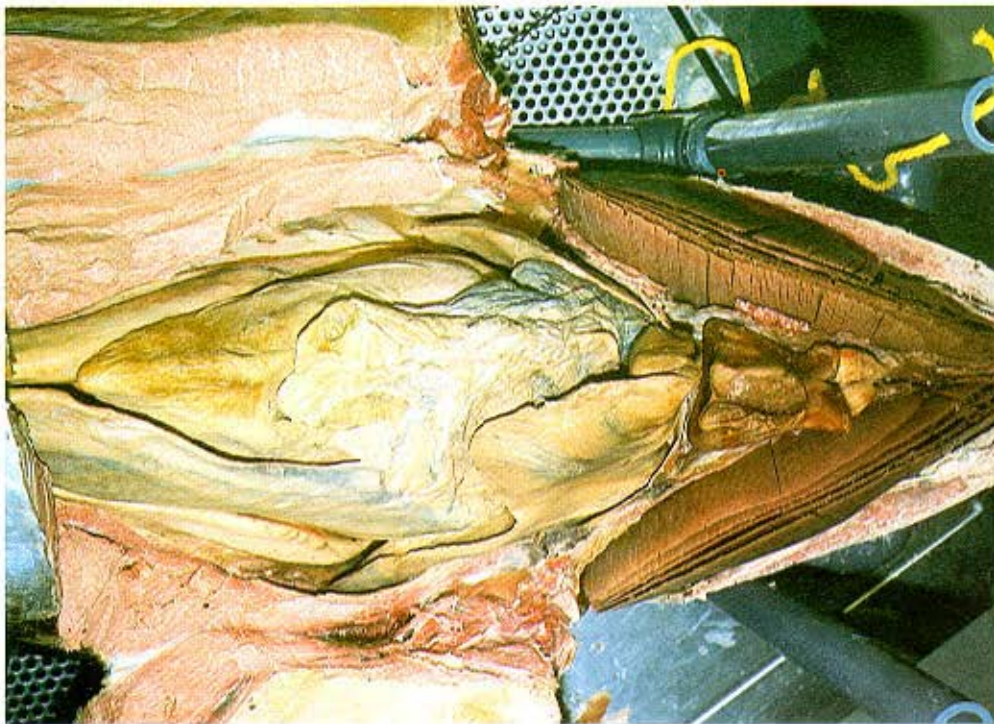


Fig. 9. Ventral view of the viscera in the same fish described in Fig. 7. The body walls and gill plates were removed to expose the viscera in their natural positions.

Fig. 10. Close-up of one of the stomach *retia* from a 250 kg bluefin in which one of the major portal veins leading from the stomach was injected with blue paint. Note that the paint proceeded as an almost linear front across the width of the entire *rete*, implying that the vessel that was injected is the only venous vessel served by this *rete*. This linear front also implies that resistance to flow through the *rete* appears to be uniform across the entire width. Note also the prominent branch of the coeliac artery running across the top of the *rete*. Smaller white structures appearing to descend off of the coeliac artery into or along the surface of the *rete* are large visceral nerves.

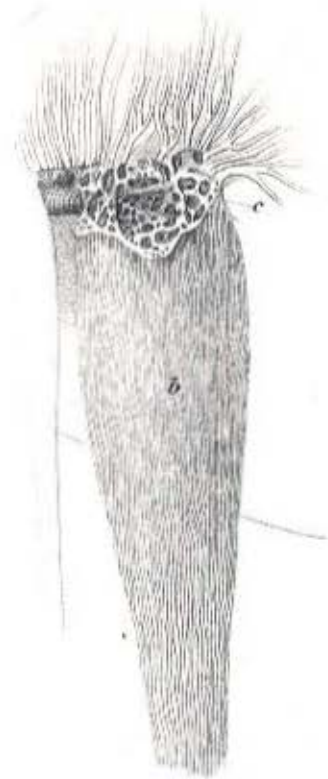


Fig. 11. Close up of the connection between a stomach *rete*, a branch of the coeliac artery and the liver from a 250 kg bluefin. This photograph is analogous to Plate III, Fig. 3 from the Eschricht & Müller text which is enlarged here beside the photograph. The *rete* has been cut open at this junction to show more clearly the nature of the relationship between these structures. The yellow and blue colors are leftover from a previous injection experiment in which the coeliac artery was injected with yellow paint and a portal vein from the stomach was injected with blue paint. The green color at the point of incision is not due to mixing within the intact *rete*, but occurred when the *rete* was cut open and the excess paint wiped off.

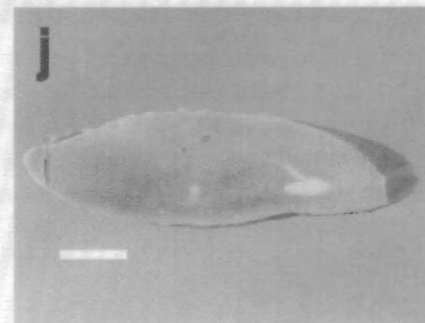
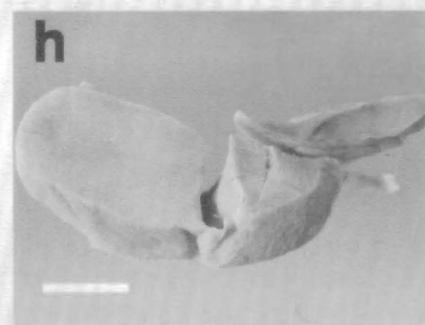
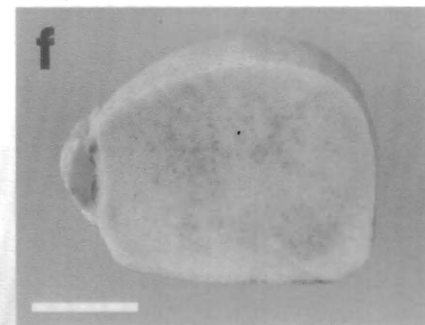
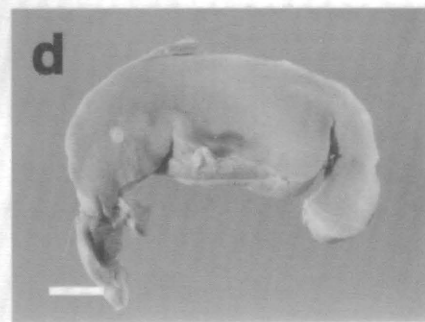
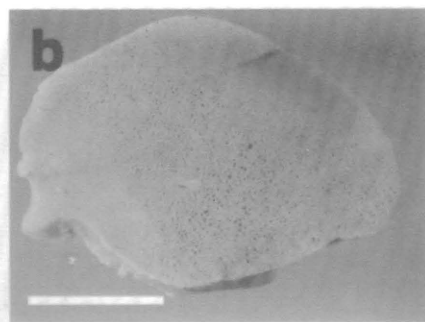
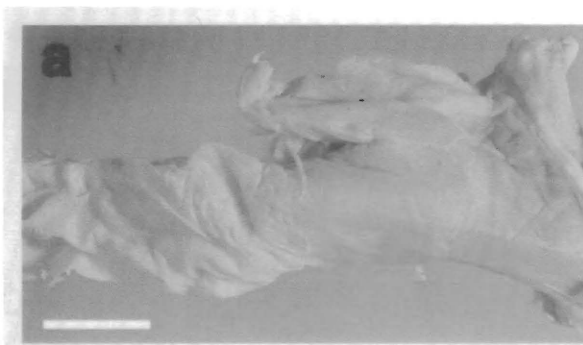




Fig. 12. Previous Page. Five major *retia* from a 250 kg bluefin tuna. Whole *retia* are in the left column and the corresponding cross-sections are in the right column. Scale bars in the left column are 20 mm, those in the right column are 10 mm. The whole *retia* are oriented so that the ends attached to the liver are on the right. a - *Rete* associated with the right side of the stomach. c - *Rete* which serves part of the caecum and the ventral part of the stomach. e - *Rete* which serves the left part of the stomach and attaches near the pylorus. g - *Rete* which serves part of the caecum. i - *Rete* which serves the spleen, intestine, and part of the caecum. The prominent white structures seen in cross-sections d and e are large nerves which pass through (and perhaps branch) within these *retia*.

Fig. 13. The same *retia* depicted in Fig. 12 *in situ*. The *retia* depicted in a, c, e, g, and i of Fig. 12 and 13 correspond to the *retia* denoted by S, CS, SP, C, and SIC in Fig. 1, respectively.

Fig. 14. Cross-section through a piece of liver in which the radiating liver vessels are especially prominent. Note that the vessels which give the bluefin liver its characteristic radiating appearance occur only on the convex (anterior) surface and do not penetrate into the liver interior.

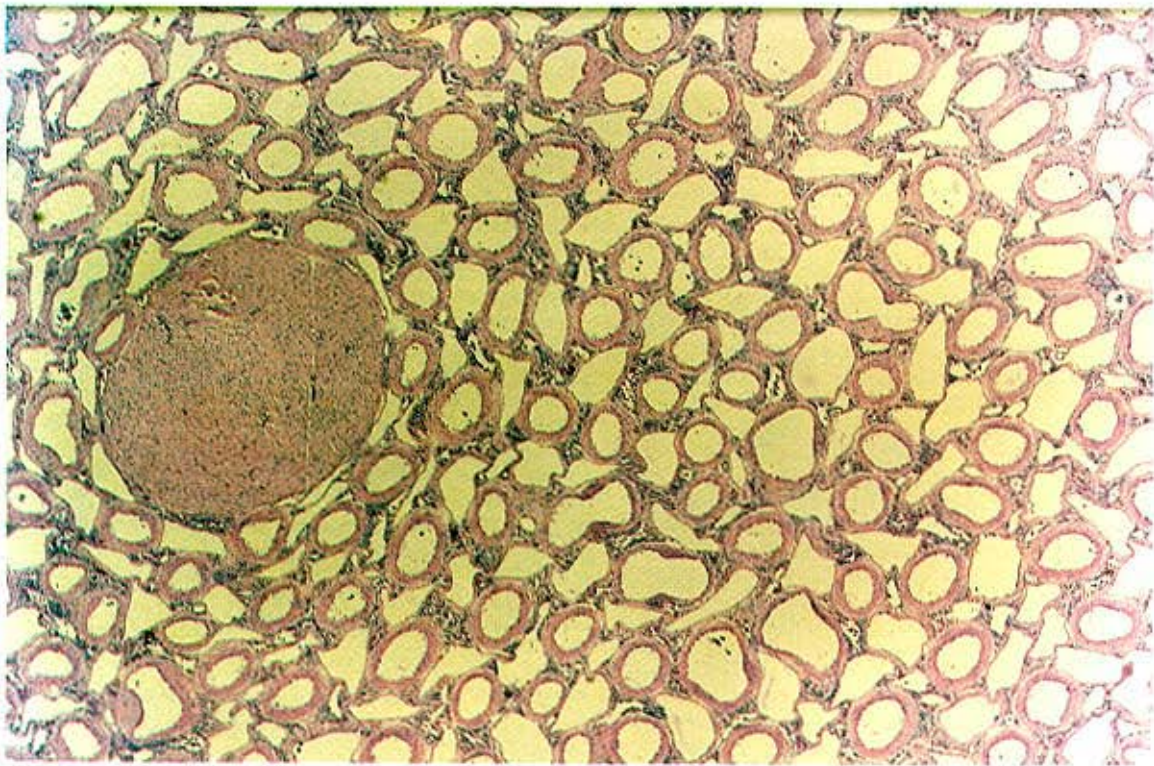
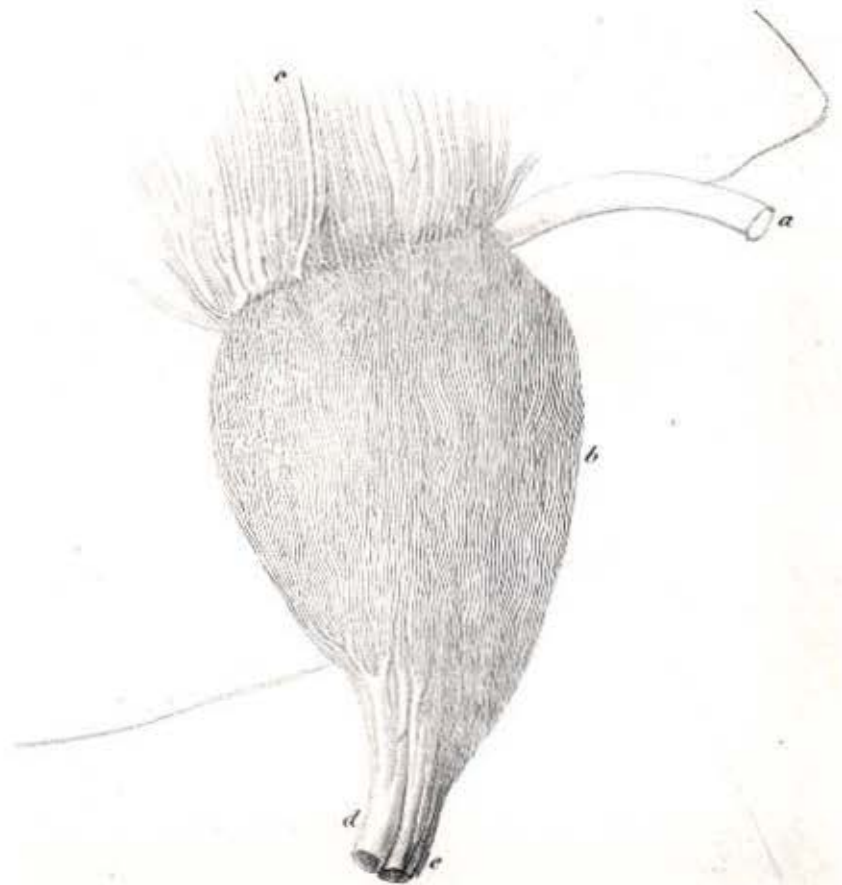


Fig. 15. Cross-section of a caecum rete from a 410 kg specimen of *T. thynnus*, magnified 40X. Rete vessels were filled with buffered formalin and fixed under pressure to reduce collapse of the vessel walls. Arterial vessels are smaller and thicker than venous vessels and arterial vessels have a significant layer of smooth muscle. Note the approximate checkerboard arrangement of the arterioles and venules. The large circular structure on the left is a nerve (nerve diameter is 0.71 mm) which runs through the center of the rete and possibly innervates it.

Fig. 16. The photographs below are of the visceral *retia* from a 450 kg bluefin tuna. The *rete* on the left is still connected to the liver and caecum. The *rete* on the right has been dissected out of the gut and perfused with saline. The blanched color of the latter emphasizes the fact that the vascular and connective tissue which make up the *rete* are translucent white, and it is blood which gives the intact *rete* its purplish-red color. The drawing to the right of a *rete in situ* is an enlargement of Plate III Fig. 4.



7. The first mention in the scientific literature that tunas are warm-blooded: Two historic papers and their abstracts by John Davy.

His intimate friendship with [Eshcricht] continued uninterrupted until his death. In the spring of 1835 he and Eschricht described the *retia mirabilia* on the liver of the tuna, which he suggested to have some relationship to John Davy's observations of the warm-blooded nature of these fish. This suggestion could represent new evidence for the idea that the liver is the seat of heat generation in animal bodies, which was first put forth by Claude Bernard in his investigations of animal thermal topography.

From the homage to Johannes Müller
by Emil du Bois-Reymond, p. 98

In this section we include two papers and their abstracts by John Davy. We include the full papers and their abstracts because, to our knowledge, only one of the abstracts has ever been cited by any worker. It was difficult to locate these papers and they should be of interest to both comparative physiologists and tuna biologists. In addition there are some important differences between what is said in the full papers and what is said in the abstracts. Because the abstracts were written by others, Davy is referred to in the third person. In each case the abstracts were published after the full papers and we present the four in chronological order of publication.

Davy (1790-1868) graduated with a medical degree from Edinburgh in 1814 and was elected as a fellow of the Royal Society of London in the same year. He entered the army as a surgeon and ultimately rose to the position of Inspector General of Army Hospitals. In the course of his service he visited the West Indies and India and was on the medical staff in Ceylon (now Sri Lanka) from 1816 to 1820. Although he published many papers on a variety of topics, he was best known for his research on animal temperature. He made very precise observations of the body temperature of many different animals under diverse conditions. He measured the temperature of a diverse collection of animals including jackals, leopards, tigers, elephants, elk, sharks, flying fish, and adders, to name a few. Davy certainly was not a fish biologist, but he did make some contributions to the study of fishes. In brief biography published in the list of fellows of the Royal Society of London, he is credited with, in addition to his temperature measurements, the discovery of "the connection of the electric columns of the torpedo with the organs of respiration". We are not sure why this

was viewed as a discovery at the time, because the nature of the connection is not obvious.

The taxonomic names used by Davy are confusing, but it must be appreciated that he was not an ichthyologist. We are relatively certain that the species to which Davy refers are the skipjack tuna and the bluefin tuna. In the first full paper and its abstract he reports muscle temperature measurements from "the Bonito (*Thynnus pelamys*)". This is confusing, because *Thynnus pelamys* is an outdated name which refers to the skipjack tuna, *Katsuwonus pelamis*, and not the Atlantic bonito *Sarda sarda*. The title of the paper refers to the genus *Thynnus*, and the implication from the discussion in the paper is that tunas (all five members of the genus *Thynnus*) are warm-blooded. He states that fishers report that *Pelamys sarda* is cold-blooded but based on morphological similarities with the tunas, he thinks that they may be somewhat warm-blooded.

Unfortunately, the confusion is made worse in the second full paper and its abstract. He claims that the measurements were performed on *Pelamys sarda*, which is the old name for the Atlantic bonito, *Sarda sarda*, but, he does not use the term bonito. Thus, for the fish on which he actually made measurements of muscle temperature and found them to be warm-blooded, in the first paper he used the scientific name for tuna and the common name bonito and in the second paper he used the scientific name for bonito and no common name. We conclude that Davy misidentified the skipjack tuna as *Pelamys sarda*. Modern measurements of muscle temperature in bonito, *Sarda sarda* show its maximum muscle temperature does not exceed water temperature by more than 1.8° C (Carey et al. 1971). The other unlikely possibilities are: (1) Davy made

erroneous measurements and his reported values of body temperature are for bonito but do not reflect reality; or (2) the few modern measurements for bonito are grossly inaccurate and bonito are actually warm blooded.

In these texts, Davy reports some measurements of the body temperatures of one skipjack (*Katsuwonus pelamis*, referred to by Davy as *Thynnus palamys* in the first paper and as *Pelamys sarda* in the second paper) which indicate that the temperature of these animals is about 10°C warmer than the water they inhabit. His conclusions are based on actual measurements. These are the first reports in the scientific literature of the elevated body temperature of any fish. Most of Davy's subsequent conjecture about how tunas generate and conserve heat appear quite primitive in light of what we now know about metabolism, thermogenesis and thermoregulation.

In the first paper, Davy reports a datum for a single measurement from a single fish that has a muscle temperature of 37.2° C in water of 26.9° C; which incidentally, is very similar to the muscle temperature reported by Stevens & Fry (1971) for *Katsuwonus pelamis* caught at sea. In addition, Davy argues that the bluefin tuna (*Thunnus thynnus*, referred to by Davy as *Thynnus vulgaris*), like the skipjack, is also "warm-blooded" based on reports from "intelligent" fishermen. He also draws attention to the fact that the bluefin is very similar to the skipjack in many regards. It is interesting to note which attributes Davy selects in trying to demonstrate a similarity between the two species. He remarks on the innervation of the gills, the unusually large heart, large gills, large amount of blood, and the dark red color of the swimming muscle. Although any modern-day fish physiologist would immediately think of aerobic capacity if confronted with the terms "large gills, large heart, and dark swimming muscle", it appears that Davy had little understanding of the significance of the relationship between these structures. While Davy understands that animals which produce a lot of heat typically have a large respiratory surface, he erroneously concludes that the respiratory surface itself must therefore be the site of heat production.

Another misconception that underlies these texts is that endothermic ("warm-blooded") animals produce heat whereas ectothermic ("cold-blooded") animals produce none. This idea is expressed in a sentence in the second abstract, "(Davy) thinks it not improbable that these fish may possess means of generating heat peculiar to themselves". In the second abstract, Davy attempts to explain the mechanism by which some fish are warmer than their environment. His approach is at first logical; he looks for other ways in which the warm fishes are different from ectothermic ones. His next step is somewhat strange. Instead of examining the characteristics he lists in the first

abstract (such as heart size or muscle redness) or other unique characteristics such as *retia*, he decides that the "peculiarities" of the blood of three fish, the skipjack tuna, the bluefin tuna, and the swordfish, *Xiphias gladius*, are the key to answering the question of how these fish generate heat. (It is strange that Davy includes the swordfish in the comparison, since he gives no indication that he suspects it of being endothermic.) The "peculiarity" to which he refers is the fact that the "globules" (erythrocytes) of these fishes are nucleate, in contrast to mammalian erythrocytes which are enucleate. Unfortunately, this line of reasoning is doomed from the start, as the erythrocytes of all fishes (at least those that have erythrocytes) are nucleate. In 1835 it was known that blood circulates and that arterial and venous blood differ in color. But, the fact that the pigment in red blood cells, haemoglobin, reversibly binds with oxygen in respiratory organs and releases it at the tissues was not known until 1864. Davy illustrates this general lack of understanding of the respiratory function of blood in the last sentence in the first paper "... especially the question, Whether any oxygen is absorbed by the blood in the lungs, and carried into the circulation".

Although the actual mechanism he proposes sounds downright ludicrous to the modern ear, it is worth examining. The fact that Davy assumes the site of heat production to be the erythrocytes is at least partly consistent with his conception that heat production occurs primarily in the gills (since the gills contain a conspicuous amount of blood). The details of the mechanism also show that Davy understood that the consumption of oxygen is linked to the process of thermogenesis. His theory about separations of charges within the erythrocyte is his attempt to explain how exactly tunas achieve rapid rates of oxygen consumption, and therefore, heat generation.

Davy makes one other important observation and that is the unusually large size of the branchial nerves found in tunas. It is interesting that Eschricht & Müller make a similar observation about the unusual size of the visceral nerves found in the bluefin. To this date there are no explanations in the literature of the function of these large nerves, and, as far as we know, there are no subsequent studies of these nerves. We have been able to confirm in our dissections that these nerves are not only large, they are in fact an order of magnitude larger than the analogous nerves in mammals of comparable size.

In the four texts that follow, endnotes are denoted by a number in brackets. In addition, some units are converted to metric and some current species names are given. In these cases the additions to the original text are set apart from the text with brackets. The only changes made to the text are that genus and species names have been italicized.

1. Davy, J. 1835. On the temperature of some fishes of the genus *Thynnus*. Edinburgh New Philosophical Journal XIX: 325-330.

On the temperature of some fishes of the genus *Thynnus*

By John Davy, M.D., F.R.S., Assistant-Inspector of Army Hospitals. Read before the Royal Society of London. Communicated by the Author.

It is commonly believed and asserted by naturalists, that fishes generally, and without exception, are cold-blooded; thus Linnaeus, in his "Regnum Animale", characterizes them in relation to their blood, by "sanguine frigido" [1]; and Baron Cuvier, our latest and highest authority, not only admits, but undertakes to shew, that it must be so; thus in the chapter of his "Histoire Naturelle des Poissons", on the general character and essential nature of fishes, he says, "Ne respirant que par l'interméde de l'eau, c'est-à-dire, ne profitant pour rendre à leur sang les qualités artérielles, que de la petite quantité d'oxigene contenu dans l'air melé à l'eau, leur sang a dû rester froid" [2]. [Breathing through the water medium ; i.e., only profiting from the small quantity of oxygen contained in the air dissolved in water, to reestablish the arterial quality of the blood, their blood had to remain cold.]

It was many years ago, on a voyage to Ceylon, that I first met with an exception to this universally received opinion: it was in the instance of the Bonito (*Thynnus palamys*, Cuv. and Valen.), whose temperature was 99° of Fahr. [37.2°C] in the deep-seated muscles in the thickest part of the fish a little below the gills, when the surface of the sea, from which it had just before been taken, was 80.5 [26.9°C], the difference being the remarkable one of eighteen degrees and a half [10.2°C].

This fact necessarily made a strong impression on my mind, and a year or two ago, when examining the heart and gills of the tunny of the Mediterranean (*Thynnus vulgaris*, Cuv. and Valen.) my attention was recalled to it, on finding that the latter were supplied with nerves of unusual magnitude; that the heart like that of the bonito, was very powerful; that the fish equally, or even more, abounded in blood, and that its muscles, generally like those of the bonito, from the same cause, were of a dark red color. It immediately occurred to me, that its temperature also might be high, and the result of careful inquiry amongst the fishermen of most experience in the tunny fishery confirmed the conjecture. All who were asked, declared that the tunny is warm-blooded, and one of the most intelligent of them, when questioned as to the degree of heat, said it was much the same, or little less than that of the blood of a pig, when flowing from the divided vessels of the neck in being killed. And this man was very competent to give an opinion on the subject, having been much employed in the fisheries on the Sicilian coast, in which the

viscera of the fish are the perquisite of the common fishermen, and are immediately taken out when the fish are caught.

From the tunny, I extended my inquiries to other fish of the same family, and learnt, that the analogy holds good, applied to all the species of the genus *Thynnus* of Cuvier and Valenciennes, with which the Maltese fishermen are acquainted, viz. (besides the two already mentioned [*T. palamys*, *T. vulgaris*]), *T. brevipinnis* [*Euthynnus alleratus*], *T. thunnina* [*E. alleratus*], and *T. alalunga* [*T. alalunga*], all of which abound in blood, have a powerful heart, red or reddish muscles; and also, as I have ascertained by particular examination, have their gills amply provided with large nerves. Not having been able to procure any of these fish alive their exact temperature, of course, I have not been able to determine; but from the reports of the fishermen, it would appear that the common tunny is the warmest of the species; and in accordance with this, I have found its branchial nerves proportionally largest.

These nerves (the branchial), immediately after quitting the cranium, enter or swell out into ganglia of considerable size, and more or less connected together, from which five principal trunks proceed, the first four chiefly to the branchiae, and are the respiratory nerves; the fifth, the lowest, to the branchiae and stomach. In point of magnitude, those respiratory nerves almost rival the electrical nerves of the torpedo, and their origin is very similar, and their direction and associations, but with this marked difference between them, that the torpedinal nerves are entirely destitute of ganglia.

The respiratory nerves of the other species of *thynnus* [sic] which I have examined, very much resemble the preceding. Those which are smallest belong to *Thynnus brevipinnis*, and yet, even in this fish, in comparison with the fish of other tribes, the respiratory nerves are large, and their ganglia considerable. This fish, perhaps, may be considered as a link between the tunny family and the mackerel on one side, and the pelamides on the other, and the respiratory nerves of one of each of those genera of fish, which I have dissected, viz., of *Scomber pneumatophorus* [*S. japonicus*] and *Pelamys sarda*, have approached in magnitude those of the *thynnus* [sic] last mentioned. What the temperature of those fish is, I have not had an opportunity of determining by trial; according to the statement of the fishermen I have consulted, they are all cold-blooded. Reasoning from analogy, the natural inference is, that they will be found to be of somewhat higher temperature than other fishes less amply supplied with respiratory nerves.

As regards the rationale of the high temperature of the thynni,

there appears to me less difficulty, than in accounting for the electrical power exercised by the torpedo, and other electrical fish. The peculiar function of the latter is performed by means of a particular organ, the most striking feature of which is a vast apparatus of nerves; but this organization bears little or no analogy to any other natural, or to any artificial process hitherto known, by which electricity is generated. Not so the respiratory apparatus, and associated organs in these fish of high temperature; they are essentially analogous in organization to the warm-blooded animals of the other two classes, and hardly more different from those of the mammalia are from the respiratory apparatus and associated organs of birds. The function of respiration in water is commonly considered the same as in the atmosphere; the same change, it is supposed, takes place in the blood; the same change is ascertained to take place in the air dissolved; and, increase of temperature in one instance and the other, is referred to the conversion of carbon into carbonic acid. The difficulty is not as regards the kind of effect, but the degree of that effect; not an augmentation of one or two degrees above the temperature of the surrounding medium, but of many degrees. The consideration of some of the peculiarities of these fish may help to diminish this difficulty, which I have little doubt will be removed entirely when we are better acquainted with their structure, and better acquainted with all the sources of animal heat.

The most important peculiarities are, I believe, chiefly the following: - a large and powerful heart; abundance of blood; large gills; and a very large apparatus of branchial nerves; - all which may be considered as concerned, either directly or indirectly, in the generation of heat: and the circumstances for its preservation are hardly less remarkable, as the manner in which the gills are defended by peculiarly strong opercula, abounding in fatty matter, and the deep situation of the principal blood vessels, surrounded by thick muscles, and in addition, the aorta surrounded by the principal abdominal viscera, the kidneys, stomach, and liver. Moreover, the habits of these fish may, in some measure, contribute to their high temperature. They are frequently to be seen near the surface, and seem to have a delight in springing into the atmosphere. Aristotle, speaking of the tunny, says, of all fish it most enjoys warmth, and on that account swims near the surface, and frequents sandy shores. I quote from the old Latin translation of Theodore Gaza. "*Thunni omnium maxime piscium gaudent tepore et ob eam rem arenam et littora adeunt; per summa etiam maris innant, quo teporis potiantur;*" [3] - confounding, as I believe in this instance he has done, a fondness for warmth, with the habits connected with its production. In this enumeration of circumstances which may contribute to the high temperature of these fish, both as regards its generation and

preservation, I have intentionally been very general. In the present state of our knowledge, I apprehend it would be useless to be more minute. It is not improbable that these fish may possess means for generating heat peculiar to themselves, and of which at present we have no adequate idea; and the situation of the kidneys, of which a considerable portion is even higher than the stomach, and posterior to the gills, of large size, and abounding in blood, and well supplied with nerves, would lead to the conjecture that these organs, in the function of imparting heat, may possibly act a part. Still, however, reflecting on the great proportional size of the branchial nerves, and guided by analogy, it is difficult to resist the conclusion, that they are not principally concerned in the performance of the function in question, and that these nerves, as means, are so very ample on account of the element inhabited, and the proportionally greater energy of function required to produce the same effect of elevation of temperature in water and in the atmosphere. On any other view, it seems difficult to account for the branchial nerves of these fish being proportionally very much larger than the pulmonary nerves of the mammalia, and vastly larger than those of birds, of all animals the warmest [4].

Whether there is any immediate relation between the ganglia on the branchial nerves and the generation of heat in these fishes, is uncertain, and must necessarily remain so, as long as there is any doubt concerning the use of ganglia. The absence of ganglia on the principal nerves of the lungs of man [5], and I believe of the mammalia generally, and of many birds, would lead to the inference that the nerves, in the instance under consideration, rather than the ganglia [6], are chiefly instrumental; and that the latter are in some way subservient to the former; but whether for giving sensation to the branchiae, or for imparting extraordinary secreting power, so as to change the blood, or for some other purpose, remains to be ascertained.

In concluding, I would remark, I am very sensible that this paper is in many respects greatly imperfect. I have been induced to contribute it chiefly with the view of calling attention to the subject, with the hope that others will engage in the inquiry as opportunities may offer; and, by more extended and minute observations, supply many desiderata, as the exact temperature of the different species of *thynnus* [sic], the temperature of the blood coming from and returning to the gills, the minute peculiarities of the structure of these fish, and their habits. It seems not improbable that the investigation, if followed up, may not only throw light on the function of respiration in these fish, and on the production of their high degree of temperature, but also that it may aid in elucidating some obscure parts of the theory of respiration in general, in connexion with that of animal heat, especially the question, Whether any oxygen is absorbed by

the blood in the lungs, and carried into the circulation.

[References and footnotes]

[1] *Systema Naturae*, tom i. p. 18

[2] *Hist. Nat. des Poissons*, tome i. p. 275

[3] *De Hist. Animal*, lib. viii. cap. 19.

[4] The size of the pulmonary nerves of birds, and indeed of their respiratory nerves generally, so far as my observations have extended, is so small as to be truly astonishing, compared with their very high temperature. And, on the hypothesis of nervous influence being essential to the production of animal heat, through the agency of respiration, the necessary inference seems to be, that birds require less of this influence than any other description of warm-blooded animals, owing to their peculiarities of structure, both in relation to the diffused ærial means they possess of generating heat, and their peculiar means, in their covering of feathers, of preserving it; and, owing probably farther to their less expenditure of it, from the peculiarities of some of their principal secretions, especially those of the kidneys, skin, and lungs; their kidneys secreting an almost solid urine; their skin exhaling little moisture, and that not in sweat, but entirely by insensible perspiration; and their lungs, though exhaling more, from the nature of the function they perform, yet less than might at first be supposed, part of the aqueous vapour contained in the air expired being, I believe, condensed before it enters the atmosphere by the trachea, mouth, and beak, especially the latter, which are always comparatively cool. And, in accordance with

this view, from the experiments by Messrs Allen and Pepys, it appears even in some instance at least, that one of the warmest of birds, the pigeon, consumes, in relation to its bulk, less oxygen, or produces less carbonic acid, than a quadruped, the Guinea pig, the temperature of which is several degrees lower.

[5] Haller, speaking of the great sympathetic nerve, which in man is so amply provided with ganglia, says, "In pectore notabiles ramos paucos edit. Neque memini me alicujus momenti truncos vidisse qui ad nervum octavi paris accederent; etsi ejusmodi nervi illustribus viris visi sunt." - *Element*.

[6] *Physiol.* iv. 260. And, according to Sir Charles Bell's view of the nervous system, none of the respiratory nerves are ganglionic nerves. Sir Everard Home (*Phil. Trans.* 1835, p.257), has endeavoured to associate the production of animal heat directly with ganglia; but the instances he has adduced seem liable to great objection; and the fact that the great sympathetic nerve in birds, is comparatively little developed, even less than in some reptiles, and destitute of large central ganglia, such as the semilunar in the mammalia (at least in every instance in which I have carefully sought for them, I have been unsuccessful), seems fatal to his hypothesis.

[7] Malta, January 8, 1835.

2. Davy, J. 1837. On the temperature of some fishes of the genus *Thunnus* [sic]. Abstracts of the papers printed in the Philosophical Transactions of the Royal Society of London from 1830 to 1837 inclusive. Vol. III: 327-328. Printed by Richard and John E. Taylor, London.

[This title of the abstract of the first paper mistakenly refers to the genus as *Thunnus*. This is the spelling used now, but is not the spelling used in 1835, nor is it the spelling used by Davy in the full paper. In addition the spelling of tunny in the full paper is given as thunny in the abstract. In other respects the abstract reflects the comments in the full paper.]

March 26, 1835. William Thomas Brande, Esq., Vice-President, in the Chair

"On the Temperature of some Fishes of the Genus *Thunnus*." By John Davy, M.D., F.R.S., Assistant Inspector of the Army Hospitals.

The author had occasion to observe, many years ago that the Bonito (*Thynnus pelamys*, Cuv.) had a temperature of 99° Fahr. [37.2°C] when the surrounding medium was 80°.5 [sic] [26.9°C], and that it, therefore, constituted an exception to the generally received rule that fishes are universally cold-blooded. Having found that the gills of the common Thunny of the Mediterranean (*Thynnus vulgaris*, Cuv.) were supplied with nerves of unusual magnitude, that the heart of this latter fish was very powerful, and that its muscles were of a dark red color, he was led to conjecture that it might, like the Bonito, be also warm-blooded; and this opinion is corroborated by the testimony of several intelligent fishermen. The author endeavours to extend this analogy to other species of the same family, which, according to the reports of the fishermen of whom he made inquiries, have a high temperature, and in whose internal structure he noticed

similar peculiarities as in the Thunny; namely, very large branchial nerves, furnished with ganglia of considerable size. In this respect he considers that in these fishes the branchial system of organs makes an approximation to the respiratory apparatus of the Mammalia, and that it probably contributes to the elevation of temperature, resulting from the more energetic respiration which he supposes to be exercised by these organs. He, however, thinks it not improbable that these fish may possess means of generating heat peculiar to themselves, and of which at present we have no adequate idea. He conceives that the situation of the kidneys, of which a considerable portion is even higher than the stomach, and posterior to the gills, and which are of large size, and well supplied with nerves and blood-vessels, may possibly act a part in the production of an elevated temperature; but, on the whole, he is disposed to ascribe the greatest share of this effect to the superior magnitude of the branchial nerves.

3. Davy, J. 1844. Miscellaneous observations on animal heat. Philosophical Transactions of the Royal Society of London. 134: 57-64.

[We have included only the first section on warm bodied fish; parts 2 and 3 concern body temperature in humans. Davy capitalizes the species name, sarda whereas current convention uses a capital for the genus but lower case for the species. Notes and unit conversions appear in brackets].

V. Miscellaneous observations on animal heat.

By JOHN DAVY M.D., F.R.S., L. and E.

Received November 2.-Read December 14, 1843.

I. On the Temperature of the Pelamides (*Pelamys Sarda* (sic), CUV. and VAL.).

Fishes generally are commonly considered as cold-blooded. In a work published in 1839, I have stated particulars tending to show, that this commonly received opinion is not universally correct, and that fishes of the genus *Thynnus*, with some others of the Scomber family, may be inferred to be an exception [1].

As this inference was founded chiefly on the reports of fishermen, it appeared very desirable to determine by actual thermometrical measurement what is the exact temperature of fishes of this family.

Hitherto, although watching for opportunities, and promised the aid of friends favorably situated, I have not been able to make any observations of the kind required, excepting on one species of these fishes, the Pelamides, the *Pelamys Sarda* [sic] of CUVIER and VALENCIENNES. The Pelamides, like most of its congeners, is migratory in its habits. In the early part of summer it appears in the sea of Marmora and the Bosphorus, and in August in the Black Sea, from whence, after spawning, it returns in September and October, on its passage to the Mediterranean. It is caught in the same manner as the Tunny.

In June 1841, whilst at Constantinople, I visited a fishing station for this fish, in an inlet of the sea of Marmora, and was present when a small capture was made, enabling me to ascertain the temperature of four specimens. This was done the instant they were taken out of the water, being in a boat alongside the net, by introducing a thermometer with a projecting bulb, through a small incision, into the muscle of the back, about inch and a half [4 cm], and immediately after into the cavity of the abdomen. In three instances, the thermometer in the back rose to 75° FAHR. [23.9° C]; in one to 74° F [23.3° C]; in all, in the abdomen it rose to 73° F [22.8° C]. The Pelamides were of moderate size, between two and three feet long. The air at the time was 71° F [21.7° C]; the sea at the surface 68° F [20.0° C], but probably at the depth from which the fishes were taken, it was a few degrees lower, the descending current of the Bosphorus then being, where

coldest, at 62° F [16.7° C].

Supposing that the water from which they were taken was 62° F [16.7° C], and it might have been lower, as the Pelamides swim in deep water, -the temperature of this fish would appear to be about 12° F [7.1° C] above the medium in which it swims, and at least 7° F [3.8° C] above that of the surface.

This result seems in accordance with the inference, that all fishes are not cold-blooded. In the work already referred to, reasoning from the smaller size of the respiratory nerves of the *Pelamys Sarda* [sic] compared with those of the Tunny, I offered the conjecture that its temperature would be found less than that of the Tunny, and somewhat higher than that of fishes of other orders with still smaller respiratory nerves, a conjecture which the observations described may be adduced as confirming.

In connexion with their temperature, my attention was directed to the blood of these fishes. I have been able to examine it only in three instances, and that partially, viz. the Sword-fish, the *Pelamys Sarda* [sic], and the common Tunny. Considering the great difficulty there is in obtaining the subjects for experiment under favorable circumstances for examination, imperfect as were my results, I am induced to offer them now.

The Sword-fish appears to abound less in blood than the Pelamides, and the Pelamides less than the common Tunny; and accordingly the muscles of the former two are of a much lighter color than those of the latter.

The blood of the Tunny is very rich in red particles: this is indicated not only by its appearance, but also by its specific gravity, which I have found as high as 1.070. The blood tried was taken from a fish, caught in the sea of Marmora, that weighed between two and three hundred pounds [91 to 136 kg].

The blood of the Pelamides appears to be less rich in red particles than that of the Tunny, but more than that of the Sword-fish: I have not ascertained its specific gravity. The specific gravity of the blood of the Sword-fish I have found to be 1.051; the fish from which the blood was taken was caught in the Bosphorus, in the month of December, and was of large size.

Under the microscope the appearance of the red particles of the blood of these three fishes is very similar. They are commonly thin oval discs (very soft), containing oval nuclei: a

few circular discs are intermixed with them. The medium dimensions of those of the Pelamides were about 1/2000th of an inch by 1/3000th [12.7 by 8.5 μm]; of the Sword-fish about 1/3000 by 1/4000th [8.5 by 6.4 μm]; and of the Tunny, about 5/8000th by 3/8000 [15.9 by 9.5 μm].

That the red particles constitute that portion of the blood which is chiefly concerned in the production of animal heat, is now generally admitted. What a contrast appears, in comparing the blood of the fishes under consideration, with that of some of the colder, especially of the cartilaginous kind, in which it is very small in quantity, accompanied by a proportionally diminutive heart, and poor in red particles! [we are not sure why this comment deserves an exclamation mark] the blood of the *Squalus Acanthias* [sic] I have found to exceed in density only a little its serum, one being of the specific gravity 1.030, the other of the specific gravity 1.027.

Whether the peculiar constitution of the red particles operates in any way in promoting their union with oxygen, seems to be deserving of consideration. It may be thrown out as a conjecture, that the circumstance of their possessing nuclei may have an effect of the kind, supposing, which is possible, the blood-

corpuscle and nucleus, or containing and contained part, to be in the electrical relation to each other of positive and negative. If it be objected to this, that as regards nuclei as well as size, there is an analogy between the blood-corpuscle of fishes, birds and reptiles, the temperature of which commonly is so very different, it may be answered, that in all these classes such a constitution of blood-corpuscle may be designed for the same end, and that birds partly owe their high temperature to it ; and that in reptiles and fishes, in most of which the proportion of red particles is small, were the constitution of blood-corpuscle different, it would be inadequate to perform the part required of it.

II. On the temperature of man in advanced age [not included here]

III. On the effect of air of different temperatures on animal heat [not included here]

[1] Researches, Physiological and Anatomical, vol. i. p. 218. [Neither the Royal Society nor we have been able to locate this paper]

[2] The Oaks, Ambleside, Nov. 1st, 1843.

4. Davy, J. 1851. Miscellaneous observations on animal heat. Abstracts of the papers communicated to The Royal Society of London from 1843 to 1850 inclusive. Vol. V: 496-497. Printed by Richard Taylor, London.

December 21, 1843. James Walker, Esq., Vice-President, in the Chair

The reading of Dr. Davy's paper, entitled, "Miscellaneous observations on animal heat," was resumed and concluded.

The author, in the first section of this paper, after adverting to the commonly received opinion that all fishes are cold-blooded, and noticing an exception, as he believes, in the instance of certain fishes of the genus *Thynnus* and of the Scomber family, describes the observations which he made whilst at Constantinople, on the temperature of the *Pelamys Sarda* [sic], when, in three different examples, he found its heat to exceed that of the surface-water by 7°, and of the deep water probably by 12°. He adduces some observations and remarks in peculiarities in the blood of the same fish, of the sword-fish and of the common tunny, which he supposes may be connected with their temperature; and throws out the conjecture, that the constitution of their blood-globule, formed of a containing and contained part, namely the globule and its nucleus, may be to each other in the electrical relation of positive and negative, and may thereby act with greater energy in separating oxygen in respiration.

In the second section, on the temperature of man in advanced old age, he relates a number of observations made for the purpose of determining the actual heat of persons exceeding eighty years of age; the result of which, contrary to the commonly received

opinion, is, that the temperature of old persons, as ascertained by a thermometer placed under the tongue, is rather above than below that of persons of middle age; and this he thinks may be explained by the circumstance, that most of the food used by old persons is expended in administering to the function of respiration.

In the third section, on the influence of air of different temperatures on animal heat, after alluding to what he had witnessed of the rise and fall of the temperature of man on entering the tropics, and, within the tropics, on descending from a cool mountainous region to a low hot country, he adduces certain observations to show that in this country similar changes of temperature take place in a few hours in breathing the air of buildings artificially heated; and, in confirmation, he describes the results of many observations made on an individual in the very variable climate of Constantinople, where, between March and July, in 1841, the thermometer ranged from 31° [-0.6°C] to 94° [34.4°C].

In the fourth section, he describes the observation which he made to determine the effect of moderate exercise, such as that of walking, on the temperature of the body, tending to prove, that while it promotes the diffusion of temperature and produces its exaltation in the extremities, it augments very little, if at all, the heat of the central and deep-seated parts.

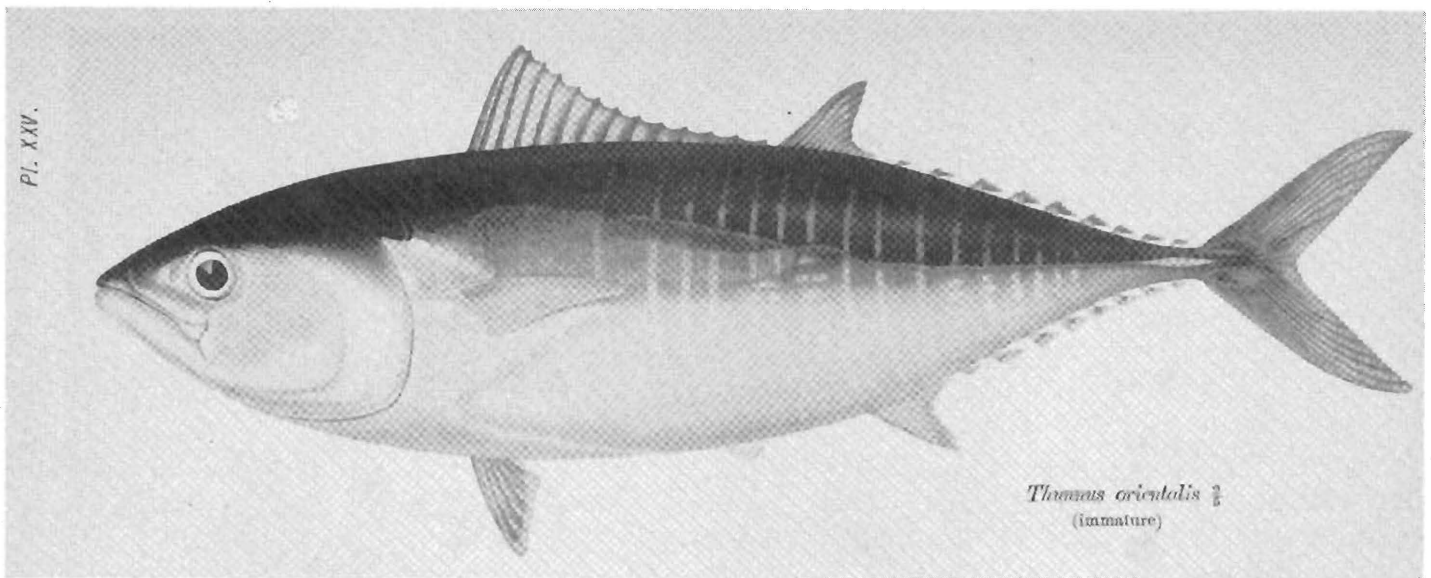


Fig. 17. This drawing of a juvenile (about six months old) bluefin tuna is taken from Kishinouye (1923).

Acknowledgments

Most importantly, we must acknowledge the major contribution made by Elisabeth Niimi with the translation. The fact that her native tongue is German was an invaluable aid in understanding the details and nuances of the sometimes interminably long sentences. We thank Ian Smith for creating the schematics. We thank those members of the fishing industry and government agencies that have been helpful in obtaining specimens for our analysis of the anatomy of visceral *retia*: Billy Raymond of Cape Ann Tuna, Gloucester, MA; Mark Godfried of Frontero Brothers, Gloucester, MA; Capt. Bill Degnan and crew (Stretch, Jamie), Harwich, USA; Robert Conrad and his crew, Nova Scotia, Canada; Brad Chase and his crew, Division of Marine Fisheries, MA, USA; Dick Stone, NFMS- USA. We also thank Ron and Marilyn Fudge who allowed the use of their garage as a tuna mortuary. Others helped considerably with taxonomic problems in a variety of languages: Christine Flegler-Balon, Eugene Balon, Bill Eschmeyer, and Bruce Collette. Jim Ballantyne, Esta Spalding, and David Noakes proofread versions of the paper. Tracey Dart, Royal Society of Edinburgh was of invaluable assistance in learning about John Davy and his papers. Catherine Norton, Marine Biological Laboratory Library gratefully loaned us the journal volume that contained the original copy of the Eschricht & Müller paper and supplement. EDS thanks the many individual tuna that have been a continued source of inspiration and have allowed him to combine his vocation with his avocation. NSERC has provided funding to EDS for many tuna projects over the years.

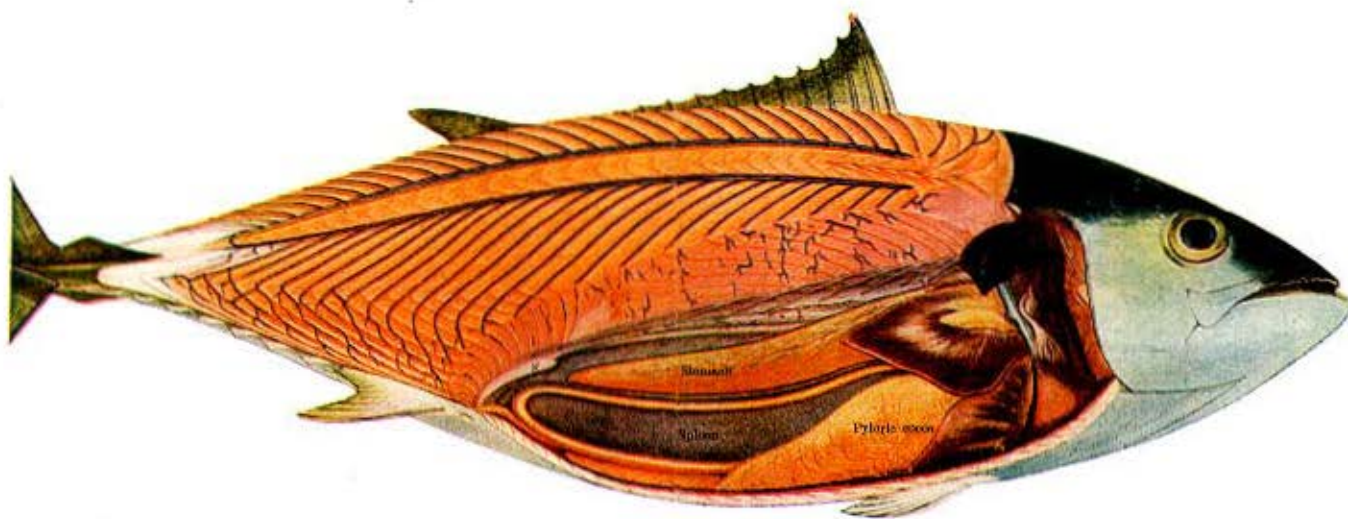


Fig. 18. Drawing of a dissection of a bluefin tuna, lateral view taken from Kishinouye (1923). The skin, anterior portion of the hypaxial lateral muscle, and part of the gills and operculum have been removed, exposing the cutaneous vascular system and the viscera. The radiating vessels on the surface of the liver can be seen, and the drawing also shows how liver envelopes the rest of the viscera.

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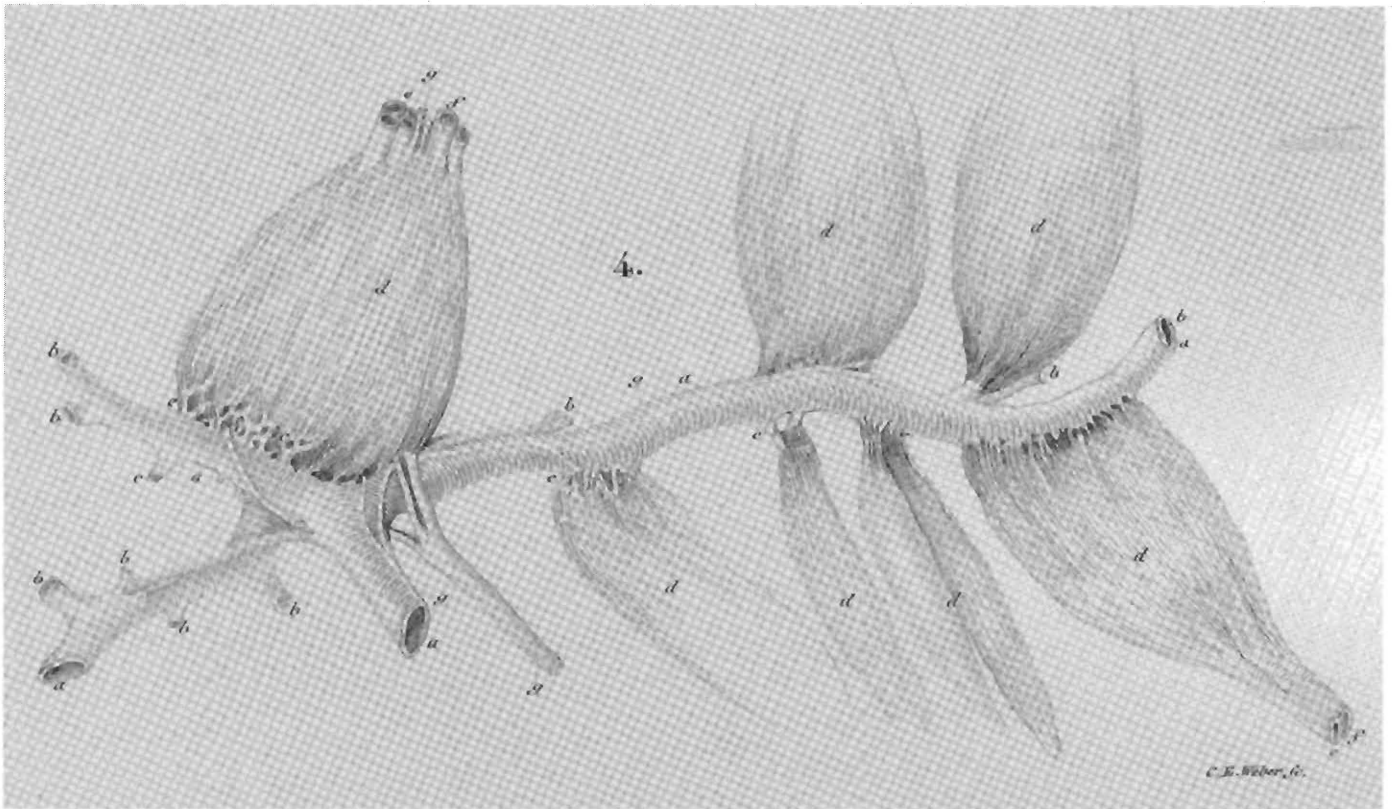
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9. Facsimile of the original text of the Eschricht & Müller paper on tuna *retia*

Eschricht, D. F. & Müller, J. 1835. Über die arteriösen und venösen Wundernetze an der Leber und einen merkwürdigen Bau dieses Organes beim Thunfische, *Thynnus vulgaris*. Physik. Abhdl. d. K. Wissensch. Berlin pp. 1-32.

Fig. 19. The drawing below is an enlargement of plate III, Fig. 4 of the original. It shows the *retia* and their branches the coeliac artery. It also shows the large nerve that runs beside the artery and its branches into the *retia*. a = artery, b = hepatic branches of the artery, c = branches of the artery into the *retia*, d = *retia*, e = visceral portal vein branches which come from the organs of the digestive system and enter the *retia*, f = arteries which leave the *retia* and lead to the organs of the digestive system.



Abhandlungen
der
Königlichen
Akademie der Wissenschaften
zu Berlin.

Aus dem Jahre
1835.

Berlin.
Gedruckt in der Druckerei der Königlichen Akademie
der Wissenschaften.

1837.

In Commission bei F. Dümmler.

Über
die arteriösen und venösen Wundernetze an der Leber
und einen merkwürdigen Bau dieses Organes beim
Thunfische, *Thynnus vulgaris*.

Von
H^{rn}. ESCHRICHT und H^{rn}. MÜLLER.



[Mitgetheilt von dem Letztern in der Akademie der Wissenschaften am 29. Juni 1835.]

Mit einigen neueren Zusätzen.

I. Veranlassung der Untersuchung.

Wie lange bekannt auch die Thunfische in der Geschichte der Fischereien sind, so ist doch die Naturgeschichte derselben bis auf Cuvier an Dunkelheiten und Verwechslungen reich gewesen und die anatomischen Eigenthümlichkeiten derselben in der Ordnung der Scomberoiden sind größtentheils bis jetzt unbekannt geblieben. Aristoteles hatte zwar schon Thiere dieser Familie untersucht, und die außerordentlich lange und enge Gallenblase seiner Amia (*Pelamis sarda*) entdeckt ⁽¹⁾, mit welcher die Gallenblase der Thunfische (*Thynnus vulgaris, alalonga*) nach Cuvier's ⁽²⁾ Beobachtungen übereinstimmt. Eine allgemeine sehr unvollständige Kenntniss von der Form und Lage der Eingeweide und von den Eigenthümlichkeiten des Skelets ist indeß das einzige, was wir von der Anatomie dieser Thiere kennen. Die physiologischen Verhältnisse dieser Familie sind in mehr als einer Hinsicht merkwürdig. Man denke nur an die regelmäßigen Wanderungen, über welche freilich noch vieles zu untersuchen übrig bleibt. Noch eigenthümlicher ist die hohe eigene Temperatur der Thunfische, auf welche ganz vor Kurzem

⁽¹⁾ *Hist. anim. ed. Schneid.* Lib. II, 11. vulg. 15.

⁽²⁾ *Hist. nat. des poissons.* T. VIII, p. 66. 125.

John Davy ⁽¹⁾ aufmerksam geworden. *Thynnus pelamys*, ein Thunfisch des atlantischen Meeres, hat nach J. Davy's Beobachtung 99° F. eigene Temperatur bei 80°,5 F. des Mediums, und auch bei anderen Thunfischen soll die Temperatur nach weniger sicheren Nachrichten beträchtlich sein. Die Beobachtungen, die wir hier mitzuthellen haben, betreffen eine in anatomischer wie physiologischer Hinsicht gleich wichtige Eigenthümlichkeit in dem Bau der Unterleibseingeweide und ihrer Gefäße, wovon sich bis jetzt keine Spuren bei irgend einem andern Thiere gezeigt haben. Die nächste Veranlassung zu den folgenden Beobachtungen war eine Entdeckung meines verehrten Freundes Herrn Eschricht in Copenhagen. Derselbe schickte mir unter dem 1. November 1833 ein Stück von der Leber des Thunfisches mit der Bemerkung, daß er nirgends eine so eigenthümliche Structur der Leber erkannt habe. Sie bestehe aus lauter parallelen Gängen mit sehr kleinen Anhängseln und die Masse reisse sich nur in Längsschichten, die ganz faserig erscheinen. Das von Herrn Eschricht gesandte Stück erregte meine Aufmerksamkeit in hohem Grade; in der That schien die ganze Lebermasse nur aus solchen mit den kleinen *acini* besetzten Röhren zu bestehen; da die Stämme der Gefäße nicht mehr an diesem Stück erhalten waren, so blieb es mir ungewiß, ob diese Röhrenbildung der eigentlichen Drüsensubstanz der Leber oder den Blutgefäßen angehörte und der erstern fremd war. Glücklicherweise befand sich die Leber und der Darmkanal eines Thunfisches auf dem Königlichen anatomischen Museum. Hier bestätigte sich nicht bloß die von Herrn Eschricht entdeckte Bildung; sondern ich konnte auch ermitteln, daß diese zum Theil parallelen, größtentheils aber strahligen Röhren, woraus die Leber zu bestehen schien, in der That nicht die eigentliche Drüsensubstanz der Leber, sondern nur Blutgefäße waren, welche von großen Blutbehältern an der convexen Fläche der Leber ausgingen; daß dagegen die Drüsensubstanz der Leber nur in den kleinen, mit bloßen Augen noch ganz gut erkennbaren Anhängseln bestand, womit die Röhren besetzt waren. Ein solcher Blutbehälter war im convexen Theile jedes der 3 Leberlappen. Der Blutbehälter des rechten Leberlappens ging nach außen in einen dicken kurzen Gefäßstamm, die vereinigten Blutbehälter des linken und mittleren Leberlappens in einen gleichen Gefäßstamm über. Beide Ge-

(¹) *L'Institut. Journal général des sociétés et travaux scientifiques.* N. 108.

fäfsstämme waren dicht an der Leber abgeschnitten. Beim Aufblasen jener Behälter schwollen alle strahlenförmigen Röhren der Leber auf. Die Gallengänge dagegen nahmen an dem Zerfallen in parallele und in strahlenförmige Röhren keinen Antheil; überhaupt konnte ich die Lebersubstanz durch Aufblasen des *Ductus hepaticus* nicht aufblasen. Keine jener Röhren füllte sich. Es war nun zu ermitteln, welche der Blutgefäße, die Arterien, die Venen oder die Pfortaderzweige jene Röhren bilden. Leider waren auch die Stämme der Blutgefäße auf der concaven Seite der Leber abgeschnitten und die Leber hing durch keine Blutgefäße weder mit dem Darmkanal noch mit der Milz zusammen. Indefs bewies die Ausmündung der *Sinus* auf der convexen Fläche der Leber, daß diese, wie die von ihnen ausgehenden Röhren, den Lebervenen angehören; denn jene Seite ist die dem Herzen zugewandte. Auch liefs sich von dem Hauptstamm an der concaven Seite der Leber nicht die ganze Leber aufblasen, und obgleich er auch viele Gefäße in die Leber abgab, so war doch die Bildung sehr von der der Lebervenen auf der andern Seite verschieden, deren ganze strahlenförmige Verbreitung mit einemale von dem Sinus aufgeblasen werden konnte.

Was vorläufig an unserm Präparat gewifs wurde, daß der strahlig röhriche Bau der Leber des Thunfisches von den Lebervenen herrührt, theilte ich meinem Freunde Eschricht mit, mit der Aufforderung, an seinem Präparate weitere Untersuchungen anzustellen. Doch war an den isolirten Theilen der Leber weiteres nicht zu ermitteln. Mein Freund bemerkte, daß er diese Gänge wenigstens hauptsächlich für Gefäfsfortsetzungen gehalten habe, und daß es ihm sehr willkommen sei, zu erfahren, daß sie es wirklich sind. Er glaube auch, daß man in neueren Zeiten vielleicht etwas zu wenig Rücksicht genommen auf die Rolle der Blutgefäße in den Drüsen, vor allem in der Leber. Denn wenn es deutlich ist, daß bei Embryonen der Ausführungsgang die Hauptrolle spielt als Fortsetzung der Darmhöhle, so ändere sich dieses Verhältnifs wenigstens der Masse nach in der Leber doch ganz sicher. Auf den vortrefflichen Injectionspräparaten von Ibsen in Copenhagen, wo die drei Gefäfsysteme und die Gallengänge mit vier verschieden gefärbten Massen injicirt, dann das Ganze ungemein sorgsam corrodirt ist, zeige sich dieses sehr deutlich, obgleich allerdings von den Haargefäßen und den letzten blinden Endigungen der Gallengänge dabei nicht die Rede sein könne.

Er rathe die Leber von Delphinembryonen nachzusehen, wo dasselbe Verhältniß ihm sehr deutlich zu sein scheine.

Etwas Eigenthümliches, was ich an der Thunfischleber des hiesigen anatomischen Museums sah und zum Theil noch an dem von Herrn Eschricht gesandten Stück der Leber erkannte, konnte ohne neue Hülfsmittel keine Erklärung finden. Diefs waren 2 Zoll lange und über 1-2 Zoll dicke und dichte Büschel von mehr röthlich grauen, nicht mit Lebersubstanz besetzten Röhren, welche von der eigentlichen Leber verschieden, auf die concave Seite der Leber, da wo die Gefäße verliefen, aufgesetzt und damit verwachsen waren. Diese Lappen enthielten auch in ihrem Innern keine Spur von Lebersubstanz; sie ließen sich von irgend einer stärkern Röhre am Anfang der Quäste aus oder auf dem Querdurchschnitt aufblasen. Die quastartigen Lappen waren sehr viel fester als die eigentliche Lebersubstanz und doch zugleich noch viel poröser durch die darin enthaltenen Röhren. Was nun diese mit der Leber verwachsenen Massen waren, ließ sich an unserem Präparat nicht ausmachen. Obgleich nämlich die unzähligen durch Zellgewebe verbundenen Röhrchen an der von der Leber abgewandten Spitze sich plötzlich in stärkere Gefäße sammelten, so waren doch wieder diese Stämme durchschnitten und ich konnte also nicht ausmitteln, ob diese röhrigen, der Leber angewachsenen Massen eine eigene den Thunfischen zukommende Drüse bilden oder dem Gefäßsystem angehören. Mit den ungeheuren Massen der *appendices pyloricae* waren diese Lappen nicht zu verwechseln. Auf dem Durchschnitt glichen dieselben einigermaßen dem Durchschnitt der Hoden einiger Fische. Auch der Hoden des Thunfisches kann ganz aufgeblasen werden. Aber diese Massen gehören nicht zu den Geschlechtstheilen. Nachdem so viel Merkwürdiges erkannt war, mußte uns alles daran gelegen sein, die besser erhaltenen Eingeweide eines Thunfisches zu erwerben. Hierzu gelangte ich durch die Gefälligkeit des Hrn. Lichtenstein, Königl. Preufs. Consuls in Montpellier. Die Eingeweide dieses Thieres von 3 Fufs Länge waren zwar schon etwas macerirt, aber über die Hauptfragen konnte man bald ins Klare kommen. Ich entdeckte nämlich, daß die auf die concave Seite der Leber aufgesetzten Massen Wundernetze darstellen, zwischen den in der Leber sich verbreitenden Zweigen der Pfortader und den Darmvenen, Milzvenen und Magenvenen, so zwar, daß alle Venen des chylopoetischen Systems sich erst in diese röhrigen Massen auflösen und aus den Wundernetzen erst

das Blut in die Leber sich verbreitet. Diese Bildung ist einzig in der Thierwelt und ist um so merkwürdiger, als sie allen bisherigen Ideen über den Zweck der Wundernetze an verschiedenen Arterien und Venen entgegen scheint. Die Wundernetze an der Leber der Thunfische sind aber zusammengesetzter als alles, was wir bis jetzt von den Wundernetzen der einzelnen Gefäße bei den Wiederkäuern, Tardigraden, Stenops, Delphinen u. a. wissen. Denn eines der mehrfachen größeren Wundernetze an der Leber des Thunfisches besteht allein schon aus vielen Hunderten von Röhren.

Ehe ich zur genauern Beschreibung der Leber und der Wundernetze des Thunfisches übergehe, muß ich eine kurze Beschreibung der Verdauungseingeweide dieses Thieres vorausschicken.

II. Allgemeines von den Verdauungsorganen des Thunfisches.

Die Verdauungseingeweide des Thunfisches und anderer Scomberoiden hat Cuvier bereits in seiner *Histoire des poissons* T. VIII. im allgemeinen beschrieben; er kennt die lange darmähnliche Gallenblase des *Thynnus vulgaris*, *alalonga*, des *Pelamis sarda* und die gleichfalls lange Gallenblase der *Scomber*, *Auxis*, *Thyrsites*, *Lepidopus*. Meckel hat in seinem System der vergleichenden Anatomie die Scomberoiden, wohl aus Mangel an Materialien, vernachlässigt, und auch Rathke giebt uns in seiner Abhandlung über das Pfortadersystem der Fische in Meckel's Archiv 1826 keine Mittheilungen von der Leber und der Pfortader der Scomberoiden.

Der Magen des Thunfisches Taf. III. Fig. 1. *K.* ist ein langer conischer, bis in den hintern Theil der Bauchhöhle ragender Blindsack von fleischigen Wänden, die unmittelbare Fortsetzung des Schlundes. Das blinde stumpfspitze Ende sieht nach hinten. Der *pylorus* befindet sich am obern Seitentheile des Sackes. Die *pars pylorica* des Darms, worin die Stämme der *appendices pyloricae* (*M.*) einmünden, liegt vor dem Magen, die *appendices pyloricae* theils vor dem Magen, theils links von demselben. Der Darm steigt von der *pars pylorica* anfangs vorwärts unter die Leber, biegt sich dann um und steigt rückwärts bis zur Länge des Magens, dann wieder vorwärts bis unter die erste obere Biegung, nun wieder rückwärts, dicht an dem letzten aufsteigenden Theil bis zum After, ohne seinen Durchmesser zu verändern. Die Milz (*S.*) ist lang und schmal und liegt zwischen dem ersten absteigenden und

dem wieder aufsteigenden Theil des Darms. In Hinsicht der sehr zahlreichen Bündel der *appendices pyloricae* und ihres Baues verweise ich auf die Abbildung und Beschreibung, welche ich in der Schrift *de glandularum structura penitiori* p. 64 Tab. VII. Fig. 4. 5. gegeben.

Die Leber bildet drei platte Hauptlappen, wie schon Cuvier angiebt, einen mittlern (*G.*) und zwei seitliche (*F.H.*). Im allgemeinen von dreieckiger Gestalt, sind sie hie und da eingeschnitten, wodurch Nebenlappen entstehen; die Nebenlappen sind indeß bei verschiedenen Individuen durchaus ungleich und ihre Zahl unconstant. Die drei Hauptlappen der Leber hängen durch dünne lappige Streifen von Lebersubstanz zusammen; überdieß verschmilzt der mittlere Lappen mit dem linken an seiner Basis ganz; wie denn auch diese zwei Lappen nur einen gemeinsamen Lebervenenstamm haben.

Die Gallenblase (*I.*) ist ein sehr langer, bei kleineren Thunfischen selbst gegen 1 Fuß langer, enger Kanal, mit unterem blindem Ende. Ihre Länge entspricht der Länge des ersten absteigenden Theiles des Darms, an welchem sie anliegt, und ihr blindes Ende reicht bis nahe zum After. In zweien Fällen war ihr Ausführungsgang, da wo er die Lebergänge aufnimmt, etwas erweitert. Die Einmündung des Gallenganges in den Darm befindet sich an der Stelle, wo der letztere die fünf Stämme der *appendices pyloricae* aufnimmt. Lage und Zusammenhang der Verdauungseingeweide sind in Fig. 1. Taf. III. abgebildet.

III. Strahlenförmiger Bau der Lebervenen. Wundernetze des Pfortadersystems.

Auf der convexen Seite der Leber sieht man die Abgangsstellen der beiden Lebervenenstämme (Taf. I.). Der kleinere gegen 4 Linien breite Stamm führt das Blut aus dem rechten Leberlappen, der zweite stärkere aus dem linken und mittlern Lappen. Die beiden Stämme der Lebervenen durchbohren das Diaphragma und senken sich in den gemeinschaftlichen, auch die rechte und linke gemeinschaftliche Hohlader aufnehmenden Sinus aller Körperven, von wo das Blut in den Vorhof gelangt. Das mit der Leber verbundene Ende der Lebervenenstämme dehnt sich in dem oberen Theile der Leber sinuös aus. Die sinuöse Erweiterung des rechten Lebervenenstammes im Innern des rechten Leberlappens ist gegen 2 Zoll lang; im linken und rechten Leberlappen, wo die Erweiterung gemeinschaftlich, gegen 4 Zoll lang; beide Er-

weiterungen gegen 8 Linien bis 1 Zoll breit. Die inneren Wände dieser Höhlen, welche der Lebersubstanz zugekehrt sind, bestehen aus den Häuten der Venen und zeigen viele beckenartige Vertiefungen, von welchen die strahlenförmigen Zweige der Lebervenen entspringen. Diese gehen an den verschiedenen Stellen theils abwärts, theils auswärts, alle mehr oder weniger strahlig divergirend, ab. Jeder strahlige Lebervenenzweig theilt sich bald wieder in mehrere Zweige, die so wie ihre dichotomischen Zweigelchen wieder in derselben Richtung durchaus gerade gegen den Rand der Leber und die untere Fläche derselben fortgehen. Die stärksten radialen Gefäße haben einen Durchmesser von $\frac{1}{2}$ -1 Linie, die feinsten von $\frac{1}{4}$ und weniger. Die feinsten Röhrchen sind nun mit der flockenartigen Substanz der Leber besetzt, was man an den macerirten Stücken sieht. Wahrscheinlich findet also hier, trotz der strahligen Vertheilung der Lebervenenzweige, doch ein ähnliches Verhältniß wie beim Menschen und den Säugethieren statt, wo nach Kiernan's vortrefflichen Untersuchungen die Lebervenen auch mit den *acini* besetzt sind und durch unzählige kleine Öffnungen die *venulae centrales* der *acini* aufnehmen.

Auf der untern Fläche der Leber sieht man die Wundernetze des Pfortadersystems. Die Wundernetze sind verschiedene 2 Zoll lange und $\frac{1}{2}$ Zoll bis 2 Zoll dicke Quäste von feinen gestreckten, hier und da anastomosirenden Blutgefäßen, die untereinander durch dichtes Zellgewebe vereinigt sind. Jede zum Pfortadersystem gehörende Vene geht abgesondert, ehe sie ihr Blut der Leber zuführt, in ein solches Wundernetz über und meist treten in den Anfang des Wundernetzes mehrere Venen zugleich ein. An der Basis des Wundernetzes sammelt sich das Blut wieder in stärkere Gefäße, welche sich dann in der Leber als Pfortaderzweige verbreiten. Einige der Quäste der Wundernetze haben eine birnförmige Gestalt, die Spitze ist dann von der Leber abgewendet und nimmt die Venen auf; die Basis sitzt auf der Leber auf; diese angewachsene Basis ist schmaler als der Körper. Andere namentlich kleinere Wundernetze sind spindelförmig; doch ist der gegen die Leber gerichtete Theil immer dicker als der Stiel. Eines der größten Wundernetze ist fast so breit als lang und ist platt. Diese Form entsteht dadurch, daß die Zahl der in das Wundernetz tretenden Venen zunimmt und daß diese in einer Reihe nebeneinander eintreten. An einem solchen zusammengesetzten Wundernetz sieht man dann wieder die den einzelnen Venen angehörenden kleineren Büschel; und so wie die kleineren Büschel birnförmig

oder spindelförmig sind, so ist auch das Ganze, wo es auf der Leber aufsitzt, etwas zusammengezogen, der schmalern Basis der Büschel entsprechend. Der im Stiel des Wundernetzes liegende Gefäßstamm zerfällt sogleich in eine Menge von Ästen, diese wieder in kleinere Zweige, so daß nun die Hauptmasse des Wundernetzes viele Hunderte nebeneinander liegende, meist gestreckte Röhrchen von $\frac{1}{4}$ - $\frac{1}{3}$ Linie darstellt, welche hier und da untereinander anastomosiren und alle die Richtung gegen die Leber nehmen. Bläst man die Gefäße im Stiel auf, so schwellen die verschiedenen Theile des Wundernetzes auf, deren Röhrchen von jenen Gefäßen ausgehen. An der Basis hängen die Röhrchen wieder, in größere sich sammelnd, auf das mannigfaltigste zusammen.

Vom Magen gehen drei Gefäße zu den Wundernetzen, eines an der rechten Seite des Magens, eines an der linken, ein drittes auf der hintern Fläche. Ein starker Gefäßstamm tritt von der Milz zu einem besondern Wundernetz und viele Blutgefäße kommen von den *appendices pyloricae* und dem Darm, um sich einzeln in das größte aller Wundernetze einzusenken. Diese bilden eine ganze Reihe über das *pars pylorica* des Darms.

Der rechte Leberlappen hat zwei große Wundernetze, welche von einander getrennt sind. Sie sitzen mit ihren Basen an dem breitem Theil der concaven Fläche des rechten Leberlappens; das eine ist birnförmig, das andere mehr spindelförmig. Das spindelförmige Wundernetz nimmt ein Gefäß von der rechten Seite des Magens auf; in die Mitte und den vordern Theil des Büschels treten noch mehrere kleine Gefäße von dem vordern Theil der untern Fläche des Magens. Das birnförmige Wundernetz nimmt die große Milzvene auf. Am dünnern Theil dieses Wundernetzes treten überdies noch einige kleine Venenstämmchen vom Darm ein.

Der mittlere Leberlappen besitzt ein sehr breites plattes Wundernetz, das keinen einfachen Stiel hat, sondern in viele Zipfel nach der freien Seite hin zerfällt. Es ist 2 Zoll lang und eben so breit, 1 Zoll dick. In die Zipfel treten viele einzelne kleinere Venenstämmchen von der *pars pylorica* des Darms und von den *appendices pyloricae*. Jeder Zipfel erhält ein oder mehrere Stämmchen. In dieses Wundernetz tritt auch noch ein Gefäß vom Magen, welches hinter der Gallenblase und Milz hergeht.

Die Wundernetze des linken Leberlappens sind mehrere Büschel, zwei größere und drei kleinere Büschel. Von den größeren erhält der eine das

Blut von der hintern linken Seite des Magens, die anderen von den *appendices pyloricae*, von letzteren noch mehrere kleinere Venen. An der concaven Seite der Leber liegt noch ein sehr starkes, dickhäutiges Gefäß, welches auch theils in der Leber sich verzweigt, theils mit der Basis der Wundernetze zusammenhängt. Es ist in Taf. II. Y. abgebildet. Dieses Gefäß, dessen Ursprung an dem letzten Präparat nicht ermittelt werden konnte, weil der Stamm beim Herausnehmen der Eingeweide von anderen Gefäßen des Rumpfes abgeschnitten worden, theilt sich in zwei Aste, einen der an der concaven Seite des rechten, den andern, der an der concaven Seite des mittlern Leberlappens und des mit ihm verbundenen linken Leberlappens hergeht. Bläst man diese Gefäßstämme auf, so schwellen die Wundernetze auch an. Da aus den Wundernetzen theils viele Zweige unmittelbar sich in der Leber verbreiten, aber auch die letzterwähnten Gefäßstämme sowohl in der Leber als in den Wundernetzen sich verzweigen, so wurden diese Gefäße noch räthselhafter. Ist jener Stamm Arterie oder Vene? ist er ein Stamm der Pfortader, der sich aus den Wundernetzen wieder bildet und sie untereinander in Communication setzt? aber woher dann das abgeschnittene Hauptgefäß, in welches sich die beiden Äste vereinigen. Nimmt dieß vielleicht, fragte ich mich, Venen des Rumpfes oder der Geschlechtstheile auf, die an den Wundernetzen keinen Antheil nehmen, aber doch ihr Blut in die Pfortader ergießen? Dagegen spricht die Stärke der Wände an diesem Gefäßstamm und seinen Ästen. Dieß so wie die ganz außerordentliche Stärke der dieses Gefäß begleitenden Nerven blieben mir räthselhaft. Um darüber ins Klare zu kommen, mußte ein neuer Thunfisch und die Gefäße *in situ* untersucht werden.

Die vorhergehenden Beobachtungen über die Leber und die Wundernetze des Thunfisches wurden mit dem letzten Abschnitte der Abhandlung und den Tafeln I. und II. der Königl. Akademie der Wissenschaften am 29. Juni 1835 mitgetheilt. Neue Materialien, die sowohl in Copenhagen als hier gewonnen wurden, veranlaßten seither noch weitere Aufschlüsse, als sie unsere gemeinschaftliche Untersuchungen bisher ergeben hatten. Die späteren Ergebnisse, bestehend aus neuen und wichtigen Mittheilungen von Herrn Eschricht und aus den Resultaten der Untersuchung eines zweiten hier angelangten Thunfisches sind in den zwei nächsten Abschnitten enthalten. Die gemeinsame Angelegenheit war uns, nachdem ich meinem Freunde im Herbste 1835 in Copenhagen persönlich über die Wundernetze der Pfortader

berichtet hatte, immer wichtiger geworden. Eine reiche Quelle eröffnete sich plötzlich in Copenhagen. Bald nach meiner Abreise von Copenhagen kam dort ein frischer im Sunde gefangener sehr großer Thunfisch an. Herr Eschricht hat daran nicht bloß die Wundernetze der Venen des chylopoetischen Systems bestätigt, sondern eine neue und wichtige Entdeckung gemacht, daß ein Theil der Röhren der Wundernetze arteriös ist und daß die Arterie des chylopoetischen Systems, eben jenes mir noch räthselhafte Gefäß, wovon vorher die Rede war, sich einestheils in die Leber verzweigt, andernteils an der Basis der Wundernetze sich in unzählige Röhren auflöst, die einen Theil der Röhren der Wundernetze ausmachen und sich an den freien Enden der Wundernetze wieder in einzelne Gefäße sammeln, um zu den Eingeweiden hinzugehen. Besondere Röhren der Wundernetze nehmen daher das Blut aus den Darmvenen, Magenvenen, pancreatischen Venen und aus der Milzvene auf, um es zur Leber zu bringen und besondere Röhren, die zwischen den anderen liegen, nehmen das Arterienblut auf, um es zu den Eingeweiden, zur Milz, zum *pancreas*, Magen, Darm zu bringen, während die arteriösen Gefäße der Leber nicht erst durch die Wundernetze durchgehen. Die Wundernetze haben daher die doppelte Beziehung, zur Leber einestheils durch die Pfortader, zu allen übrigen Eingeweiden des chylopoetischen Systems durch die Arterien. Obgleich sie an der Leber liegen und an ihr angewachsen sind, haben sie doch eine gleich große Beziehung zu allen übrigen Organen des *systema chylopoeticum*.

Das Resultat der Untersuchungen von Hrn. Eschricht an dem letztgenannten Thunfische theile ich nun wörtlich mit.

IV. Wundernetze der Arterien des chylopoetischen Systems. Verhalten derselben zu den Wundernetzen der Pfortader und zu den Lebervenen.

(Beitrag zur Anatomie der Thunfischleber von Herrn ESCHRICHT.)

Der Thunfisch, dessen Leber zu folgender Untersuchung benutzt wurde, kam am 29. September 1835 in Copenhagen an. Er war (angeblich am 27.) bei Helsingör in einem großen Fischernetz gefangen worden, das er größtentheils zerrissen hatte. Sein Gewicht wurde auf 400 Pfund geschätzt,

seine Länge betrug von der Schnautze zum Schwanzende 8' 10", zum Rande des *Operculum* 2' 2½", sein Umfang, wo er am größten war, 4' 2½". Er war männlichen Geschlechts (wie sich später ergab).

Es wurde die Bauchhöhle weit aufgeschnitten bis ans *Pericardium*, und, da die Lebermasse sehr weich war, so daß sie bei dem Anfassen leicht rifs, näherte man sich mit vieler Vorsicht den Hauptästen ihrer Gefäße, denen am leichtesten anzukommen war, und Herr Ibsen injicirte die zwei großen Lebervenenstämme, die dicht am *Pericardium* eingeschnitten wurden, mit grüner Masse; einige Arterienstämme, die an der rechten Seite der Leber neben mehreren Pfortaderzweigen verliefen, mit rother, und mehrere Pfortaderzweige mit gelber Masse. Auch wurden die Gallengänge von dem *Ductus cysticus* aus mit weißer Masse injicirt, allein mit wenigem Erfolg. Die Injectionsmassen waren sämmtlich aus gefärbtem Leim bestehend. Es dauerte diese Arbeit an dem colossalen Thiere von 1 Uhr Mittag bis in den Abend hinein, und da unterdessen die Leber noch viel mürber geworden war, wurde sie herausgenommen und in starkem Weingeist aufbewahrt. Einige Tage später versuchte Herr Ibsen wieder noch mehrere Zweige zu injiciren, was jedoch nur einen unvollkommenen Erfolg hatte. Die Leber lag darauf mehrere Wochen im Weingeist und wurde erst untersucht, nachdem die Haut längst zum Ausstopfen benutzt, das Fleisch aber in sehr vielen Portionen als essbar vertheilt war. Die Breite der Leber betrug 2' 3½", von vorn nach hinten 11".

Die Thunfischleber ist sowohl an dem vordern convexen, als an dem hintern etwas concaven Rande mehrfach eingeschnitten und dadurch stark gelappt. Man kann auf jenem Rande 6, auf diesem 4 solcher Lappen unterscheiden, die in verschiedenem Grade getrennt sind, und selbst wiederum mehrere weniger tiefe Einschnitte haben, oder mit kleineren Anhängen versehen sind.

Die obere Leberfläche ist im Ganzen genommen convex; die untere etwas concav. Auf dieser unteren Fläche zeichnen sich einige kegelförmige Massen von den eigentlichen Lappen sogleich aus. Es sind deren 8. Die 6 größten stehen paarweise und können als rechtes, mittleres und linkes Paar unterschieden werden. Jedes dieser Paare besteht aus einem vordern und einem hintern Kegel, die an ihrer Basis mehr oder weniger verbunden

sind. Außerdem aber finden sich zwischen dem linken und dem mittlern Paare 2 nicht gepaarte kleinere Kegel.

Wo die Kegel mit ihrer Basis auf der unteren Leberfläche ansitzen, kann man mit einem Spatel zum Theil zwischen ihnen und der eigentlichen Leber eindringen, wenn man bloß etwas Zellengewebe entfernt. Sie sitzen also nicht mit ihrer ganzen Basis, als sich hiemit in die Lebersubstanz verlängernd, an; der Umkreis derselben ist nur *contiguus* damit, nicht *continuus*.

An der Anheftungsstelle der Kegel ist die Leber selbst ungemein dünn, an meinem colossalen Exemplare höchstens 3''' dick, Diese dünneren Stellen der Leber lassen sich auf der obern Leberfläche nicht unterscheiden, auf der untern Fläche aber erscheinen sie als Vertiefungen, die sämtliche Kegel umfassen, und mit einander mittelst schmalerer Gänge zusammenfließen. Sie bilden die Leberpforte.

In der Leberpforte finden sich 1) die Gallengänge, 2) einige Nervenstämme und 3) eine große Arterie, die wir wegen ihrer fast knorpligen Wände die dickhäutige nennen werden. Die Pfortader tritt hingegen in die Spitzen der Kegel hinein, und die Leberblutadern aus der convexen Leberfläche heraus, ohnweit des hintern Leberrandes. An den Spitzen der Kegel befinden sich aber außer den eintretenden Venen noch mehrere Arterienstämme mit ungleich dünneren Häuten als jene in der Pforte; und an dem rechten vordern Kegel (der besonders gut injicirt und deshalb auch besonders genau untersucht wurde), ein Nervenstamm von der Dicke eines Federkiels. Ein ähnlicher noch dickerer Nervenstamm war an der Basis desselben Kegels, oder an dem damit paarigen Kegel zu sehen.

Unter den Gallengängen ist der *Ductus choledochus* ziemlich eng, noch mehr aber sein einer Zweig, der *D. cysticus*, obgleich dieser in eine enorme (trocken 2' 9" lange) Gallenblase übergang, die längs der Mittellinie des ganzen Unterleibes lag, so daß sie beim Aufschneiden des Unterleibes mit Noth entging beschädigt zu werden. Der *D. hepaticus* wechselte in seiner Weite mehrmals und sehr bedeutend ab, und verlief quer über die untere Leberfläche, sich in der Pforte für die verschiedenen Leberlappen verästelnd. Auffallend war der Verlauf seines einen Zweiges zwischen den beiden mittleren Kegeln, woselbst er von der diese verbindenden Mittelsubstanz brückenartig bedeckt wurde.

In der Leber scheinen die Lebergänge hauptsächlich dem *Tractus* der Arterienzweige zu folgen; doch sind sie in der Tiefe, wegen ihrer dünnen Wandungen, sehr schwer zu verfolgen, und ihre Injection war nur sehr unvollkommen gelungen.

Die Pfortader wird aus sehr vielen kleineren Zweigen gebildet, die in die Kegelspitzen hineintreten. Diese Zweige kommen hauptsächlich von den Verdauungswerkzeugen, vielleicht auch, wie sich vermuthen läßt, von anderen Theilen der hintern Körperhälfte (¹). Die drei vorderen der gepaarten Kegel scheinen vorzugsweise Eingeweideblutadern, die hinteren sowohl Venen der Eingeweide als der umliegenden Theile aufzunehmen. Der Eintritt des letztern Blutes, also in die hinteren Kegel, geschieht durch viele Stämme, z. B. 14-16 für die hinteren mittleren Kegel; jeder dieser Stämme wandelt sich aber alsbald in eine platte Masse um, dem Anschein nach einen Theil der Lebermasse.

Schon vor der Injection hatte die Oberfläche der Leber zum allergrößten Theil, nämlich überall an den Kegeln und an der convexen Oberfläche, ein gestreiftes Aussehen, wie es mir schon vor langer Zeit an einer in Spiritus lange aufbewahrten Thunfischleber aufgefallen war, und wodurch im Grunde diese Untersuchungen zuerst veranlaßt wurden. Nach der Injection wurde dieses auf einmal ganz klar. Die Arterien waren roth, die Pfortader gelb, die Blutadern grün, die Gallengänge (sehr unvollkommen) weiß angefüllt.

Nach der Injection hatten die verschiedenen Leberparthieen ein auffallend buntes Aussehen, indem es fast überall gestreift mit abwechselnden Farben erschien. Die Kegel wurden durchaus roth und gelb gestreift, ohne Spur der grünen Masse oder sonst irgend einer zwischenliegenden Substanz. Die convexe Oberfläche der Leber zeigte sich fächerförmig gestreift; die Streifen hauptsächlich grüner Farbe mit weniger rothen, noch viel weniger gelben und einzelnen weißen Streifen. Die untere Leberfläche war der Pforte zunächst ebenfalls mittelst derselben Farben gestreift; mehr nach dem vorderen Rande hin aber ohne Streifen, graubräunlich gefärbt mit isolirten dunkleren rundlichen Flecken von etwa 1''' Durchmesser.

(¹) Diese Vermuthung, die ich theilte, hat sich an dem letzten Thunfisch nicht bestätigt.

Nachdem mehrere Einschnitte in die Substanz gemacht und viele Versuche angestellt worden, die einzelnen Stämme dorthinein zu verfolgen, ergab sich Folgendes.

Bau der Kegel. Sie sind wahrhafte *Corpora spongiosa*, indem sie nur aus Gefäßgeflechten der Pfortader und der Pulsadern bestehen. Diese Geflechte von beiderlei Blutgefäßen sind aber von einander durchaus getrennt, so daß die Injectionsmasse nirgends aus jenem in dieses System gedrungen war. Die Gefäßgeflechte bilden ferner keine Zellen, sondern nur sehr viele lange, ohngefähr gleich breite Röhren (etwa $\frac{1}{3}$ ''' breit) [alle Messungen nur nach dem Augenmaafs genommen], die ziemlich gerade und mit der Axe der Kegel parallel durch deren ganze Länge verlaufen. Dies sieht man sowohl an der Oberfläche der Kegel, als auch bei Einschnitten in dieselbe. Bei Querdurchschnitten nehmen die Schnittflächen sich siebförmig aus durch die Menge ohngefähr gleich starker Löcher der durchgeschnittenen Röhren. An mehreren Stellen weichen jedoch die Röhren von diesem gradlinigen Verlaufe ab. So namentlich um den oben erwähnten großen Nervenstamm herum, welcher sich nur wenig in dem Kegel selbst verzweigend, auch ohngefähr mit der Kegelaxe durch die röhrlige Substanz verläuft, und daselbst von einer zelligen Scheide eingeschlossen ist, ohngefähr wie die *Commisura anterior* im Gehirn. Um diese Scheide herum liegen die Gefäßröhren nicht grade, sondern bilden eine Art Geflecht um sie herum. An der Basis der Kegel weichen die Röhren ganz und gar von ihrer Richtung ab, indem sie sich in die Quere legen, sich erst nach dem Centrum der Kegelbasis wendend, dann aber sich umbiegend und auswärts strahlend, um alsbald als wahre Gefäßstämme zu erscheinen.

Die Gefäßröhren der Kegel stehen also sowohl an deren Spitze als an deren Grundfläche mit Gefäßstämmen in Verbindung, und dies gilt sowohl von den zum Arteriensysteme als von den zum Pfortadersysteme gehörigen Röhren. Die Gefäßröhren sind analog den Wundernetzen überhaupt, zumal aber denen an den Pulsadern der Extremitäten der trägen Säugethiere. Die Thunfische wären Leberfaulthiere zu nennen, wenn nicht im Grunde diese Kegel gar nicht wesentlich zur eigentlichen Leber gehörten, sondern nur als Divertikel anzusehen wären des Kreislaufs der hinteren Körperhälfte überhaupt, zumal aber al-

lerdings des Kreislaufs in den Verdauungseingeweiden, wie sich sogleich ergeben wird.

Es entsteht nämlich jetzt die Frage, ob die Blutbahn in jedem Kegel von der Spitze nach der Basis, oder von dieser nach der Spitze hingeht, eine Frage, deren Lösung bei der Untersuchung der Theile im Zusammenhange sich sogleich ergeben muß, jedoch auch durch die Untersuchung der isolirten Leber sich entscheiden läßt.

Die Gefäßstämme, mit denen die Kegelröhren an den Grundflächen in Verbindung stehen, liegen in der Pforte, und von hier aus verzweigen sich die Pfortaderstämme in die Leberlappen hinein und nur in diese; also offenbar eine spätere oder zweite Verästelung. Für die Pfortaderblutröhren wäre also die Frage leicht beantwortet; das Blut tritt aus den Verdauungseingeweiden in die Spitzen der Kegel, um darin in mannigfaltige Röhren zu zerfallen, und wiederum in der Pforte zusammenzutreten und sich dann erst auf die gewöhnliche Weise für die Leberlappen zu vertheilen.

Daß die Blutbahn für die Arterien hiermit übereinstimmend sei, ließe sich vielleicht daraus vermuthen, daß auch sonst das Arterienblut mit dem Pfortaderblute einen Weg nimmt, es ist hier aber offenbar umgekehrt. Erstlich kommen die Pfortaderzweige von den Unterleibseingeweiden her, das Arterienblut kann nicht daher kommen, sondern muß dorthin gehen. Zweitens sind die Arterienstämme in den Kegelspitzen ziemlich dünnwandig, die in der Pforte hingegen sind sehr dickhäutig, so daß das Durchschneiden der sogenannten dünnen Leberstellen etwas Knorpeliges spüren läßt. Sie sind Äste der dickhäutigen Arterie in der Leberpforte, und sie verzweigen sich wiederum, die secundären oder wahren Pfortaderäste begleitend, in die Leberlappen hinein. Für diese Ansicht spricht außerdem auch noch der Umstand, daß jener große Nervenstamm (*Vagus*) des rechten vordern Kegels auch nur ein durchgehender ist und zwar so, daß er an der Basis hinein, an der Spitze austritt, in dem Kegel nur wenige Äste von sich schickend, alle mehr nach der Spitze hingerichtet, den letzten an der Spitze ausgenommen, der allerdings in die Kegelspitze hinein zurückläuft.

Die Blutbahn des arteriellen Blutes ist demnach folgende. Die dickhäutige Arterie ist der gemeinsame Stamm der Leberarterien und der Arterien für die Verdauungseingeweide. In der Pforte verzweigt sie sich eines-

theils als wahre Leberarterie in die Leberlappen hinein, mit ihren Zweigen denen der Pfortader folgend, anderntheils aber zerfällt sie in unzählige dünne Röhren, die in ziemlich stumpfen Winkeln von ihren Hauptzweigen entspringen und darauf (mit den ähnlichen Wundernetzröhren der Pfortaderstämme) die schwammigen Kegel bilden, um sich wieder, aber in sehr spitzen Winkeln, in Äste zu sammeln (an den Spitzen der Kegel) und ihrer Bestimmung gemäß an die Verdauungseingeweide zu treten.

Wir gehen jetzt zur Beschreibung der eigentlichen Leberlappen. Es ist bereits angeführt worden, daß die Lebervenen von der convexen Leberfläche dicht an ihrem hintern Rande entspringen; daß dieselbe Fläche durch die Injection sehr dicht mit grünen (Farbe der Leberblutadern) Streifen bedeckt wurde, die fächerförmig über die ganze Fläche nach dem vordern Rande ausstrahlen, und daß hiermit seltene Zweige der Pfortader, der Leberarterien und einzelne der Gallengänge parallel verlaufen. Ferner wurde bemerkt, daß zwar auch an der untern Fläche, wenigstens an ihrem zunächst der Pforte liegenden Theile, eine ähnliche fächerförmige Ausbreitung Statt hatte, sonst aber hier die Leberoberfläche mehr gleichförmig graubräunlich erschien mit isolirten dunkleren Flecken.

Die Streifen, die sich an der Oberfläche der Leberlappen zeigen, rühren allerdings auch von ziemlich gleichdicken, gerade gestreckten, also röhrenförmigen Gefäßzweigen her, und namentlich von allen drei Gefäßklassen (besonders aber den Leberblutadern), so viel ich weiß, auch von den Gallengängen. Doch haben diese Röhren eine ganz andere Bedeutung als die der Kegel. Es sind keine Wundernetze. Ihre lineare Form rührt nur daher, daß überhaupt die Leber sehr regelmäfsig von der Pforte aus in Unterabtheilungen zerfällt, ohngefähr in folgender Form:

Zunächst der Pforte ist die ganze Lebersubstanz allerdings röhrenförmig. Von hier aus verästeln sämmtliche Zweige sich auch nur schwach, verbreiten sich aber erst nach dem vorderen Rande hin, dann gebogen mehr der unteren Fläche zu. Auf diesem Wege tritt aber mehr und mehr eine körnige Substanz zwischen die Gefäßröhren, und zunächst an der untern Fläche und dem vordern Rande zu macht diese Substanz einen grofsen Theil des Ganzen aus. Zerreißt man die Lebersubstanz, zumal an etwas macerirten Stücken, so bricht sie immer parallel mit der angegebenen Richtung, erscheint aber nicht zellig, wie jene Kegel, sondern körnig, durch

die den Gefäßen anhängende Substanz. Die Gefäße erscheinen hiedurch wieder oft wie mit blinden Anhängen versehen, doch fand ich nirgends die Injectionsmasse von einem Aste aus in sie hineingetreten.

Wenn die Natur dieser körnigen Masse genügend erläutert werden könnte, so würden wir beim Thunfisch wohl die erste Leber haben, deren Bau hinlänglich ergründet wäre. So bleibt uns aber gewöhnlich eine — oft nur eine kleine — allein leider eine wichtige Brücke übrig, wo wir nicht hinüberkommen können.

Gehen wir also auf einem Umwege jenseits dieser Brücke, und folgen dem zurückkehrenden Lebervenenblut, so sammelt sich dies in zwei große Becken, die auf der convexen Fläche der Leber transversal liegen, ohnweit des hintern Randes verlaufen, und von dort aus ergießt es sich in zwei sehr große Stämme, die alsbald in den venösen Sinus sich ergießen.

So weit reichen die besonderen Mittheilungen von Herrn Eschricht.

V. Verhalten der übrigen Eingeweide und Gefäße.

Das Wesentliche der ganzen Untersuchung war nun ermittelt. Was noch aufzuklären übrig blieb, war das Verhältniß der Venen der Geschlechtstheile und Harnwerkzeuge zu den übrigen Venen. Frühe genug, um auch dieses vor dem Abschluß unserer Arbeit aufzuhellen, langte in Berlin noch gegen Mitte April ein schon im Herbste 1835 von Montpellier abgegangener Thunfisch (*Thynnus vulgaris*) von 3 Fufs Länge an, dessen Besorgung wir abermals der Gefälligkeit des Herrn Lichtenstein in Montpellier verdanken. Zugleich war Herr Eschricht so gütig, mit dem vorher mitgetheilten Bericht die injicirte Leber des für Copenhagen acquirirten Thunfisches hieher zur Vergleichung zu senden, nachdem derselbe schon lange vorher die Resultate seiner Untersuchung brieflich mitgetheilt hatte. Zur Vervollständigung der letztern habe ich nach Untersuchung der injicirten Leber nichts zuzusetzen.

Eine Beobachtung, die ich zuletzt noch hier an dem zweiten Thunfisch von Montpellier gemacht habe, betrifft eine merkwürdige Eigenthümlichkeit im Bau der Nieren. Die Eingeweide dieses Thieres wurden *in situ* präparirt, nachdem die Seitenwände des Rumpfes abgeschnitten worden, und hiernach wurde die Zeichnung Tab. III. Fig. 6. entworfen.

Physikal. Abhandl. 1835.

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Die Nieren des Thunfisches liegen nicht wie bei den meisten Fischen in der Länge der obern Bauchwand, sondern blofs über dem vordern Theile der Bauchhöhle, und zwar die Hauptmassen, innerhalb des Schultergürtels zu beiden Seiten des Anfangs der Aorta, wo sie aus der Vereinigung der Kiemenvenen entsteht, über dem Schlund und über und hinter den Kiemen. Siehe Tab. III. Fig. 5. Ihr vorderes Ende reicht bis an die vorderen Kiemenvenen und fast bis in die Nähe des Hinterhaupts; die beiden hinteren Kiemenvenen jeder Seite sind schon von den Nieren von oben bedeckt. Von dem Anfang der Aorta bis zu der Stelle, wo rechts und links die grofsen Arterien für die seitlichen Rumpfwände abgehen, sind die Nieren getheilt und zwischen ihnen liegt der stärkste Theil der Aorta. Von dieser Stelle an verschmelzen die Nieren, vor der Fortsetzung der Aorta als *arteria caudalis*, mit einander zu einer Masse und von dem verschmolzenen Theil der beiden Hauptmassen setzt sich die untere Hälfte der Nieren unpaarig und schmal an der Mitte der obern Bauchwand noch eine Strecke fort, ohne jedoch die Hälfte der Länge der Bauchhöhle zu erreichen. Der vordere paarige Theil der Nieren ist sehr dick und breit, liegt mit der äufsern und obern Fläche dicht an dem äufsern und obern Theil der inneren Rumpfwandungen und des Schultergürtels an; der schmalere hintere Theil ist hingegen sehr dünne. Die Niere besteht deutlich aus kleinen platten Lappen, wie man besonders an dem obern Theil und an dem hintern schmalen Theil derselben sieht. Dicht vor dem hintern Ende theilt sich die unpaarig gewordene Niere wieder in zwei kurze Endlappen, aus denen jederseits ein Ast des Ureters hervorgeht. Beide Äste vereinigen sich sogleich unter spitzem Winkel zu einem unpaaren Kanal, welcher als eine dickhäutige Röhre in der Mittellinie der hintern Bauchwand herab läuft. Nur der Anfang des Ureters der Thunfische ist also doppelt; der durch den gröfsten Theil der Bauchhöhle herabgehende Stamm ist unpaarig, eine Bildung, die uns noch von keinem Fische bekannt ist. Nach Eröffnung der Bauchhöhle werden weder die Nieren noch der Ureter sogleich sichtbar. Sie sind durch eine fibröse Haut von der Bauchhöhle geschieden, die man erst wegnehmen mufs, um sie zu sehen. Wo diese Haut vor dem unpaarigen Ureter herabgeht, ist sie sehr stark und fest. Mit der untern Wand des hintersten Endes des Ureters ist der Körper der 1 Zoll langen, festen Urinblase verbunden. Die Harnröhre geht hinter dem Mastdarm in den für die Geschlechtstheile und Harnwerkzeuge

bestimmten Ausgang über, dessen Mündung, wie gewöhnlich bei den Fischen, hinter dem After liegt.

Der Anfang der Aorta entsteht aus den zwei ersten Paaren der Kiemenvenen. Die beiden ersten Kiemenvenen verbinden sich jederseits zuerst zu einem gemeinschaftlichen Stamm, beide gemeinschaftliche Stämme, *venae branchiales communes*, gehen unter spitzem Winkel, rückwärts gerichtet, zusammen. Hierdurch entsteht der unpaare Anfang der Aorta zwischen den vorderen Enden des paarigen Theiles der Nieren. Der Anfang der Aorta nimmt dann noch die zwei hinteren Kiemenvenen jeder Seite auf. Vom Anfang der Aorta bis zum Abgang der Arterien der seitlichen Rumpfwände, *arteriae axillares* (?), ist die Aorta sehr dick. Von diesem Theil der Aorta gehen mehrere Nierenarterien seitlich und die einzige große Arterie des chylopoetischen Systems nach unten und hinten ab. Die *arteriae axillares* selbst durchbohren mit den *venae axillares* die hinteren Theile der seitlichen Hauptmassen der Nieren, um zu den Muskeln der Bauchwände zu gelangen, schief. Während des Durchganges geben die *arteriae axillares* auch noch Zweige für die Nieren ab. Nach dem Abgang der *arteriae axillares* wird die Aorta plötzlich mehr als um die Hälfte dünner im Durchmesser. Dieser Theil der Aorta läuft nur eine kurze Strecke noch über dem hintern unpaaren Theil der Nieren, der hier noch Zweige erhält, weiter und tritt dann in den Kanal der unteren Dornfortsätze, bis er als *arteria caudalis* endigt. Der Kanal der unteren Dornfortsätze beginnt beim Thunfisch schon über dem vordern Theil der Bauchhöhle am neunten Wirbel, indem die hinteren Rippen an den unteren Dornen hängen; erst am neunzehnten Wirbel beginnt der Schwanz. In dieser ganzen Länge liegt also die Aorta schon in dem Kanal der unteren Dornfortsätze.

Die *arteria systematis chylopoetici* geht mit den starken Nerven der Verdauungsorgane zwischen Schlund und Niere abwärts, kommt rechts vom Schlunde zur concaven Fläche der Leber und theilt, Zweigelchen an das Diaphragma und die Umgegend gebend, sich hier in zwei Äste, wovon der eine an der concaven Fläche des rechten Leberlappens, der andere an derselben Fläche des mittlern und linken Leberlappens hergeht. Da wo sie an der Basis der Wundernetze ihrer Lappen hergehen, geben sie viele Zweige in die concave Fläche der Leber, *arteriae hepaticae*, der ganze übrige Theil dieser zwei Arterienäste vertheilt sich ganz in die Basis der Wundernetze und bildet den

arteriösen Theil derselben. Aus den Wundernetzen sammeln sich die arteriösen Zweige wieder in die früher beschriebenen Stämme von viel dünneren Wänden als vor dem Eintritt der Arterien in die Wundernetze. Die aus den Wundernetzen entstehenden arteriösen Stämme verzweigen sich überall in Begleitung der Venen am Magen, Darm, an der Milz und an den *appendices pyloricae*. Alle Arterien des ganzen chylopoetischen Systems mit Einschluss der Leber kommen aus jener einzigen Arterie, und alle Zweige derselben, die für den Magen, Darm, die Milz, das Pancreas bestimmt waren, lösen sich erst in die Wundernetze auf. Die Arterien der Geschlechtstheile konnte ich ohne Injection nicht finden.

Der Sinus aller Körpervenen, der mit dem Vorhof zusammenhängt, hat links einen zipfelförmigen Anhang. Der Sinus nimmt von unten die beiden Lebervenenstämme, nachdem sie das Diaphragma durchbohrt haben, auf; von unten und vorn empfängt er eine Vene von der untern Wand der Kehlgegend, *vena jugularis inferior*, links und rechts nimmt er die *venae cavae communes* auf, wovon jede aus einem vordern und hintern Ast entsteht, der vordere Ast liegt an der untern Seite des obern paarigen Theils der Nieren zwischen diesem und dem Herzbeutel, *vena jugularis* der hintere durchbohrt den untern Theil der paarigen Hauptmasse der Niere auf jeder Seite, nimmt Nierenvenen auf diesem Wege, dann auch die Venen des Hodens auf und endigt als hintere Hauptvene der muskulösen Seitenwände *vena axillaris* oder *vena lateralis posterior*. Da wo die Fortsetzung der Aorta in den Kanal der unteren Dornfortsätze kommt, tritt kein Venenstamm aus diesem Kanal heraus. Man sieht, dass die Anordnung der Hauptvenenstämme von derjenigen bei anderen Fischen etwas verschieden ist.

VI. Wundernetze bei anderen Fischen.

Die Wundernetze des Thunfisches sind nicht die einzigen Erscheinungen dieser Art in der Klasse der Fische. Für's erste scheint diese Bildung bei den Arten der Gattung *Thynnus* allgemein zu sein. Wir haben Gelegenheit gehabt außer *Thynnus vulgaris* auch *Thynnus brachypterus* zu untersuchen. Herr Dr. Grube hatte die Gefälligkeit, aus Cette das Bauchstück eines Thunfisches hieher zu senden, woran ich den *Thynnus brachypterus* Cuv. erkennen konnte, weil gerade dieser Thunfisch eine kleine silberglänzende Schwimmblase hat, wie Cuvier angiebt. Die Wundernetze verhalten

sich ganz wie bei *Thynnus vulgaris*, auch die Nieren liegen an derselben Stelle und der Ureter ist unpaarig wie dort. Die Wundernetze nehmen auch hier von denselben Theilen das Blut auf, nur gelangt hier das Blut der kleinen Schwimmblase auch in die Pfortader und zwar in das hintere der Wundernetze der rechten Seite; diese kleine Vene nimmt das Blut von der Oberfläche der Schwimmblase und der hintern Fläche des Peritoneums, wo es auf der Schwimmblase liegt, auf; noch andere Venen als die des chylopoetischen Systems gehen auch hier nicht in die Wundernetze ein. *Pelamis* und *Thyrsites* habe ich noch nicht untersuchen können. Bei *Scomber scombrus* habe ich keine Wundernetze gefunden. Aber schon habe ich Gelegenheit gehabt, eine ähnliche Bildung bei einem Knorpelfische aus der Ordnung der Plagiostomen, bei *Squalus (Lamna) cornubicus* zu beobachten. Vor Kurzem erhielt das Königliche anatomische Museum ein sehr großes Exemplar von *Squalus cornubicus*, das bei Copenhagen gefangen war, in Salz. Herr Eschricht hat diesen großen weiblichen Hai als Tauschgegenstand für uns acquirirt und frisch abgesandt. Obgleich die Tonne lange Zeit unterwegs gewesen, so hatten sich doch die Eingeweide in so weit erhalten, daß sie untersucht werden konnten. Beim Herausnehmen derselben wurde ich auf zwei aus lauter Blutgefäßen zusammengesetzte Massen aufmerksam, welche im obersten Theile der Bauchhöhle zu jeder Seite des Schlundes, zum Theil noch über der Leber lagen. Sie hatten eine pyramidale plattgedrückte Form; so daß die Basis der Pyramiden nach hinten gerichtet war. Sowohl ihre Form als ihr Bau stimmten ganz mit den Wundernetzen des Thunfisches überein. Sie bestanden nämlich aus lauter der Länge nach verlaufenden anastomosirenden Blutgefäßen, welche vom obern und untern Theil der Massen vollständig aufgeblasen werden konnten. Am obern und untern Theil der Gefäßkörper bildeten die Gefäße weitläufige Communicationen und gingen in Stämme über. Ich konnte auch arteriöse und venöse Gefäße an diesen Körpern unterscheiden. Die abgeschnittenen Gefäße gingen vom obern Theil der Massen büschelförmig aus. Hier traten sie auf jeder Seite des Schlundes in das Innere der Wundernetze. Woher die Stämme kamen, ließ sich an den ausgeschnittenen Eingeweiden nicht mehr unterscheiden. Der arteriöse Theil der Wundernetze schien überall von venösen Geflechten durchflochten. An der Basis der Wundernetze sammelten sich viele (arteriöse?) Gefäße wieder in Stämme, welche sich an den Eingeweiden des

chylopoetischen Systems aber auch in der Leber selbst verbreiteten. In letzterm Punkt schien die Bildung mit den Wundernetzen des Thunfisches nicht überein zu kommen. Der venöse Theil der Wundernetze verhielt sich aber entschieden anders. Er wurde nicht von der Pfortader gebildet, denn diese trat ganz und unmittelbar zur Pforte, um sich in den beiden gar langen platten Leberlappen zu verbreiten. Die Lebervenenstämme hingegen, statt sogleich zum Sinus der Körpervenen zu gelangen, verliefen an der Basis der Wundernetze her und gaben eine große Menge von Büscheln in die Wundernetze ab; während am obern Theil der Wundernetze diese Gefäße sich wieder in große Becken sammelten. Diese letzteren Becken waren indeß beim Ablösen der Eingeweide von der obern Bauchwand gerade durchgeschnitten. Wie sich die Gefäße weiter verhalten, ließ sich nicht mehr ermitteln. Überhaupt konnte bei dem verdorbenen Zustande der Eingeweide nur das Allgemeinste erkannt werden; und wird es von weiteren Untersuchungen abhängen, wie weit diese vorläufige Mittheilung erweitert und ergänzt werden kann. Die Nieren des *Squalus cornubicus* liegen nicht wie beim Thunfisch im vordersten Theil der Bauchhöhle, sondern in der hintern Gegend derselben, wie gewöhnlich bei Haifischen. Auffallend war das Zerfallen der Milz in eine große Menge von Läppchen und die außerordentliche Dicke des *Ductus choledochus*, die von seinen ungemein starken Wänden abhängt. Dieser ganz von einem muskulösen Gewebe mit deutlichen Längsfasern umgeben, senkt sich in den Anfang des mit der Spiralklappe versehenen Theils des Darms. Nach dem Herausnehmen der Augen fand sich beim Skeletiren auf dem Grunde der Augenhöhle auch ein Gewebe von gewundenen Röhren, dessen Zusammenhang nicht mehr erkannt werden konnte. Ich habe mehrere Haie aus den Gattungen *Scyllium*, *Galeus*, *Squatina*, *Mustelus*, *Spinax*, *Centrina*, *Zygaena* (*Tiburo*) auf die Wundernetze der Bauchhöhle untersucht, aber bei keinem eine analoge Bildung vorgefunden. Die einzelnen Gattungen der Familie der Haifische haben so viele anatomische Eigenthümlichkeiten, daß uns diese Verschiedenheit nicht sehr wundern darf. Auch die Rochen der Gattungen *Myliobates*, *Raja*, *Trygon*, *Torpedo*, *Rhinobatus*, die ich untersuchte, zeigten keine analoge Bildung. Die Leber des *Squalus cornubicus* besitzt nicht den ausgezeichnet strahligen Bau der Lebervenen, wie die Leber des Thunfisches, obgleich die Gefäße zum Theil divergirend lange Strecken hingehen.

VII. Bedeutung der Wundernetze.

Dafs die verschiedenen Venen, welche die Pfortader zusammensetzen, einzeln zur Leber treten, kommt bei den Fischen öfter vor. Rathke hat davon mehrere Beispiele beobachtet. Aber die ungeheuren Wundernetze bei diesem Übergang sind eine noch nicht beobachtete Bildung. Eben so wenig hat man bisher einen Fall bemerkt, der einigermaßen eine Parallele zu den Wundernetzen der Arterien des chylopoetischen Systems bildete. Dafs die Arterien des Darmkanals bei allen Thieren anastomotische Bogen erster, zweiter, dritter Ordnung bilden, kann hier nicht angeführt werden. Denn zum Wesen eines Wundernetzes gehört, dafs die Stämme wieder einfach oder in geringer Zahl aus der netzförmigen Auflösung hervorgehen. Eine geflechtartige Vertheilung einer Arterie, ohne Entwicklung eines neuen Stammes, mag wohl mit dem wahren Wundernetze einige Verwandtschaft haben, indess steht sie doch dem gewöhnlichen anastomotischen Verhalten der kleineren Arterien näher, welche überall, lange vor dem Übergang in die Capillarnetze, Netzwerke bilden. Die Auflösung eines Arterienstammes in ein Netz, das nicht zur bequemern Vertheilung des Blutes bestimmt ist, sondern das Blut in einen neuen Stamm sammelt, zeigt hingegen einen geheimen besondern Zweck der Natur in der Anordnung dieser Apparate an. Vergleicht man die Wundernetze der Eingeweide der Thunfische mit ähnlichen Bildungen anderer Thiere, so erkennt man, dafs sie zu den wenigen wahren Wundernetzen gehören, und dafs sie die zusammengesetztesten aller bis jetzt bekannt gewordenen Bildungen dieser Art sind. Ohne Zweifel müssen sich die Erklärungen des Zwecks der Wundernetze an ihnen prüfen lassen.

Die Wundernetze an den Extremitäten der Stenops und Tarsius, der Faulthiere, der Ameisenfresser und am Schwanz der letztern, an der *carotis cerebialis* der Wiederkäuer, an der *arteria ophthalmica* einiger Säugethiere und Vögel, am Penis der Vögel, an den *venae iliacae* und Intercostalarterien der Delphine, an der sogenannten Carotisdrüse der Frösche sind bekannt ⁽¹⁾.

⁽¹⁾ Wir verweisen in dieser Hinsicht auf die Schriften von Carlisle, Vrolik, Rapp, Huschke, Barkow, v. Baer, Breschet.

Carlisle *Philos. Transact.* 1800. *Account of a peculiarity in the distribution of the arteries sent to the limbs of slowmowing animals. Continuation Philos. Transact.* 1804.

Vrolik *disquisitio anatomico-physiologica de peculiari arteriarum extremitatum in nonnullis animalibus dispositione. Amstelod.* 1826.

Die Erklärungen, welche sich für diese Bildungen anführen lassen, legen ihnen zum Theil einen mechanischen Zweck zu Grunde, wie man in der Vermehrung der Oberflächen und in der Kleinheit der Röhren eine Ursache zur örtlichen Verlangsamung des Blutstroms im Gegensatz der Geschwindigkeit desselben in den übrigen Theilen erkennt, indem die Wirkungen der Reibung und der Capillarität in diesen Bildungen zunehmen. Hieran hat man bei dem Wundernetz der *Carotis cerebialis* gedacht. Es ist merkwürdig daß die Thiere, bei denen wahre Wundernetze an den Extremitäten vorkommen, wie die Faulthiere und Stenops, sich durch die Langsamkeit ihrer Bewegungen auszeichnen. Andernthails hat man bei den Wundernetzen der Arterien der Extremitäten und des Schwanzes daran gedacht, daß diese Bildungen bei den anhaltenden Anstrengungen der Muskeln beim Klettern die Strömung des Blutes erleichtern und die Hindernisse aufheben, welche durch die Zusammenziehung der Muskeln für die Bewegung des Blutes entstehen können. Die letztere Erklärung läßt sich nicht auf die Wundernetze anwenden, welche dem Muskeldrucke nicht ausgesetzt sind, wie die Wundernetze der *Carotis cerebialis* der Wiederkäuer, der *Carotis* der Frösche, die arteriösen und venösen Wundernetze des Thunfisches und des *Squalus cornubicus*. Der Umstand, daß bei den Thieren mit einem Wundernetz der *Carotis cerebialis* nach Rapp's Beobachtung die *arteria vertebralis* gar nicht das Gehirn mit Blut versieht, zeigt ziemlich deutlich, daß in diesen Fällen mehr eine Retardation der Blutströmung bezweckt ist. Diese Erklärung hat den Vortheil, daß sie auf alle Wundernetze angewandt werden kann, wenn man auch den Zweck einer örtlichen Retardation der Blutströmung im Gegensatz der übrigen Theile nicht einsieht. Auf die arteriösen und venösen Wundernetze des Thunfisches und des *Squalus cornubicus* liefse sich jene Erklärung folgendermaßen anwenden. Die gewöhnliche Anordnung des Pfortadersystems bei allen Thieren wird schon Ursache zu einer localen Verlangsamung des Blutstroms in den Capillargefäßen des Darms, der Milz und der Leber sein.

Rapp über das Wundernetz (der Carotis). Meckel's Archiv für Anat. und Physiol. 1827.
 Huschke über die Carotidendrüse einiger Amphibien. Tiedemann's Zeitschr. f. Phys. IV. 1.
 Barkow anatom. physiol. Beobachtungen. Meckel's Archiv für Anat. und Physiol. 1829.
 v. Baer über das Gefäßsystem des Braunfisches. Nov. Act. Nat. Cur. XVII.
 Breschet hist. anat. et physiol. d'un organe de nature vasculaire de couverte dans les cetacés.
 Paris 1836.

Dadurch daß das vom Darm, von der Milz und dem Pancreas kommende Blut noch ein zweites Capillargefäßsystem, nämlich das der Pfortader in der Leber durchgehen muß, muß die Bewegung des Blutes in den Gefäßen des ganzen chylopoetischen Systems etwas langsamer als in den übrigen Theilen des Körpers sein, deren Blut, nachdem es den Widerstand der Reibung und Capillarität eines einfachen Capillargefäßsystems überwunden hat, sogleich wieder in die allgemeine Strömung gelangt. Die Wundernetze des Pfortadersystems beim Thunfisch werden die Blutbewegung noch mehr verlangsamen als es schon im Pfortadersystem der übrigen Thiere geschieht. Die tausende von feinen Röhren, durch welche alles Blut der Pfortadern durchgehen muß, ehe es in die Leber gelangt, vermehren die Hindernisse durch einen neuen Widerstand der Reibung und der Capillarität, und dem zufolge wird das Blut sowohl in den Capillargefäßen des Darms als der Pfortaderzweige der Leber noch langsamer als bei anderen Thieren fließen. Die Wundernetze der Arterien des chylopoetischen Systems beim Thunfisch bilden abermals ein neues Hinderniß, welches auf alle in Hinsicht des Blutstromes hinter diesen Netzen liegenden Theile zurückwirkt, also auch wieder den Durchgang durch die Gefäße des Darms, der Milz und der Leber verlangsamt. Beim Thunfisch könnte man aus den Wundernetzen der Pfortadern auf eine Beziehung dieser Wundernetze zur Leber schließen. Bei den Wundernetzen des *Squalus cornubicus*, an welchen die Pfortader keinen Antheil nimmt, fällt diese Beziehung weg. Nimmt man indeß die obige Erklärung des Zwecks der Wundernetze an, so paßt dieselbe ebensogut auch auf die Wundernetze des *Squalus cornubicus*. Denn die Bewegung des Blutes wird hier in denselben Theilen gleich stark local gehemmt werden. Der Ursprung des arteriösen Theils der Wundernetze hat dort nicht aufgeklärt werden können; in Hinsicht des Hindernisses, welches aus den venösen Netzen hervorgeht, ist es aber für das ganze chylopoetische System gleich, mag die Hemmung vor dem Durchgang des Blutes durch die Leber oder nach demselben angebracht sein. In beiden Fällen wird die Blutbewegung im ganzen chylopoetischen System langsamer werden.

Es läßt sich vor der Hand nicht erweisen, ob diese Erklärung richtig ist. Die Verschiedenheit in der Anordnung des venösen Theils der Wundernetze beim Thunfische und *Squalus cornubicus* spricht aber dafür. Denn daß das Blut, nachdem es das ganze chylopoetische System verlassen, ehe es zur

Masse des übrigen venösen Blutes gelangt, noch Wundernetze durchkreisen soll, kann wohl mechanisch auf die Bewegung des Blutes im ganzen chylopoetischen System zurückwirken, aber das Blut nicht qualitativ für die Verbreitung in der Leber verändern. Letztere Voraussetzung ist nur beim Thunfisch möglich, wo die venösen Wundernetze vor dem Durchgang des Blutes durch die Leber liegen.

Ob nun in den Wundernetzen des Thunfisches und überhaupt in Wundernetzen nicht auch qualitative Umänderungen des Blutes statt finden, läßt sich nicht bestimmt entscheiden. Mehrere Gründe veranlassen uns indess vor der Hand diese Idee nicht aus den Augen zu verlieren.

Die lymphatischen *plexus* und ihr Übergang in Lymphdrüsen, die wesentlich aus feinerer Vertheilung der Lymphgefäße bestehen, liefern eine gute Parallele zu den Blutgefäßbildungen, die hier genannt sind. Was sind die Lymphdrüsen anders als Wundernetze der lymphatischen Gefäße, die zwischen die *casa adferentia* und *efferentia* gelegt sind? Hier sind die qualitativen Veränderungen, die chemische Einwirkung der vermehrten thierischen Oberflächen offenbar der Zweck und ganz dasselbe könnte in den analogen Bildungen der Blutgefäßwundernetze der Eingeweide angenommen werden.

Vielleicht liegt in den Wundernetzen der Thunfische und in der chemischen Action der Gefäßwände und des Blutes eine Hauptquelle der bedeutenden eigenthümlichen Temperatur der Thunfische, die J. Davy entdeckte ⁽¹⁾. Derselbe beobachtete schon vor mehreren Jahren, daß *Thynnus Pelamys* Cuv. eine Temperatur von 99° F. hatte, während das Medium 80°,5 zeigte. Nach Schiffernachrichten soll der gemeine Thunfisch, *Thynnus vulgaris*, auch warmblütig sein und nach denselben Aussagen sollen auch die anderen Arten dieser Gattung eine höhere Temperatur besitzen. J. Davy vermuthet, daß die hohe Lage der Nieren in der Nähe der Kiemen bei den Thunfischen mit der Wärmeerzeugung im Zusammenhange stehe, insofern die Kiemennerven so außerordentlich stark und mit großen Ganglien versehen sind. Diese Vermuthung ist unwahrscheinlich. Aus der bloßen Lage der Organe läßt sich für ihre Functionen kaum jemals etwas folgern. Die Nebennieren z. B., in der Nähe der Nieren, haben mit diesen nicht den geringsten physiologischen Zusammenhang; sie könnten ebensogut im Becken oder

(¹) *L'institut. Journal général des sociétés et travaux scientifiques.* No. 108.

gar in der Brusthöhle liegen, und oft trennen sich Nebennieren und Nieren ganz von einander, indem die letzteren ihre Lage verlassen und tief herabsinken. Der Versuch, aus der Lage der Eingeweide Schlüsse in Beziehung auf den physiologischen Zusammenhang zu machen, hat sich auch in Hinsicht des Verhältnisses der Wolffschen Körper, der Nieren, Nebennieren und Hoden nicht gerechtfertigt.

Von *Thynnus Pelamys*, an welchem J. Davy allein seine Beobachtung anstellte, während das vom gemeinen Thunfisch Beigebrachte auf Fischernachrichten beruht, haben wir noch keine Kenntnisse in Hinsicht des Vorhandenseins der Wundernetze. Indessen läßt es sich nicht bezweifeln, daß eine so ausgezeichnete Bildung den verschiedenen Arten der Gattung *Thynnus* zugleich zukommen werde. Da die außerordentlich starken Eingeweidenerven nach Hrn. Eschricht's Beobachtung nicht bloß durch die Wundernetze durchgehen, sondern ihnen auch Äste abgeben, so wird es einigermassen wahrscheinlich, daß in diesen Organen ein eigenthümlicher chemischer Prozeß stattfindet. An noch lebenden Thunfischen angestellte Beobachtungen über die Temperatur verschiedener Theile des Körpers, namentlich der Wundernetze und der davon entfernteren Organe werden die Richtigkeit oder Unrichtigkeit dieser Supposition bald entdecken lassen. Eben so wichtig werden in dieser Hinsicht Beobachtungen über die eigene Temperatur des *Squalus cornubicus* werden können.

VIII. Analogien des eigenthümlichen Baues der Lebergefäße.

Nachdem das Wesentliche der vorher beschriebenen Bildungen erkannt war, suchte ich nach Analogien bei anderen Fischen. Bei unseren Flusssischen liefs sich nichts ähnliches erkennen. Vorzüglich begierig war ich indeß andere Scomberoiden zu untersuchen. Bei *Caranx trachurus* suchte ich vergebens ähnliche Bildungen der Blutgefäße. Die Exemplare von *Scomber colias*, die ich untersuchen konnte, waren ohne Eingeweide; indessen habe ich mich in Copenhagen an der frischen Makrele *Scomber scombrus* überzeugt, daß der Bau ihrer Leber sich ganz vom Thunfisch entfernt und daß sie keine Wundernetze besitzt. Dagegen fand ich bei *Auxis vulgaris* des mittelländischen Meeres einen Anfang von strahliger Bildung der Lebervenen, ohne Sinus. Unter vielen anderen von mir unter-

suchten Fischen des mittelländischen Meeres, welche Hr. Dr. C. W. Schultz (jetzt in Neapel) dem anatomischen Museum als sehr schätzbares Geschenk überwiesen hat, ist mir nur noch ein einziges Beispiel von strahliger Bildung der Lebergefäße vorgekommen. Bei der Bestimmung und Ordnung der Fische der Schultzschen Sammlung traf ich in einem Glase zwei von einander getrennte große Leberlappen mit dem davon getrennten Darmkanal eines großen Knorpelfisches aus der Ordnung der Plagiostomen, wie sich aus dem gleichzeitigen Vorhandensein des dichten Pancreas und der Spiralklappe des Darmes ergab. Die ganz platten Leberlappen mit parallelen Seitenrändern, abgerundetem Endrande gehören offenbar zusammen; der eine ist 1 Fuß, der andere 8 Zoll lang, beide $3\frac{1}{2}$ Zoll breit. An dem Seitenrand des einen Endes der Leberlappen treten alle Gefäße aus und ein, von wo aus der ganze Leberlappen aufgeblasen werden konnte. Diese Gefäßstämme laufen oberflächlich der Länge nach auf der platten Fläche der Lappen hin, ohne Sinus zu bilden, und schicken lauter schief abgehende theils parallele, theils (am Ende der Leber) strahlige Zweige nach der Peripherie hin, so daß diese Gefäße durchaus einer Federfahne gleichen. Beim Aufblasen zeigte sich ihre strahlige Verbreitung nur auf der flachen Seite der Leber. Alle vom stumpfen abgeschnittenen Ende der Leber in sie eindringenden Gefäße zeigten jenes Verhalten. Nach der Größe der Leber konnte sie nur einem der größten Knochenfische oder einem schon ansehnlichen Knorpelfische des Mittelmeers angehören.

Von Thunfischen fand sich in der Schultzschen Sammlung nichts vor. Die Beschreibung der Leber anderer Thunfischarten durch Cuvier paßt auch nicht auf diese Leber. *Thynnus brachypterus* habe ich selbst untersucht; die Leberlappen sind dreiseitig. Eben so wenig paßt die Beschreibung der zweilappigen Leber des *Thynnus alalunga*, wovon der eine Lappen kartenherzförmig, der andere dreiseitig ist. Mehr würde noch die Leber von *Pelamis sarda* passen, der aber nur 2 Fuß und einige Zoll Länge erreichen soll. Cuvier sagt, seine Leber ist in zwei Lappen getheilt, wovon der linke breit mehr als ein Drittheil der Länge des Unterleibs einnimmt, der rechte ein wenig schmaler ist. Indefs die fraglichen Leberlappen sind ungleich lang, dagegen gleich breit und sehr viel länger als breit. Unter die großen Knochenfische des Mittelmeers gehören noch der Schwertfisch, *Sciaena aquila* und *Coryphaena hippurus*. Die Leber der letztern

ist nach Cuvier's Beschreibung ganz von der fraglichen verschieden. Über die Leber der *Sciaena aquila* theilt Cuvier nichts mit und leider war ein in der Nordsee gefangenes, hieher gesandtes Exemplar dieses großen Fisches ohne Eingeweide. Doch deutet Cuvier's Bemerkung über die Leber der *Sciaena hololepidota* vom Cap eine gänzliche Verschiedenheit an. Die Leber des Schwertfisches ist auch ganz verschieden. Ich erhielt die Eingeweide ganz frisch aus einem ansehnlichen Exemplar, das zur Zeit meiner Anwesenheit in Swinemünde dort gefangen wurde.

Hiernach wurde es wahrscheinlicher, daß die fraglichen Leberlappen mit strahliger Bildung der Gefäße und der Darm eines großen Plagiostomen, die sich zusammen in demselben Glase vorfanden, in der That zusammengehören. Freilich zeigte bei allen wohlerhaltenen Rochen und Haifischen der Schultzschen Sammlung die Leber keine solche strahligen Gefäße, obgleich die Form unserer Leberlappen im Allgemeinen sehr mit der Leber der Haifische übereinstimmte. Die Rochen und Haifische der Schultzschen Sammlung aus den Gattungen *Spinax*, *Mustelus*, *Scyllium*, *Galeus*, *Squatina*, *Centrina*, *Raja*, *Rhinobatus*, *Trygon*, *Myliobates* hatten ihre größtentheils wohlerhaltenen Eingeweide noch und konnten untersucht werden. Ein Exemplar von *Carcharias Vulpes* der Schultzschen Sammlung war ohne Eingeweide. Auch fand sich ein einzelner Kopf von einem großen Hammerfisch, nämlich *Zygaena malleus* vor. Von einem von beiden konnten Darm und Leber herrühren. Ich konnte nur die Eingeweide der von Hrn. Erman aus Brasilien mitgebrachten kleinen *Zygaena Tiburo* vergleichen. Hier zeigte sich die Form der Leber im Allgemeinen ähnlich; beide Leberlappen waren sehr lang, schmal und platt; aber sie waren gleich lang, die Lage der Gefäßstämme war auch ähnlich, aber die strahlige oder federartige Vertheilung ihrer Äste fehlte; die übrigen Baueingeweide paßten. Herr Dr. Schultz hat mir auf meine Anfrage brieflich mitgetheilt, daß die Leber *Zygaena malleus* angehören könne ⁽¹⁾. Ich bedaure sehr, daß dieser Punkt nicht zur

(¹) Denn außer den Eingeweiden dieses Thieres besaß Herr Dr. Schultz von einzelnen Eingeweiden von Fischen nur noch die eines großen *Squalus*. Letztere seien jedoch in seiner Abwesenheit von Palermo verpackt und daher bis auf die Leber, die er in einem besondern Glase verschlossen habe, verdorben in Berlin angekommen. Die Leber der verschiedenen *genera* von *Squalus*, die ich untersuchte, zeigt nur die gewöhnliche Anordnung der Blutgefäße. *Squalus cornubicus* zeigt kaum eine ganz schwache Spur der divergirenden Vertheilung der

Gewissheit erhoben werden kann und bitte die Naturforscher, welche Gelegenheit haben, die genannte Art der Gattung *Zygaena* zu untersuchen, zu entscheiden, ob diese Species in der That, abweichend von *Zygaena Tiburo*, jenen Bau der Leber besitzt oder nicht.

Was übrigens das Verhältniß des strahligen Baues der Lebergefäße zu den Wundernetzen der Pfortadern und der Eingeweidearterien betrifft, so stehen beide offenbar in keinem abhängigen Verhältniß. Die Leber des *Auxis vulgaris*, wo eine Andeutung des strahligen Baues vorhanden ist und die zuletzt beschriebene strahlige Leber haben keine Wundernetze. Dafs der strahlige Bau der Lebervenen nicht zu den Wundernetzen gehöre, ist schon vorher bemerkt worden. Die Ursachen einer solchen Bildung sind gänzlich unbekannt.

Erklärung der Abbildungen.

Taf. I.

Convexe Seite der Leber des Thunfisches nach einem Präparat des anatomischen Museums.

- A. Sinus der Lebervenen auf der convexen Seite des rechten Leberlappens. a. Stamm, der aus dem Sinus hervorgeht und die Oberfläche der Leber verläßt.
- B. Sinus der Lebervenen des mittlern und linken Leberlappens. b. Stamm, der aus dem Sinus hervorgeht.
- C. Strahlige Lebervenenzweige.

Taf. II.

Die Wundernetze der Thunfischleber *in situ*, nach dem Präparat des ersten Thunfisches (*Thynnus vulgaris*) von Montpellier. Die Leberlappen sind aufwärts geschlagen und die Verdauungsorgane aus der natürlichen Lage so gezogen, dafs man Alles übersehen kann. Die natürliche Lage siehe Taf. III.

- D. E. Lebervenenstämme. D. Rechter, E. linker aus dem mittlern und linken Leberlappen.
- F. Rechter Leberlappen.
- G. Mittlerer Leberlappen.
- H. Linker Leberlappen.
- I. Gallenblase. I'. Anschwellung ihres Ausführungsganges. I". Gemeinschaftlicher Gallengang kommt hinter dem Wundernetz V. des mittlern Leberlappens zum Vorschein, liegt zwischen den Blutgefäßen der *appendices pyloricae* und senkt sich in die *pars pylorica* des Darms.
- K. Magen, nach rechts gezogen. K'. Seitenast des Magens, *pars pylorica* desselben.

Lebervenenäste. Sollten die fraglichen Leberlappen und der Darm von einem großen *Squalus* herrühren, so sind sie doch keinesfalls von *Squalus cornubicus*. Die Milz paßt ohnehin gar nicht auf diesen.

- L.* *Pars pylorica* des Darms.
- M.* *Appendices pyloricae*.
- N.* Schief aufsteigender Theil des Darms.
- O.* Erster absteigender Theil des Darms.
- P.* Zweiter aufsteigender Theil des Darms.
- Q.* Zweiter absteigender Theil des Darms.
- R.* Mastdarm.
- S.* Milz.
- T.* Spindelförmiges Wundernetz des rechten Leberlappens.
- T'*. Magenvene, die es aufnimmt. *T''*. Kleine Venenzweige vom Magen.
- U.* Birnförmiges Wundernetz des rechten Leberlappens.
- U'*. Milzvene, die es aufnimmt. *U''*. Kleine Darmvenenzweige.
- V.* Plattes Wundernetz des mittlern Leberlappens.
- V'*. Venen vom Darmkanal und den *Appendices pyloricae*, welche in die Zipfel des Wundernetzes eintreten. *V''*. Magenvene, welche in dieses Wundernetz tritt.
- X.* Kleine Wundernetze des linken Leberlappens.
- X'*. Venen von den *Appendices pyloricae*, welche hineintreten.
- Y.* Arterie des chylopoetischen Systems.
- Y'. Y''*. Ihre beiden Äste. *Y'* tritt an die Basis des Wundernetzes *T.* und *U.* verzweigt sich theils im rechten Leberlappen, theils löst er sich in die Wundernetze auf, aus deren Spitzen die die Venen begleitenden Arterien für den Magen *Z.* und die Milz *Z'* entstehen.

Taf. III.

Fig. 1. Abbildung der Eingeweide des Thunfisches *in situ*, nach dem zweiten Thunfisch (*Thynnus vulgaris*) von Montpellier (verkleinert). Der Magen ist etwas nach links gezogen.

- A.* Herzkammer.
- B.* *Bulbus aortae*.
- C.* Vorhof.
- D.* Sinus der Körperven. *D'*. Zipfel von diesem Sinus.
 - a. a.* Lebervenen.
 - b. b.* Quervenenstämme. *c.* *Vena iugularis*, *d.* *Vena lateralis posterior*. Die letztere geht durch die Nieren *E.* durch und empfängt Venen aus den Nieren und Genitalien und tritt in die Rumpfmuskeln.
- F.* Rechter, *G.* mittlerer, *H.* linker Leberlappen.
- I.* Gallenblase. *I'*. Erweiterung am Anfang derselben, hier treten einige Lebergänge aus dem rechten Lappen ein. *I''*. *Ductus choledochus*.
- K.* Magen. *K'*. *Pars pylorica* desselben.
- L.* *Pars pylorica* des Darms.
- M.* *Appendices pyloricae*. *N. O. P. Q. R.* wie in Taf. II.
- S.* Milz.
- T. U.* Wundernetze des rechten Leberlappens.
- V.* Wundernetze des mittlern Leberlappens.
- X.* Wundernetze des linken Leberlappens.

Fig. 2. Stück des rechten Leberlappens (natürliche Größe).

- a.* Zweig der Eingeweidearterie, der sich sowohl in der Leber als im Wundernetz verbreitet.
- b.* Wundernetz.
- c.* Pfortaderzweige, die aus dem Wundernetz hervorkommen.

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- d. Pfortaderzweig, der in das Wundernetz führt.
- e. Arterie, die aus dem Wundernetz kommt.

Fig. 3. Zusammenhang eines Astes der Eingeweidearterie mit der Leber und seinem Wundernetz, aufgeschnitten.

- a. Arterie. b. b. Wundernetz.
- c. Zusammenhang der Arterie mit dem Wundernetz.

Fig. 4. Ein Ast der Eingeweidearterie mit den davon abhängigen Wundernetzen; aus der von Copenhagen gesandten injicirten Leber.

- a. Arterie.
- b. b. Leberzweige der Arterie.
- c. c. Zweige der Arterie in die Wundernetze.
- d. d. Wundernetze.
- e. f. Pfortaderzweige, die von den Organen des chylopoetischen Systems kommend, in die Wundernetze eintreten, Arterien, welche heraustreten und zu den Organen des chylopoetischen Systems sich begeben.

Fig. 5. Querdurchschnitt eines Stückchens von einem Wundernetz der Thunfischleber.

Fig. 6. Hauptarterienstämme und Nieren des Thunfisches von der Rückseite (etwas verkleinert).

- A. A. Oberer paariger Theil der Nieren, über dem vordersten Theil der Bauchhöhle dicht hinter und über den Kiemen.
- B. Commissur der paarigen Theile der Nieren.
- C. Unterer unpaariger platter und schmaler Theil der Nieren, C' C". Theilung desselben nach unten.
- D. Unpaariger Ureter. D' D'. Paariger Anfang desselben. D". Harnblase. D". Harnröhre.
- E. Samengänge. E'. Gemeinschaftlicher Samengang, liegt vor der Harnröhre und ist bis zur gemeinschaftlichen Ausmündung davon getrennt. F. Mastdarm.
- a. Vordere Wurzel der Aorta, aus den beiden ersten Kiemenvenen a' a'.
- b. b. Hintere Wurzeln der Aorta aus den beiden hinteren Kiemenvenen.
- c. Stamm der Aorta zwischen den paarigen Theilen der Nieren.
- d. d. d. Nierenarterien. d' d". Hintere Nierenarterien aus der Aorta.
- e. Gemeinschaftlicher Arterienstamm des chylopoetischen Systems (Y Taf. II.). e' e'. Seine beiden Äste (Y' Y" Taf. II.)
- f. Arteria axillaris durchbohrt mit der vena lateralis posterior, die Nieren.
- g. Dünne Fortsetzung der Aorta für die Mittellinie, sie tritt in den Kanal der unteren Dornfortsätze.
- h. Vena lateralis posterior.
- h'. Vena lateralis anterior, iugularis.



10. Facsimile of the original text of the Eschricht & Müller paper on shark *retia*

Eschricht, D. F. & Müller, J. 1835. Nachtrag zu der Abhandlung der Herren Eschricht und Müller, über die Wundernetze an der Leber des Thunfisches: Über die Wundernetze am Darmkanal des *Squalus vulpes* L., *Alopecias vulpes* Nob. Physik. Abhndl. d. K. Wissensch. Berlin pp. 325-328.

Nachtrag

zu der Abhandlung der Herren Eschricht und
Müller über die Wundernetze an der Leber des
Thunfisches.



Über die Wundernetze am Darmkanal des *Squalus vulpes* L.,
Alopecias vulpes Nob.

Die im letzten Abschnitt der Abhandlung angeführten Eingeweide eines Haifisches, von welchen es wahrscheinlich gemacht wurde, daß sie entweder *Zygaena malleus* oder *Carcharias vulpes* Cuv. angehören, sind, wie jetzt bestimmt zu erweisen ist, von *Carcharias vulpes* Cuv., *Squalus vulpes* L. Herr Duvernoy hat neulich (*Annales des sciences naturelles*, 1835 Mai) gezeigt, daß sich *Zygaena tudes* von den übrigen Haien durch die eigenthümliche Bildung der Spiralklappe des Mittelstücks des Darms, wohin Galle und Pancreassaft gelangen, unterscheidet. Diese Klappe ist gemeiniglich bei den Plagiostomen schraubenartig, d. h. ihre Insertion an den Darmwänden sowohl als ihr freier Rand bilden eine schraubenförmige Spirale; bei *Squalus thalassinus* Val., der den Typus eines neuen Genus in der Nähe von *Galeus* bildet, und bei *Zygaena tudes* entdeckte indess Hr. Duvernoy eine in einer longitudinalen Linie angeheftete segelartige Klappe, welche nur spiralförmig gerollt ist und einen starken Ast der Pfortader im freien Rande der Klappe enthält. Da sich dieselbe Bildung, wie ich hierauf sah, bei *Zygaena Tiburo* findet, so wurde es schon sehr wahrscheinlich, daß die erwähnten Eingeweide in der Schultzschen Sammlung mit der *Structura pinnatifida* der Lebergefaße nicht *Zygaena malleus* angehören. Denn die Spiralklappe war an jenen Eingeweiden schraubenförmig, und so wurde es höchst wahrscheinlich, daß die Eingeweide von *Squalus vulpes* waren, außer *Zygaena*

malleus, dem einzigen Haifisch der Schultzschen Sammlung, dessen Eingeweide ausgenommen waren. Dieß wurde zur völligen Gewißheit durch die Untersuchung eines andern Exemplars von *Squalus vulpes* im zoologischen Museum, dessen Untersuchung Hr. Lichtenstein gefälligst gewährte. Dieser Fisch war vom Cap gesandt, er stimmt aber ganz mit *Squalus vulpes* des Mittelmeers überein. Bei der Untersuchung dieses Fisches fand ich nicht allein die *Structura pinnatifida* der Lebergefäße, dieselbe Form der Leber, Milz, des Pancreas wieder, sondern überzeugte mich auch, daß die Stelle, welche Cuvier dem *Squalus vulpes* L. angewiesen, nicht richtig ist. Er gehört zwar mit den Gattungen *Carcharias* und *Lamna* zur Abtheilung der Haifische ohne Spritzlöcher mit Afterflosse, aber unter die Gattung *Carcharias* kann er nicht gebracht werden. *Squalus vulpes* hat eine schraubenförmige Spiralklappe des Darms. Die wahren *Carcharias* haben aber, wie ich bei *Carcharias vulgaris* und *Carcharias glaucus* gefunden, dieselbe segelartige Spiralklappe wie die Zygaenen und der *Squalus thalassinus* Val. Schon an den von Hrn. Meyen mitgebrachten Eingeweiden eines *Squalus glaucus* fand sich die longitudinale Klappe. Da jedoch der *Carcharias glaucus* Cuv., *Squalus glaucus* Bloch, mit dem *Squalus thalassinus* Val. in der Färbung ganz übereinstimmt, so war eine noch bestimmtere Nachweisung nöthig. Diese gewann ich durch die Untersuchung des *Carcharias vulgaris* und *Carcharias glaucus* des zoologischen Museums. Der letztere ist das von Bloch beschriebene und abgebildete Exemplar. Also die wahren *Carcharias* haben eine longitudinale segelartige Darmklappe, *Squalus vulpes*, wie die Gattung *Lamna* in derselben Familie, eine schraubenförmige Klappe. Die Zähne der *Carcharias* sind von denen des *Squalus vulpes* nicht ganz verschieden; bei beiden sind sie dreieckig, platt, aber nur bei den *Carcharias* am Rande meist sägeartig gezähnt. Allein die abortive Afterflosse und abortive zweite Rückenflosse und der ungeheuer verlängerte obere Lappen der Schwanzflosse sind bei *Squalus vulpes* eigenthümlich. Ich bilde daher aus *Squalus vulpes* L., *Carcharias vulpes* Cuv. mit *Rafinesque* eine eigene Gattung, *Alopecias Nobis*, *Alopias Rafinesque*. Man kennt bis jetzt nur eine Art, *Alopecias vulpes*. Die Familie der Haifische ohne Spritzlöcher mit Afterflosse enthält also die Gattungen *Carcharias*, *Alopecias*, *Lamna*. Der Name *Alopecias* kommt schon in der Ichthyologie der Alten vor. *Artedi synonymia piscium* ed. Schneider. Lips. 1789. 134. 138. Was die Verbreitung der segel-

artigen Klappe betrifft, so habe ich sie in anderen Gattungen von Haifischen und auch bei Rochen nicht vorgefunden. Untersucht wurden die Gattungen *Lamna*, *Scyllium*, *Galeus*, *Mustelus*, *Spinax*, *Centrina*, *Squatina*, *Rhinobatus*, *Torpedo*, *Narcine*, *Raja*, *Myliobates*. Sie alle haben die schraubenförmige Spiralklappe. Die segelartige longitudinale Klappe ist also bis jetzt nur von den Gattungen *Carcharias*, *Zygaena* und dem *Squalus thalassinus* Val. bekannt. Die Eingeweide der Gattungen *Notidanus*, *Selache*, *Cestracion*, *Scymnus*, *Pristis*, *Rhina*, *Anacanthus*, *Propterygia*, *Rhinoptera*, *Cephaloptera* sind noch nicht untersucht.

Der zweite Theil dieses Nachtrags betrifft die von mir bei *Alopecias vulpes* beobachteten Wundernetze am Darmkanal, die ich an den von der Leber isolirten Eingeweiden der Schultzschen Sammlung nicht wahrnehmen konnte. An der Seite des Magens liegt ein großes quastförmiges Wundernetz von vielen hunderten strahlenförmigen Röhren, welche von allen Seiten zusammentreten und ihr Blut an einer gemeinsamen Stelle in den Stamm der Pfortader, noch in einiger Entfernung von der Leber ergießen. Sie kommen theils parallel, theils büschelartig aus den Wänden des Magens und haben eine Dicke von $\frac{1}{4}$ bis $\frac{1}{2}$ Linie. Sie anastomosiren unter einander. Dicht vor dem Eintritt der Pfortader in die Leber nimmt sie noch ein kleines Wundernetz vom obersten Theile des Magens oder vom Schlunde auf. Aber der Stamm der Pfortader, der vom Darmkanal her aufsteigt, nimmt schon viel früher und lange vor der Aufnahme des großen Wundernetzes des Magens, kleine Büschel von gehäuften Adern von der Milz, vom Pancreas und ein sehr großes Wundernetz von dem Theil des Darms auf, worin sich die Spiralklappe befindet. Das letztere Wundernetz ist ebenso groß wie das des Magens. Eine große Darmvene, der Anfang der Pfortader, steigt wie bei den übrigen Plagiostomen mit schraubenförmiger Darmklappe von dem untersten Theil des Darms herauf, dicht auf der Oberfläche des Darms gelegen; bei *Alopecias vulpes* befindet sich an dieser Stelle eine Anschwellung, so weit der Venenstamm über den Theil des Darms hingeht, der mit der Klappe versehen ist. Sie entsteht durch das Wundernetz. Alle von diesem Darmstück kommenden Gefäße bilden lauter feine, parallele, hier und da unter einander anastomosirende Röhren, auf das dichteste gedrängt, so daß man an dieser Stelle die Wände des Darms selbst wegen der gehäuften Gefäße nicht sieht. Die Gefäße treten unter geradem oder wenig schiefem

Winkel in den Stamm, und zwar von beiden Seiten, so daß das Ganze die vollkommenste Ähnlichkeit mit einer Federfahne darbietet. Das Wundernetz hört unten, wo die Spiralklappe im Darm aufhört, auch auf und hier auf dem Mastdarm haben die Blutgefäße die gewöhnliche Anordnung, die baumförmige Verästelung.

Diese Art der Wundernetze unterscheidet sich von denen an der Leber der Thunfische und den Wundernetzen des *Squalus cornubicus*, daß die quastförmig in einer Richtung vertheilten Gefäße nicht wieder sich in neue Stämme sammeln und hat mehr Ähnlichkeit mit den Wundernetzen an den Extremitäten der Tardigraden, wo wenigstens diese Sammlung nicht vollständig ist. Die Arterien der Eingeweide nehmen innerhalb der Wundernetze des *Alopecias vulpes* ein ähnliches Verhalten wie die Venen an. Ich habe viele Rochen und Haifische auf diese Bildung untersucht, sie aber nicht wiedergefunden. Die Fische, bei denen bis jetzt Wundernetze beobachtet sind, sind demnach unter den Knochenfischen *Thynnus vulgaris*, *Th. brachypterus*, unter den Knorpelfischen *Lamna cornubica* und *Alopecias vulpes*. Bei einer andern Gelegenheit werde ich die Wundernetze der letzteren durch Abbildungen erläutern. Noch muß ich der sehr langen canalartigen, aber geschlängelt gewundenen und von der Substanz des größern Leberlappen größtentheils verdeckten Gallenblase des *Alopecias vulpes* erwähnen, wovon ich an einem andern Ort auch eine Abbildung geben werde.





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Printed in the United States of America by T.F.H. Publications, Inc., Neptune City, New Jersey
for the Axelrod Institute of Ichthyology, University of Guelph, Ontario, Canada

Printed on acid-free paper