RETINAL CIRCULATION IN SOME LOWER VERTEBRATES

ISAO HANYU

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ISAO HANYU

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ABSTRACT

Four Elasmobranchs, 23 Teleosts, 2 Holosteans, 1 Urodele and 2 Anurans were studied. In Elasmobranchs, no vessel is found either in the vitreous cavity or on the retina. The iris artery proceeds through the ventral choroid and sends off a branch to the small lens muscle papilla. Most instances in the Teleosts are classified into 4 types; the higher falciform process, the low falciform process, the low falciform process with branches on the retina, and the vitreal vessels; depending upon the development of the hyaloid artery either into the vitreous cavity along the embryonic fissure or onto the retina. The main vessel which proceeds from the optic disc to the lens muscle tends to be obliterated in the vitreal vessels where the embryonic fissure is closed and the numerous branches on the retina are received by a peripheral annular vessel. Instances which do not fall into any of these categories are considered to be deviations. The arterial entry near the ventral ora in Holostei is associated with the ventralward elongation of the optic disc. The vitreal vessels of Liparids are unique in that their exit is through the optic disc. Urodela show an

avascular condition, while Anura have a well developed system of vitreal vessels where the entry and the exit are at the ventral margin of the ventral lens muscle represented by a small swelling in the ciliary folds. In both, the ophthalmic artery runs along the ventro-temporal meridian of the eye-ball to supply the cilio-iris region.

The falciform process type vascularization may have arisen from the vitreal vessels due to their being influenced by the development of the accommodative lens muscle, which is functional only in Neopterygii. On the other hand, both in Classes Chondrichthyes and Amphibia, it seems that the less marked lens muscle has not had any significant effect on intraocular vascularization.

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INTRODUCTION

In the vertebrate eye, the highly vascularized choroid usually plays the most important role in nourishing the photosensitive layer, the retina. The innermost part of the choroid consists of a single-layered network of capillaries called choriocapillaris which encapsule the outer surface of the retina completely.

In addition to the choroid, there are some other blood vessels which are found adjacent to the inner surface of the retina, or even in the retina itself. Among these are the vitreal vessels covering the retina of some fishes, frogs and snakes, and the retinal vessels with capillaries lying in the retina, of some Mammals as well as eel, a Teleost. Further, there are vascular structures projecting into the vitreous cavity such as the pecten of birds, the papillary cone of lizards and the falciform process of some Teleosts. These vascular projections are also believed to be primarily nourishing devices for the most demanding retina (Walls, 1942).

Although detailed information concerning these intraocular vascular structures is available in the literature (Virchow, 1901; Franz, 1913, 1934; Michaelson, 1954), it is felt, at least as far as the

Teleosts are concerned, that all important instances are not covered, nor pertinently described, thus leaving a gap in our understanding of their interrelationships (Hanyu, 1960). This may partly be due to the fact that the observations were made on a relatively limited group of fishes.

After having studied various instances of the intraocular vascularization in many Teleosts inhabiting the Japanese waters (Hanyu, 1959a), the author undertook the present work dealing with a wider range of animals including Amphibians, Elasmobranchs, Holosteans as well as Teleosts found in the north eastern part of North America. In this study, it is hoped, not only to further examine the interrelationship of various Teleostean intraocular structures, but also to compare the intraocular vascularization among the lower vertebrate groups mentioned above. The instances where the blood vessels run on the surface of the retina having been selected for intensive study, an emphasis will be laid on them in the following description of the results.

LITERATURE REVIEW

Among the authors who have attempted to study the intraocular vessels on a comparative basis are Virchow (1882b, 1901), de Waele (1902), Franz (1913, 1934), Jokl (1927) and Michaelson (1954). Virchow (1901), in the first comprehensive review in this field, was of the opinion that, commonly in vertebrates, a vascular loop seems to emerge through the embryonic fissure into the eye cup during its formation and that the primary vascular loop may be the rudiment of the various vascular structures encountered either in the vitreous cavity or on the retina of the adult eye. Franz (1934), agreeing with this view, further claimed that the embryonic vascular loop with its dorsal afferent and ventral efferent limbs (die dorsal zuführende und ventral abführende Schenkel der embryonalen Gefässschlinge) could be identified in the definitive, complex vascularization of some adult animals.

Among the Elasmobranchs, de Waele (1902) observed the primary vascular loop in the optic cup of the shark, Mustelus laevis. In 29mm embryo of Mustelus, the vascular loop with a few branches is seen passing through the embryonic fissure into the cavity of the eye cup. In 52mm embryo, however, the vessels are confined to the distal part, where the embryonic fissure is still open but is in the process of closing. This closing occurs from under the optic disc to the periphery or in the proximal to disatl direction. In the eyes of adult Mustelus, Franz (1934) proposed that the same dorsal limb of the embryonic vascular loop persists as the iris artery, Arteria iridis, proceeding along the ventral meridian of the choroid to supply the iris and the lens muscle which is formed at the corresponding part of the embryonic fissure or the ventral rim of the eye cup. Apart from this, no other blood vessel is found in the vitrous cavity or on the retina.

According to Virchow (1882b), Chimaera monstrosa belonging to the order Holocephali is also devoid of intraocular blood vessels in the definitive stage.

Adult bony fishes or Osteichthyes show various modes of intraocular vascularization. Although Chondrostei such as sturgeon Acipenser sturio still show the same avascular situation as those mentioned above (Virchow, 1882b), Cladista such as Polypterus endlicheri and Calamoichthys calabaricus have a system of vitreal vessels developing over the retina (Virchow, 1882b).

The vitreal vessels are rather common in the largest group, Neopterygii, which are the most modern fishes. Virchow (1882b) classified the vitreal vessels found in this group as well as in some other groups into the following 3 types. 1) "Carp type", where the artery enters the eye at the optic disc and sends off the branches radially or somewhat bilaterally, while the vein, lying along the ora serrata (in a circle), goes out downwards; as seen in Cyprinus, Catostomus, Myxostoma, Barbus, Leuciscus, Abramis, Tinca, Gobius. 2) "Eel type", where the arterial part is the same as in the "carp type", but the venous part uses the optic disc as exit, having received the capillaries which are distributed in the retina. This type is seen particularly in the eyes of eel-like fishes such as Conger, Synaphobranchus and, Anguilla. 3) "Bony Ganoid* and catfish type", which has the arterial entry at the most ventral part of the ora serrata, being adjacent to the point of exit of the vein which is similar to that of the "carp type"; as seen in Lepidosteus, Polypterus, Calamoichthys, Amia, Malapterurus, Amiurus. No other basic type was thought to exist. Thus, Tautogolabrus adspersus where both the entry and the exit of the

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* The category "bony ganoid", has since been abolished. It is now considered to be equivalent to Holostei.

vessels are within the embryonic fissure, and Pleuronectidae where a wide meshed vascular net covers the retina were pointed out to be the instances of differentiation in minor detail or of transition. Karsten (1923) described the vitreal vessels of Periophthalmus koelreuteri precisely and recognised a particular branch which, unlike other ones joining the peripheral annular vein along the ora, leads to the lens muscle or campanula Halleri situated at the ventral ora. Later, Franz (1934) referred to the vessel homologous to this branch in Periophthalmus eye as the main vessel. Chrustschoff (1926) and Jokl (1927), in Cyprinus and Amia, respectively, demonstrated that the vitreal vessels cling to a thin, translucent membrane composing the vitreo-retinal boundary, and not to the internal limiting membrane of the retina. After a detailed examination on the eel retina, Michaelson (1954) confirmed the above mentioned, peculiarly developed vascularization or Virchow's "eel type" vitreal vessels, which Hanyu (1959a) also observed in Astroconger. But this type with intraretinal capillaries, being found only in the eel like fishes, Apodes, was considered exceptional and therefore called retinal vessels.

In addition to these vessels on the retina, Neopterygii show another kind of intraocular vascular structure which is well known by the name of falciform process. Virchow (1901), having defined the falciform process* as a plate of connective tissue projecting into the vitreous cavity through the persisting embryonic fissure, distinguished four basic forms or "Grundformen"; 1) the very low falciform process as seen in most Acanthopterygii, 2) the distally high falciform process as seen in Salmonidae, *Esox* and herring, 3) the proximally high falciform process as seen in *Thynnus* and *Auxis* and, 4) the very short and distally present falciform process as seen in Cyprinidae. He regarded the last one as being restricted distally by the closing of the embryonic fissure in the proximal to distal, in other words, from the optic disc to the ora terminalis direction. In much the same way, Franz (1934) stated that the instances where the length of the falciform process is reduced by the partial closing of the embryonic fissure were shown by *Gasterosteus maritimus*, *Crenilabrus*, Syngnathidae and *Hippocampus*, Cyprinidae, *Gobius minutus*, *Gadus carbonarius* etc. He also

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* Virchow preferred the term "Leiste" to this.

maintained that the falciform process is supplied by the same artery, namely, Arteria centralis retinae or Arteria hyaloidea or Arteria ophthalmica interna, which also supplies the vitreal vessels and that the vitreal vessels may develop when the falciform process becomes restricted distally by the closing of the embryonic fissure. Walls (1942), similarly, suggested that where the falciform process is wholly lacking or in some instances where it is present only far distally, there is a system of vitreal vessels clinging to the inner surface of the retina. As the falciform process is fed by the same artery which would otherwise divides into the vitreal vessels, the two structures are mutually exclusive, never flourish together in one species. Recently, Hanyu (1959a), having examined over 250 Teleost species, suggested a different relation between the falciform process and the vitreal vessels. He proposed that the falciform process, is essentially a mode of vascularization into the vitreous cavity along the embryonic fissure rather than an outgrowth of the choroidal connective tissue. It has a tendency to send branches also onto the retina, especially in the less developed instances. It is to such an instance as this wherein branches onto the retina are developed thickly, that the term vitreal vessels is usually applied. On the other hand, the closing of the embryonic fissure does not restrict the falciform process as a vascular structure distally but simply prevents the main vessel from communicating with the choroidal layer through the embryonic fissure. By Neoprene injection in 13 representative species, he further demonstrated the following points (Hanyu, 1959b). Generally, the main vessel of the hyaloid artery appears at the optic disc and then runs ventrally along the embryonic fissure to the lens muscle, thus feeding the latter. The vein from the lens muscle and that from the iris congregate into the ventral choroidal vein which proceeds conspicuously along the ventral meridian of the choroid. The branches from the main vessel, either in the vitreous cavity or on the retina, go distally into the embryonic fissure, and communicate with the choriocapillaris, the ventral choroidal vein and other choroidal vessels, thus never rejoining the main vessel. When the embryonic fissure is lacking, the branches over the retina are received by the peripheral annular vessel which passes at the ventral ora into the ventral choroidal vein.

von Kittlitz (1907) noted the temporary development of a vascular net, "Glomerulus des Glaskoerpers", on the dorsal limb of the primary vascular loop in the young of _Salmo trutta_ during the last 2/3rds period of the period between the fertilisation and the complete absorption of the yolk. Confirming a similar transient vascular net in _Salmo irideus_, Hanyu (1961) further considered the following formation of the falciform process as being mainly undertaken by the communication of the remaining part of the vascular net with the choroid. He also demonstrated that in _Channa argus_, another Teleost which has well developed vitreal vessels in the definitive stage, there occurs no degeneration of intraocular blood vessels at any stage of development.

In Dipnoi, _Ceratodus_ is free from any intraocular vessels mentioned above (Virchow, 1882b), but _Protopterus annectens_ has the vitreal vessels with its artery entering at the optic disc (Hosch, 1904).

In adult amphibia, Urodela have no intraocular vitreal vessels, while Anura have a well developed system of vitreal vessels (Virchow, 1901; Franz, 1934; Michaelson, 1954). In Anura, the hyaloid artery appearing at the ventral ora divides itself into two main branches i.e. nasal and temporal ones, which run along 1/4 and 3/4 of the ora terminals, respectively, thus making up an approximate annular vessel with a little discontinuity at the nasal portion. Many branches given from these branches cover the retina and join eventually in the fundus into a 'Y' shaped venous trunk, whose exit is also at the ventral ora close to the entrance of the hyaloid artery. Just before this point two venous branches which run along the ora in a manner similar to the two main arterial branches, also meet the venous trunk, resulting in the hyaloid vein.

In Rana esculenta (Tretjakoff, 1906), the hyaloid artery is a terminal branch of the ophthalmic artery, Arteria ophthalmica. The trunk of this artery, after giving off main branches to the choroid, proceeds on the ventral surface of the sclera to its ventral part and there enters the eyeball to supply the iris-ciliary region as well as the vitreal vessels mentioned above. The hyaloid vein passes into the choroid and joins the ophthalmic vein, Vena ophthalmica which collects the venous branches from the lower half of the eyeball.

According to de Waele (1902a), the primary vascular loop emerging through the embryonic fissure in frog embryo, becomes restricted by the closing of the fissure, which starts proximally on the 5th day and reaches the ciliary region on the 10th day. As the vascular loop disappears, vitreal vessels in turn develop and persist. On the other hand, in Triton similar embryonic vitreal vessels are present only temporarily, and in Axolotl these vessels are never developed (de Waele, 1905). Jokl (1927), proved that Triton taeniatus and T. alpestris have the temporary intraocular blood vessels originating from the primary vascular loop, but T. cristatus does not show such vessels at any stage.

MATERIAL AND METHODS

A. MATERIAL

The species examined are listed below. Identifications were based upon Bigelow and Schroeder (1953) for the marine fishes and upon Hubbs and Lagler (1947) for the fresh water ones. Concerning classification of higher categories such as classes and subclasses, however, the terms used are after Weichert (1958).

The species examined.

*, injected; ** also observed ophthalmoscopically.

CLASS CHONDRICHTHYES

SUBCLASS ELASMOBRANCHII

ORDER SELACHII

FAM. SQUALIDAE

Squalus acanthias LINNAEUS,* spiny dogfish

Centroscyllium fabricii (REINHARDT), black dogfish

ORDER BATOIDEI

FAM. RAJIDAE

Raja senta GARMAN, smooth-tailed skate

R. radiata DENOVAN, thorny skate

CLASS OSTEICHTHYES

SUBCLASS NEOPTERYGII

HOLOSTEI

FAM. LEPISOSTEIDAE

Lepisosteus osseus (LINNAEUS), long-nose gar

FAM. AMIIDAE

Amia calva LINNAEUS, bowfin

TELEOSTEI

FAM. SALMONIDAE

Salmo salar LINNAEUS,** Atlantic salmon

FAM. ARGENTINIDAE

Argentina silus ASCANIUS, argentine

FAM. GADIDAE

Merluccius bilinearis (MITCHILL), silver hake

Gadus callarias LINNAEUS,*, ** cod

Urophycis chuss (WALBAUM), squirrel hake

U. chesteri (GOODE and BEAN), long-finned hake

Enchelyopus cimbrius (LINNAEUS), four-bearded rockling

FAM. MACROURIDAE

Macrourus bairdii GOODE and BEAN, common grenadier

FAM. GASTEROSTEIDAE

Apeltes quadracus (MITCHILL), bloody stickleback

FAM. ANARHICHADIDAE

Anarhichas lupus LINNAEUS, wolffish

FAM. ZOARCIDAE

Lycodes reticulatus REINHARDT, arctic eelpout

FAM. LABRIDAE

Tautogolabrus adspersus (WALBAUM),*, ** cunner

FAM. SCORPAENIDAE

Sebastes marinus (LINNAEUS), rosefish

FAM. COTTIDAE

Myoxocephalus scorpius (LINNAEUS),*, ** shorthorn sculpin

M. octodecemspinosus (MITCHILL),*, ** longhorn sculpin

FAM. CYCLOPTERIDAE

Cyclopterus lumpus LINNAEUS, lumpfish

Eumicrotremus spinosus (MÜLLER), spiny lumpfish

FAM. LIPARIDAE

Neoliparis atlanticus JORDAN and EVERMANN, sea snail

Liparis liparis (LINNAEUS), striped sea snail

FAM. BATRACHOIDIDAE

Opsanus tau (LINNAEUS), toadfish

FAM. PLEURONECTIDAE

Pseudopleuronectes americanus (WALBAUM),* winter flounder

Glyptocephalus cynoglossus (LINNAEUS), witch flounder

FAM. LOPHIIDAE

Lophius americanus VALENCIENNES, American goosefish

CLASS AMPHIBIA

ORDER URODELA

FAM. PROTEIDAE

Necturus maculosus,* mud puppy

ORDER ANURA

FAM. BUFONIDAE

Bufo americanus, *, ** toad

FAM. RANIDAE

Rana pipiens, *, ** leopord frog

Only 4 species belonging to 2 families were obtained from Subclass Elasmobranchii, which have been reported to invariably show an avascular condition (Virchow, 1901; Franz, 1934). In Subclass Neopterygii, however, 23 species belonging to 15 families were chosen as the representatives of Teleosts inhabiting North America, especially the north-eastern Atlantic coast. Two species representing two families of Holostei, or the most primitive group of Neopterygii were also examined. In Class Amphibia, which show less variation, 2 Anurans belonging to 2 families and a Urodele were studied.

B. METHODS

The animals were fixed and kept in formalin. The eyes were excised and after the removal of the cornea, the iris and the lens, the remaining part was submerged in water and examined with a binocular microscope. Sometimes, for more minute observation, injection of India ink was made into the heart of anaesthetized animal prior to fixation. Through a cut made on the ventricle wall, a blunted needle was inserted far into the aorta, and ligated together with the aorta. By injecting carefully, the India ink was observed to flow into the small vessels of the skin around the eye and the oral region, which usually indicated success of the operation. As for the spiny dogfish, *Squalus acanthias* and the mud puppy, *Necturus maculosus*, specimens injected doubly with Neoprene latex were purchased from Ward's Natural Science Establishment, Inc. In most species, several specimens were examined in order to ascertain the extent of individual variation, which turned out to be insignificant.

Ophthalmoscopy was also performed on some species in order to confirm the direction of the blood flow in the vessels. The animal was kept lightly anaesthetized by chloroform or by urethane or by cold. The fish, in particular, was placed on its side in a shallow dish with just enough water to submerge its head. In the darkness, the indirect method of ophthalmoscopy was practised using an ordinary hand ophthalmoscope (+5 - + 20 Diopter range) and an auxiliary lens (ca. + 30 Diopter) placed near the eye to be observed. The auxiliary lens served both for the magnification of the image and the convergence of the rays from the ophthalmoscope to the pupil of the eye. An upsidedown, magnified image of the illuminated fundus of the eye was obtained when the distances between the eye and the hand lens and between the hand lens and the ophthalmoscope were approximately 1.5 and 4 inches, respectively. By altering the distances and focussing sharply, the blood flow or the stream of the blood corpuscles in the intra-ocular vessels could usually be recognized.

RESULTS

A. SUBCLASS ELASMOBRANCHII

1. Order Selachii

In the two shark species examined, no vessel was found in the vitreous cavity or on the retina. But the vessel supplying the lens muscle papilla was identified in the injected specimens of *Squalus acanthias* (Fig. 1). In *S. acanthias* (Squalidae), the lens muscle papilla is represented by a small pigmented plate attached to the ventral part of the iris. In appearance the lower part of the lens muscle papilla is an upward continuation of the ciliary region which is less developed but signified by a zone consisting of many low meridional folds between the ora terminalis* and the area of the iris. The upper part of the lens muscle papilla is connected to the iris only along the mid-vertical portion, the margin being left free. Along this mid-vertical portion, there is a trace of the cleft which is believed to be the most distal part of the embryonic fissure (Rochon-Duvigneaud, 1943). It is near the end of this trace that a small branch is given off from one of the two major branches of the iris artery or

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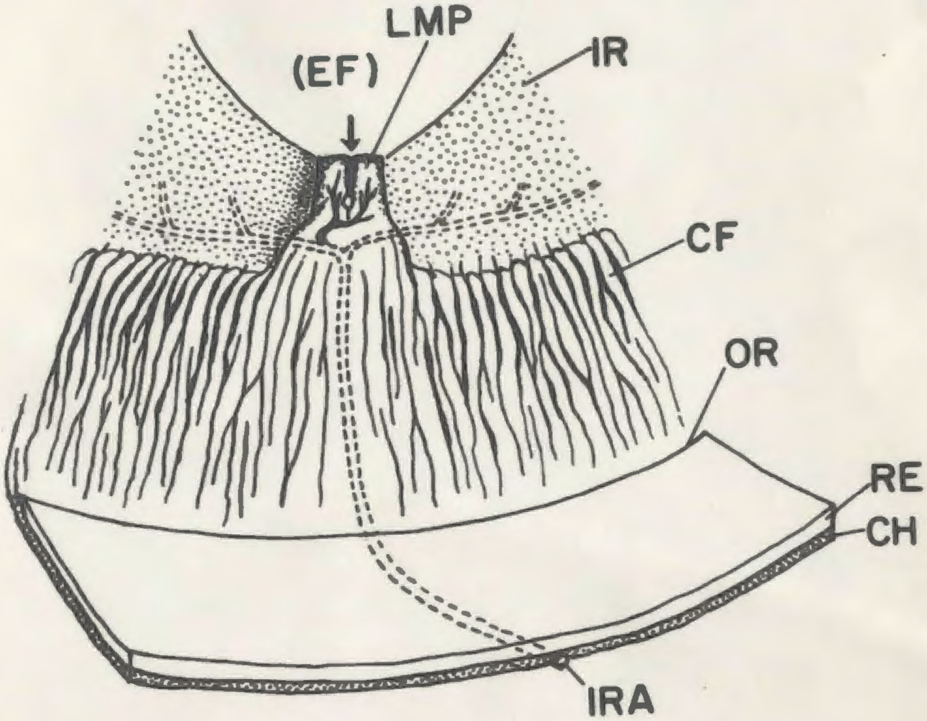
* This term is preferred to "ora serrata", because the part is not serrated.

Fig. 1. The ventral part of the eye of Squalus acanthias, viewed from the fundus. The iris artery (IRA) sends a branch to the lens muscle papilla (LMP) in which a vertical trace of the embryonic fissure (EF) is found.
CH, choroid; CF, ciliary folds; EF, embryonic fissure; IR, iris; IRA, iris artery; LMP, lens muscle papilla; OR, ora terminalis; RE, retina.


LMP
(EF)
IR
CF
OR
RE
CH
IRA

Arteria iridis (Franz, 1934) or Arteria ophthalmica minor (Virchow, 1901). The iris artery enters the eyeball with the optic nerve and proceeds ventrally, through the choroid, to the most ventral part of the iris, where it divides itself (Fig. 1). It sends off only a few minor branches, on the way to the iris. The vein draining the lens muscle papilla and the iris could not be examined because of the unsuccessful venous injection.

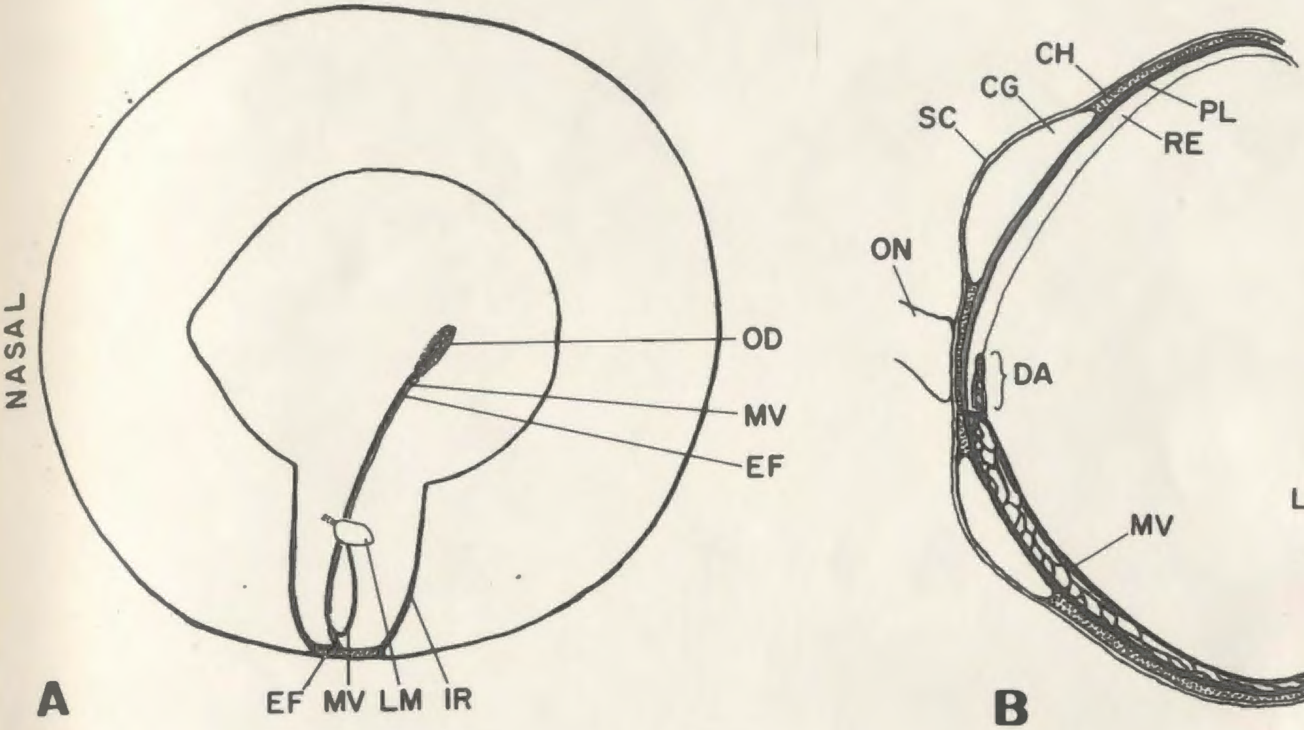
In Centroscyllium fabricii (Squalidae), the ciliary folds are less marked and the lens muscle is so reduced as to be hardly recognized as such. Yet, the remnant of the distal part of the embryonic fissure is seen as a small notch in the corresponding part of the pupillary margin of the ventral iris. The trunk of the iris artery is easily followed even in an uninjected specimen.

2. Order Batoidei

The avascular situation in the vitreous cavity was confirmed also in the two skate species, Raja senta and R. radiata (Rajidae), which show quite a similarity in every respect. Without injection, the distinct iris artery can be traced through the ventral meridian of the well pigmented choroid as well as the ventral part

Fig. 2. The low falciform process of Gadus callarias. A, front view showing the main vessel (MV) which proceeds along the embryonic fissure (EF). B, section along the embryonic fissure, showing a network which extends through the embryonic fissure and communicates with the choroid (CH).

CG, choroidal gland, or a horseshoe-shaped mass of capillaries; CH, choroid; DA, "dorsaler Anhang"; DE, "Dreiecke"; EF, embryonic fissure; IR, iris; LM, lens muscle; MV, main vessel; OD, optic disc; ON, optic nerve; PL, pigment layer of retina; RE, retina; SC, sclera.



A
B

of the iris. The lens muscle papilla is far less marked than in Squalus and is actually a very small swelling located near the upper border of the most ventral part of the ciliary zone, which consists of less distinct meridional folds than those in Squalus. Proceeding upwards from the lens muscle papilla, there is a rather marked, vertical trace of the closed embryonic fissure across the iris. Under the lens muscle papilla, the ciliary zone becomes a little wider, so that the ora terminalis gets a concavity at its most vetral part.

B. SUBCLASS NEOPTERYGII

1. Teleostei

As had been expected, the teleosts which were examined yielded a wide variety of retinal circulation types. But, the author believes that almost all these instances can reasonably be divided into four types* which show successive stages of vascularization between the typical falciform process and the so called vitreal vessels. The four types are; the higher falciform process, the low falciform process, the low falciform

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* Essentially the same classification was followed in the author's previous work dealing with Japanese Teleosts (Hanyu, 1959a).

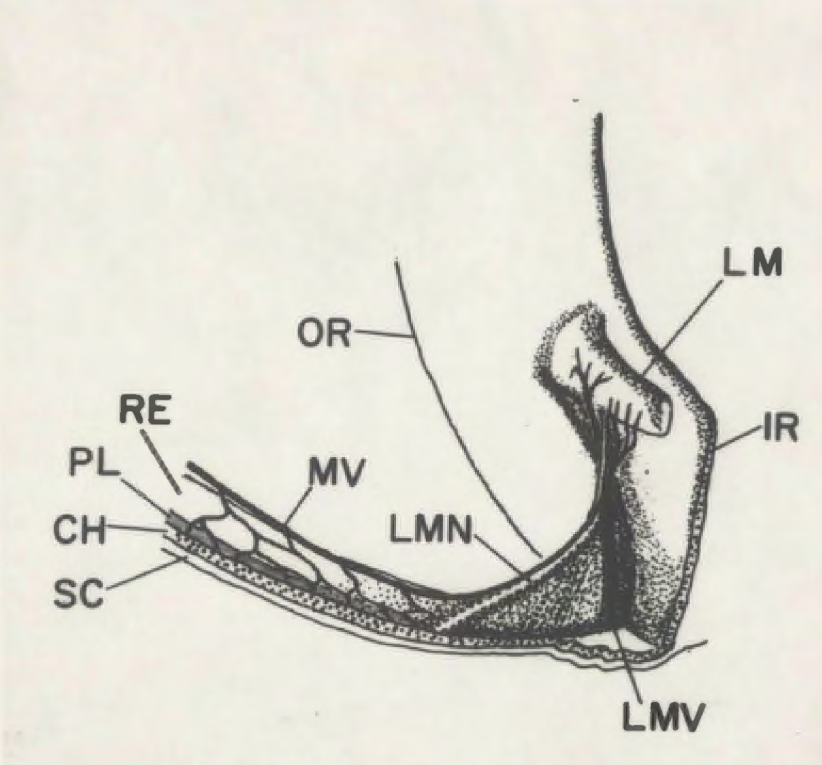
process ~~which~~ with branches on the retina, and the vitreal vessels. In referring to these types, the term 'falciform process' is used as far as possible, even though it does not appear quite relevant in describing the true situation. By doing so, the relationship between the falciform process and the vitreal vessels becomes clearer. However, it has not been possible to include some other instances in any of these four categories. Those instances have been grouped, for convenience sake, into the following two categories; special instances of vitreal vessels in Liparidae, and other unusual instances.

a. The low falciform process.

This type of falciform process is well represented by <u>Gadus</u> <u>callarias</u> (Gadidae). In this species (Fig. 2-A), a thick vessel or the hyaloid artery appears at the ventral end of the vertically elongated optic disc which is situated rather temporally on the fundus, then runs ventro-nasally as the main vessel along the remaining embryonic fissure or retinal cleft and finally turns up to reach the lens muscle or campanula Halleri, which is attached to the iris. If the retina along the embryonic fissure is removed in a well injected specimen, it is clearly seen that the main vessel, on the way to the lens muscle, sends several small branches into the embryonic fissure (Fig. 2-B). The branches both by dividing and anastomosing, make up a large-meshed network extending throughout the embryonic fissure. Another branch given proximally goes dorsally onto the optic disc, resulting in a small complex of fine vessels there. This part is considered to be identical with "Dorsaler Anhang" by Virchow (1901). It is also noticed that all the branches lie in a very thin, hardly perceptible lamella and therefore, the entire system is a flat, somewhat sickle-shaped strip situated vertically to the fundus. It should be pointed out that all these branches from the main vessel do not rejoin the main vessel, but communicate distally with the choriocapillaris layer which lies adjacent to the pigment layer of the retina. Ophthalmoscopically, the blood flow in the main vessel was confirmed to be in the optic disc to the lens muscle direction or in the proximal to distal direction.

Similar situations are found in the other Gadids examined. Of these, Urophysis chuss, U. chesteri and Merluccius bilinearis show a small, colorless, triangular body rising above the brims of the embryonic fissure from within. This particular structure, which was called

Fig. 3. The distal part of the low falciform process of Argentina silus. The main vessel (MV), the nerve for the lens muscle (LMN), and the vein from the lens muscle (LMV) form part of the membranous region attached to the retino-iris angle. CH, choroid; IR, iris; LM, lens muscle; LMN, nerve for lens muscle; LMV, vein from lens muscle; MV, main vessel; OR, ora terminalis; PL, pigment layer of retina; RE, retina; SC, sclera.


LM
OR
RE
IR
PL
MV
CH
LMN
SC
LMV

"Dreiecke" or "Kegelformiges Gebilde" by Virchow (1901), has been paid little attention since and is histologically unknown (see Fig. 5).

Argentina silus (Argentinidae) and Eumicrotremus spinosus (Cyclopteridae) also present similar instances. These instances, however, are different from those of Gadids in that the distal part of the falciform process passes into a well pigmented membrane which takes a triangular shape fitted in the retino-iris angle. Embedded in this membranous part, the nerve for the lens muscle and the vein* from the lens muscle are found in Argentina (Fig. 3). Thus, in these species the lens muscle is bigger and firmly fastened to the neighbouring part.

b. The higher falciform process.

A typical falciform process is seen in the eye of Salmo salar (Salmonidae). The falciform process of Salmo (Fig. 4), which is a pigmented, sickle-shaped membrane projecting conspicuously into the vitreous cavity, is apprently quite different from the low falciform process described in the previous section.

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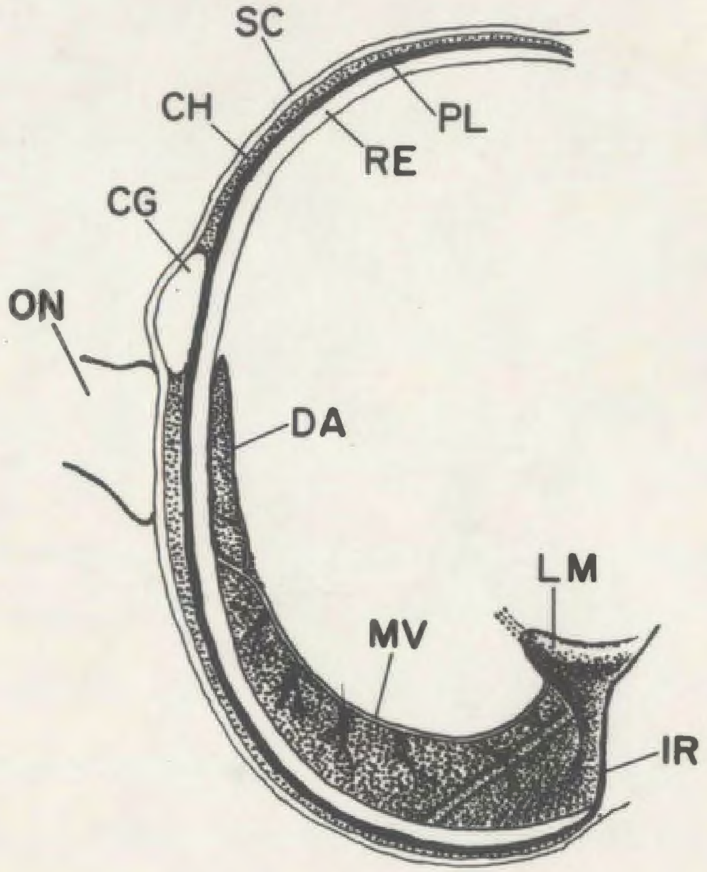
* This vein is present in many species (Hanyu, 1959b).

Fig. 4. The typical, membranous falciform process of Salmo salar. Although it is well pigmented, the included vessels, especially the thicker ones are easily seen.
CG, choroidal gland; CH, choroid; DA, "dorsaler Anhang"; IR, iris; LM, lens muscle, MV, main vessel; ON, optic nerve; PL, pigment layer of retina; RE, retina; SC, sclera.

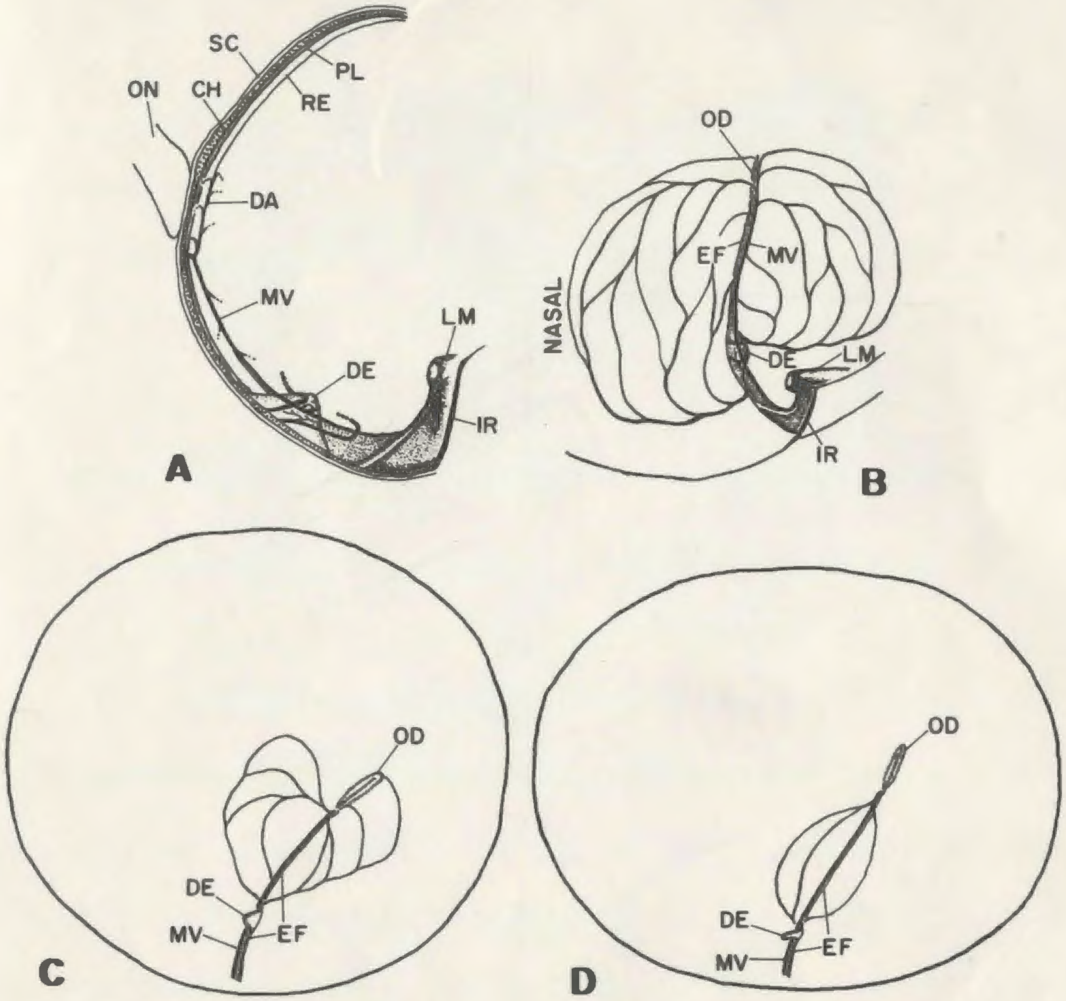

SC
CH
CG
ON
PL
RE
DA
LM
MV
IR

But, if this membranous falciform process is carefully observed from the standpoint of vascularization, it turns out to have a vascular pattern that corresponds to that, for example, in Gadus callarias (Fig. 2). Although pigmentation prevents the tracing of fine vessels, it is recognized without much difficulty that the main vessel passes along the dorsal edge of the process to supply the lens muscle and the branches from the main vessel further divide spreading throughout the falciform process including "Dorsaler Anhang". Thus, this typical falciform process should be regarded as an instance where the vascularization along the embryonic fissure rises remarkably into the vitreous cavity, being accompanied by pigmentation and some connective tissue of supposedly choroidal origin.

Because of the heavy pigmentation, the blood vessels in the falciform process were not recognized as such during ophthalmoscopy. Rather, the falciform process presented itself as a distinct, dark-red coloured ridge on the bluish fundus, indicating its high degree of vascularization.

Fig. 5. Examples of the low falciform process with branches on the retina, in front view of the eye except A which shows a section. A & B, Myoxocephalus octodecemspinosus; C, Cyclopterus lumpus; D, Sebastes marinus. The branches on the retina go distally into the embryonic fissure (EF) near "Dreiecke" (DE), not rejoining the main vessel (MV).

CH, choroid; DA, "dorsaler Anhang"; DE, Dreiecke"; EF, embryonic fissure; IR, iris; LM, lens muscle; MV, main vessel; OD, optic disc; ON, optic nerve; PL, pigment layer of retina; RE, retina; SC, sclera.


SC
PL
ON
CH
RE
DA
MV
LM
DE
IR
A
OD
EF
MV
NASAL
DE
LM
IR
B
OD
DE
MV
EF
C
OD
DE
EF
MV
D

The lens muscle is also well developed and pigmented and is firmly connected to both the iris and the distal part of the falciform process. The nerve for the lens muscle is seen to proceed through the distal part of the falciform process from within the embryonic fissure (Fig. 4).

c. The low falciform process with branches on the retina.

In contrast to the above mentioned vascularization into the vitreous cavity, there is another mode of vascularization in which branches of the hyaloid artery are sent off onto the retina, or more precisely, onto a delicate transparent membrane called "Glaskörperhaut (Chrustschoff, 1926; Jokl, 1927) which composes the vitreo-retinal boundary.

An instance of the low falciform process with such branches on the retina is seen in Myoxocephalus octodecemspinosus (Cottidae). In this species (Fig. 5-A,-B), several relatively thick branches arising from the "Dorsaler Anhang" as well as from the main vessel pass onto the retina, undergoing dichotomy and anastomosis, and make up a wide meshed network covering a considerable part of the retinal surface both nasal and temporal to the embryonic fissure. They finally congregate into a few thicker vessels which enter the fissure in the vicinity of "Dreiecke", thus not rejoining the main vessel. Although very few branches, if present, are sent directly into the embryonic fissure, there is also a membranous part along the fissure distal to "Dreiecke", showing a situation similar to that in Argentina, an instance of the low falciform process type. The blood flow was confirmed ophthalmoscopically to be in the main vessel to branches direction.

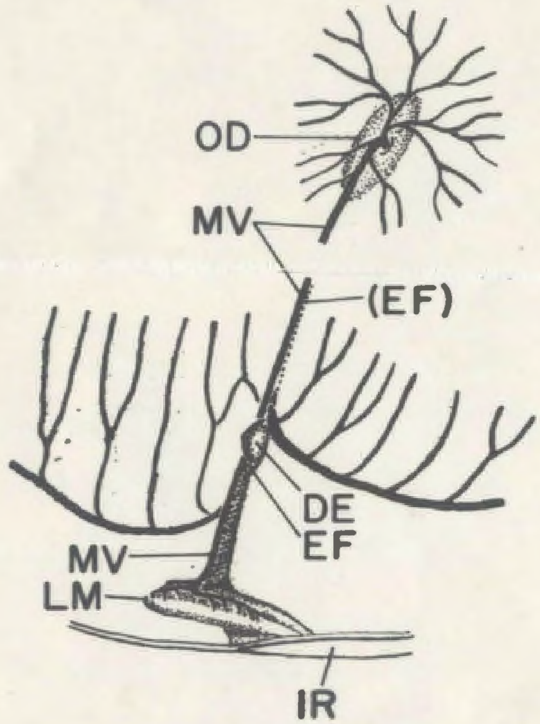
A related species, Myoxocephalus scorpius exhibits much the same vascular situation, while, as seen in Fig. 5-C,-D, Sebastes marinus (Scorpaenidae), Cyclopterus lumpus and Anarhichas lupus present far simpler cases of vascularization on the retina, suggesting a wide interspecific variation. In Anarhichas, the main vessel also sends fine branches directly into the embryonic fissure as in Gadus, and therefore proceeds along the ridge of the low falciform process to supply the lens muscle, which is rather developed and receives a prominent nerve.

d. Vitreal vessels.

Instances of so called vitreal vessels or vascular network spreading over the retina were seen in the following species; *Apeltes quadracus* (Gasterosteidae), *Lycodes reticulatus* (Zoarcidae), *Tautogolabrus adspersus* (Labridae), *Pseudopleuronectes americanus* and *Glyptocephalus cynoglossus* (Pleuronectidae), *Liparis liparis* and *Neoliparis atlanticus* (Liparidae), *Opsanus tau* (Batrachoididae). It should first be mentioned that all these instances except those in Liparids can be understood to have the above mentioned branches from the main vessel developed extensively and densely over the retina. There is, however, diversity in connection with the extent of vascularization and with the remaining embryonic fissure, as well.

In *Pseudopleuronectes* and *Glyptocephalus*, the embryonic fissure persists for its entire length and the main vessel supplying the lens muscle is clearly present, just as in the above mentioned types of falciform process. The branches from the main vessel, though denser, occupy only as much area on the retina as those in *Myoxocephalus*, an example in the previous section, do.

Fig. 6. The vitreal vessels of Tautogolabrus adspersus. Vascularization near the optic disc (OD) and the lens muscle (LM) are shown exclusively. The branches over the retina join to become two thicker ones which finally go into the embryonic fissure (EF) near "Dreiecke" (DE). The closing of the embryonic fissure, commencing from under the optic disc (OD) seems to have extended as far as "Dreiecke" (DE). IR, iris; MV, main vessel.


OD
MV
(EF)
DE
EF
MV
LM
IR

In Tautogolabrus (Fig. 6), the radially arranged branches cover a fairly large area on the retina, and then join two peripheral vessels which run a little apart from the ora terminalis. These vessels get much thicker along their courses and eventually enter the embryonic fissure near "Dreiecke". The blood flow in the main vessel and the branches was confirmed ophthalmoscopically in the coincident direction.

In Lycodes (Fig. 7), some of the branches are very thin and anastomosis is prevalent, in addition to the more marked peripheral vessels than those in Tautogolabrus, and the barely perceptible main vessel supplying the less developed lens muscle. The thinnest branches may be called capillaries.

In Apeltes, all the branches, after covering the whole surface of the retina, join into a single peripheral annular vessel which proceeds along the ora terminalis in a complete circle and go out through the distal end of the embryonic fissure.

In Opsanus, in which very dense radial branches are present, the annular vessel is situated even beyond the ora terminalis, in other words, on the iris, and has its exit adjacent to the ventral margin of the base

Fig. 7. The vitreal vessels of Lycodes reticulatus, shown only along the embryonic fissure (EF). All branches over the retina congregate into a few thicker vessels which go into the embryonic fissure. The embryonic fissure remains open for its entire length. DE, "Dreiecke"; EF, embryonic fissure; IR, iris; LM, lens muscle; MV, main vessel; OD, optic disc.


OD
EF
DE
MV
IR
LM

of the underdeveloped lens muscle, as shown in Fig. 8. There is no vessel corresponding to the main vessel which regularly proceeds from the optic disc to the lens muscle, although a vessel* probably the vein from the lens muscle was seen to join the annular vessel in the vicinity.

In Tautogolabrus, the embryonic fissure is present only distally to the "Dreiecke" and seems to have closed as far as "Dreiecke", leaving a trace of its closing (Fig. 6). A histological study will have to be undertaken to confirm this. Concerning this particular species, Virchow (1882b) pointed out that both the entry and the exit of the vitreal vessels are within the embryonic fissure and this situation represents a transition between his basic types of vitreal vessels. But, as described above, the artery enters obviously at the optic disc, not through the embryonic fissure left open distally. In Opsanus, the embryonic fissure is totally lacking and there is no vestige of it on the retina any longer.

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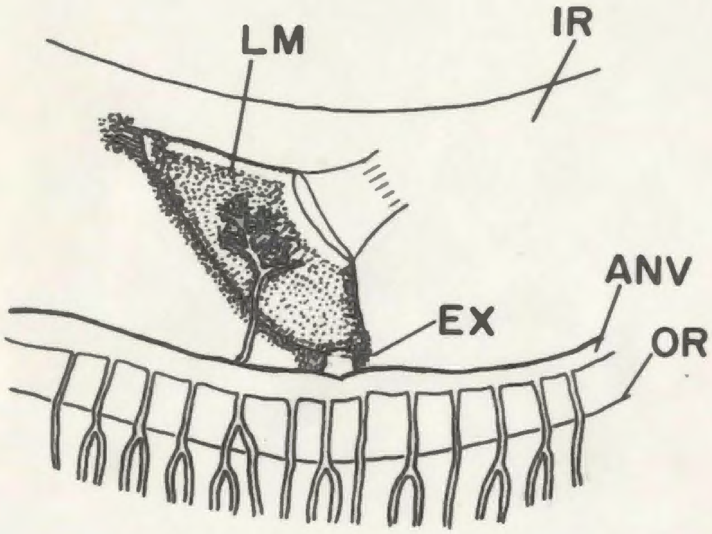
* A similar vessel was identified as the vein, in Periophthalmus (Karsten, 1923) and in Acanthogobius (Hanyu, 1959b).

Fig. 8. The vitreal vessels near the lens muscle in Opsanus tau, viewed from the fundus. The annular vessel (ANV), collecting the branches on the retina, has its exit (EX) adjacent to the lower margin of the under-developed lens muscle (LM) attached to the iris (IR). OR, ora terminalis.


LM
IR
ANV
EX
OR

e. Special instances of vitreal vessels in Liparidae.

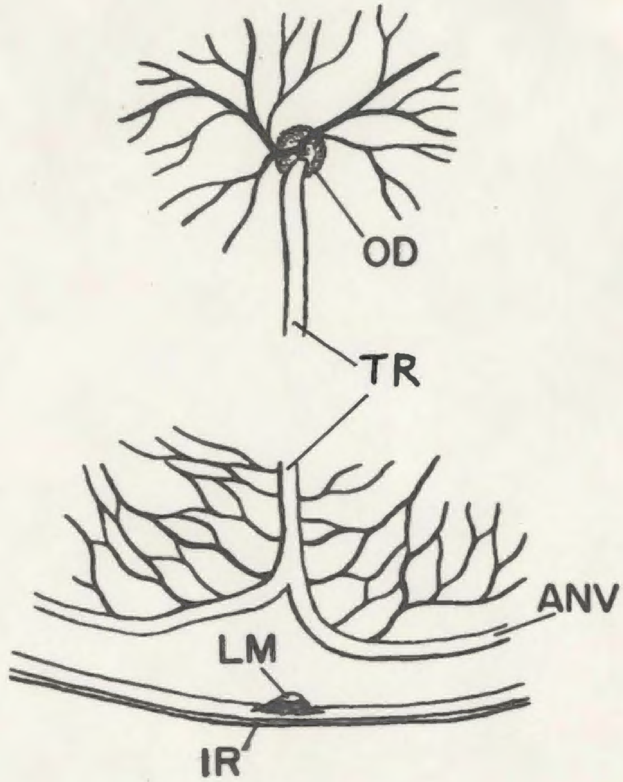
In both of the two Liparids examined, special modes of vascularization were found.

In *Liparis liparis*, the system of vitreal vessels is unique in that the peripheral annular vessel does not go out through the ventral ora or adjacent part, as is the case in the ordinary type of vitreal vessels described above. As Fig. 9 shows, the nasal and the temporal arms of the annular vessel meet near the ventral ora and pass into a single trunk, which proceeds dorsally to the optic disc and leaves there outwards.

In the vitreal vessels of *Neoliparis atlanticus*, however, there is neither an annular vessel nor an outstanding trunk such as those seen in *Liparis*. The branches over the retina, being so fine as to be called capillaries, gather into a few, somewhat thicker branches which converge radially to the optic disc, the venous exit as well as the arterial entrance.

In both instances, the lens muscle is only rudimentary and no branch is sent to them from the vitreal vessels on the retina. Nor is there any trace of the embryonic fissure.

Fig. 9. A special type of vitreal vessels in *Liparis liparis*. The annular vessel (ANV) passes on a conspicuous trunk (TR) running dorsally to the optic disc (OD), through which it goes out. The lens muscle (LM) is not supplied by the vessels on the retina and is vestigeal.
IR, iris.


OD
TR
ANV
LM
IR

f. Other unusual instances.

In Lophius americanus (Lophiidae), the situation is quite simple (Fig. 10). Only one vessel runs on the retina from the optic disc to the poorly developed lens muscle. There is no trace of the embryonic fissure on the retina.

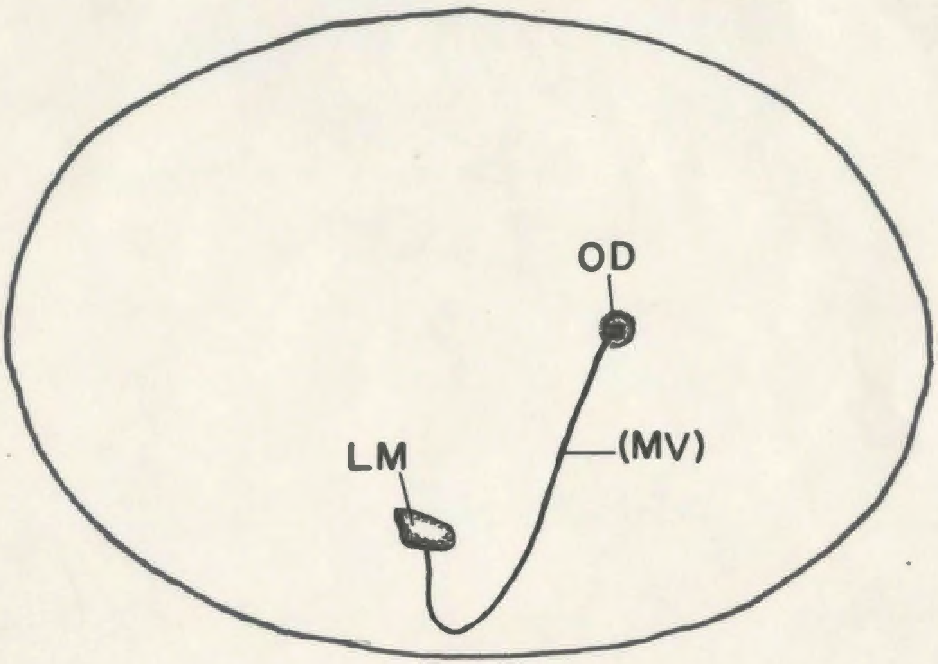
In Macrourus bairdii (Macrouridae), no intraocular vessels are found either on the retina or in the vitreous cavity. There is also no trace of the embryonic fissure. Thus, the fundus is completely free from any of the structures mentioned above. The lens muscle is very vestigeal, being small, white patch on the iris.

2. Holostei

The two representatives of Holostei, Lepisosteus osseus (Lepisosteidae) and Amia calva (Amiidae) were confirmed to have another special system of vitreal vessels which had been mentioned by Virchow (1882b).

In Lepisosteus, as shown in Fig. 11-A,-B, the hyaloid artery, instead of emerging in the fundus, appears at the medial end of the insertion of the lens muscle which is connected not only with the iris but

Fig. 10. An unusual instance in Lophius americanus. Only a vessel or the main vessel (MV) runs from the optic disc (OD) to the poorly developed lens muscle (LM).

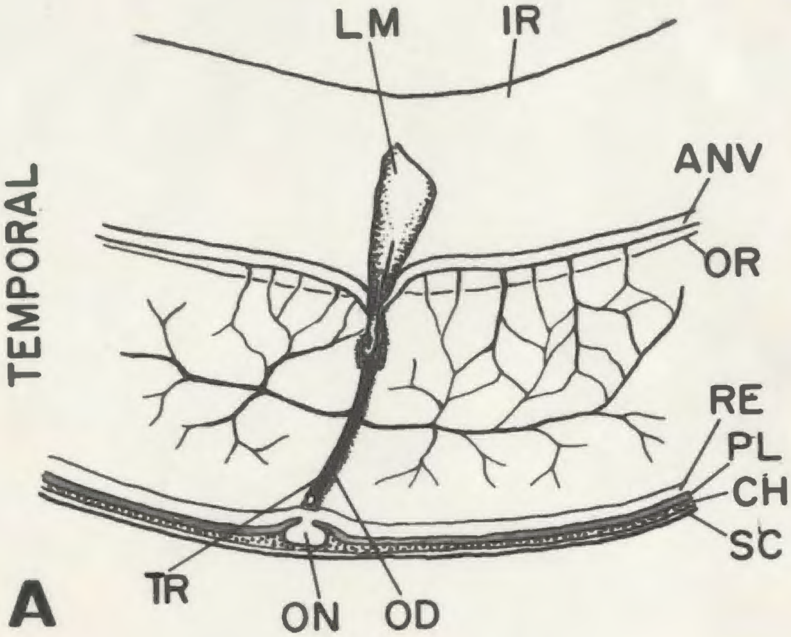

OD
(MV)
LM

also with the distally restricted embryonic fissure. The artery, proceeding dorso-temporally, gives off branches which make up a network over the retina and finally congregate into an annular vessel or vein along the ora terminalis. The annular vessel has its exit close to the entry of the hyaloid artery (Fig. 11-B). A thin branch is seen to be given to the somewhat developed lens muscle from the artery upon its entry.

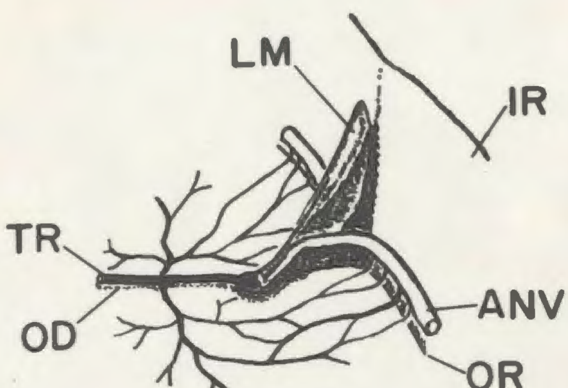
It should also be pointed out that the artery proceeds on a fairly distinct streak on the retina which, on the examination of a section, proves to be an extraordinarily elongated optic disc, naturally following the course of the embryonic fissure which has already closed (Fig. 11-A). If the retina is removed from this region, the optic disc or nerve head is left filled in a narrow choroidal cleft, which tapers toward the medial end of the base of the lens muscle. This cleft or elongated optic disc is more distinct, when observed in transmitted light.

In <u>Amia</u>, the situation is quite similar, except that the lens muscle is rather plump and well pigmented.

Fig. 11. The vitreal vessels near the lens muscle in Lepisosteus osseus. A, viewed from the fundus; B, viewed nasally. The entry of the hyaloid artery (TR) is, like the exit of the annular vessel (ANV), at the medial end of the lens muscle (LM) insertion. The arterial trunk (TR) is also noticed to proceed along the extraordinarily elongated optic disc (OD).
ANV, annular vessel; CH, choroid; IR, iris; LM, lens muscle; OD, optic disc; ON, optic nerve; OR, ora terminalis; PL, pigment layer of retina; RE, retina; SC, sclera; TR, trunk of hyaloid artery.



A



B

C. CLASS AMPHIBIA

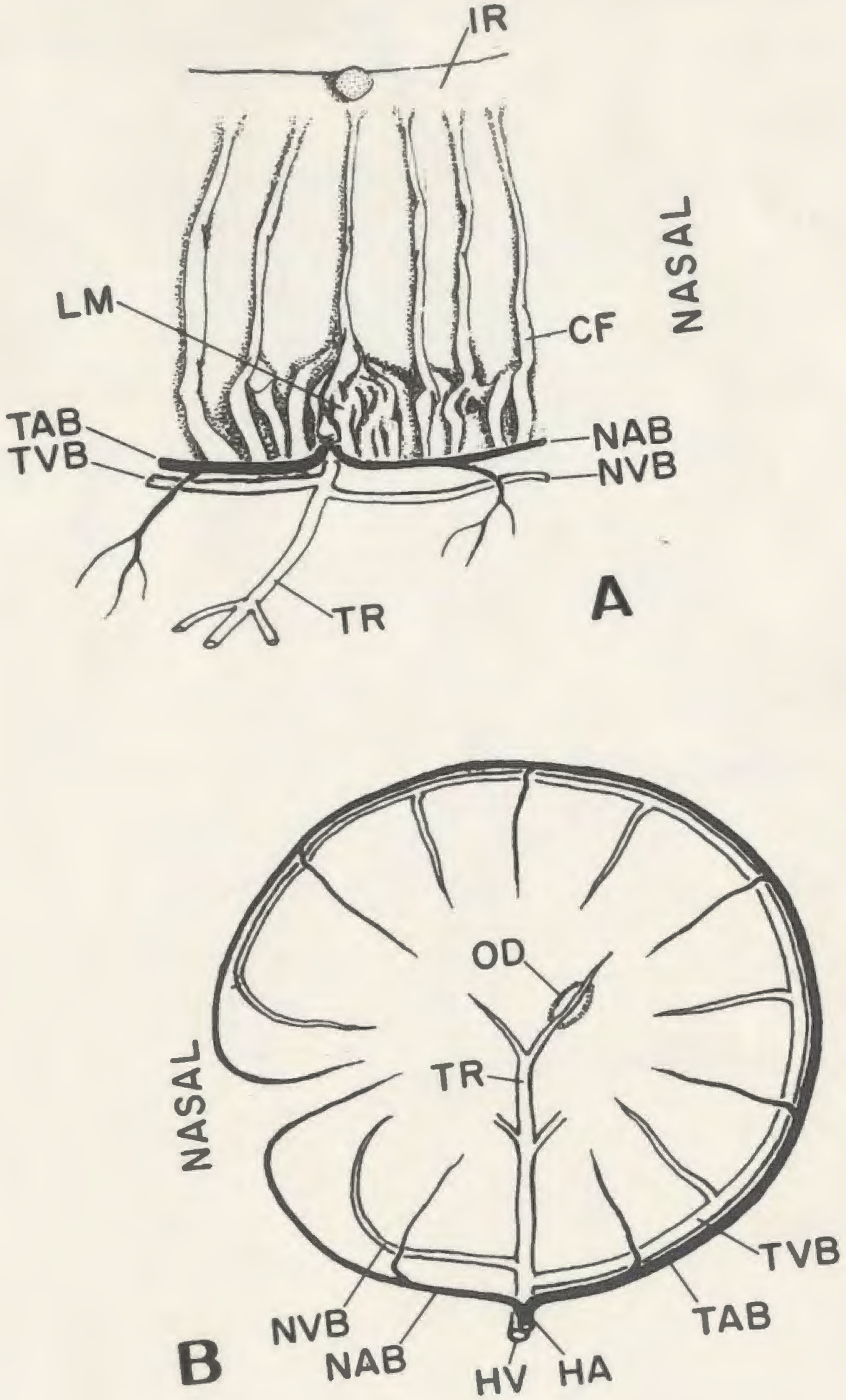
1. Order Anura

Both of the two species, *Bufo americanus* (Bufonidae) and *Rana pipiens* (Ranidae) were confirmed to have essentially the same system of vitreal vessels as has been described by earlier workers (Virchow 1901, Tretjakoff 1906, Michaelson 1954).

In *Bufo*, the hyaloid artery, a terminal portion of the ophthalmic artery, is divided into two main branches, which appear at the ventral margin of the lens muscle located at the ventral ora and then take their courses along the ora terminalis in the opposite directions, i.e. nasally and temporally (Fig. 12-A). The temporal, thicker one passes at first temporally, upward and finally reaches the nasal side, thus occupying about three quarters of the circle along the ora terminalis. The nasal one runs for the remainder of the circle but falls a little short of making a direct connection with the temporal main branches, failing to complete a peripheral annular vessel (Fig. 12-B). In more or less equal intervals, along those main branches several vertical branches are given onto the fundus and further divide dichotomously, resulting in a capillary network over the retina.

Fig. 12. The system of vitreal vessels in <u>Bufo</u> <u>americanus</u>. Small branches are omitted. A, the ventral portion viewed from the fundus. Both the arterial entry and the venous exit are located on the ventral margin of the lens muscle (LM), which is apparently a small projection of ciliary folds (CF) adjacent to the ventral ora hidden under the main arterial branches, nasal (NAB) and temporal (TAB). B, front view. The two arterial branches (NAB and TAB) are almost parallel to the two main venous branches, nasal (NVB) and temporal (TVB), respectively. The trunk (TR) of the hyaloid vein (HV) begins near the optic disc (OD).

CF, ciliary fold; HA, hyaloid artery; HV, hyaloid vein; IR, iris; LM, lens muscle; NAB, nasal arterial branch; NVB, nasal venous branch; OD, optic disc; TR, trunk of hyaloid vein; TAB, temporal arterial branch; TVB, temporal venous branch



IR
NASAL
LM
CF
TAB
TVB
NAB
NVB
TR
A
OD
NASAL
TR
TVB
TAB
NVB
NAB
HV
HA
B

Proceeding a little inward and almost parallel to the arterial main branches, there are two main venous branches, which also give several vertical branches toward the fundus to collect the capillaries there. In the neighbourhood of the optic disc, which is slightly temporal to the centre of the fundus, a conspicuous vessel, the venous trunk, begins to gain in its thickness. It runs ventrally, receiving both branches and capillaries, to the ventral ora and has its exit very close to the above mentioned entrance of the hyaloid artery (Fig. 12-A). The two main venous branches, nasal and temporal, join the trunk a little in front of the exit and give rise to the hyaloid vein. Ophthalmoscopically the blood flow along the vessels on the fundus was easily recognized.

The system of vitreal vessels lies in a membrane which is easily separated from the retina in preserved specimens. At the several arterio-venous crossings, the arterial branches are always over the venous ones.

The hyaloid artery is proximally a branch of the ophthalmic artery which is traced along the ventro-temporal meridian of the sclera. Along with the ophthalmic artery, fine nerves are seen to proceed to innervate the cilio-iris region, which is rather developed. The lens muscle is found near the ventral ora where a part of a ciliary fold is swollen into a small elevation (Fig. 12-A). Adjacent to the ventral border of the lens muscle are located the exit and the entry of the vitreal vessels.

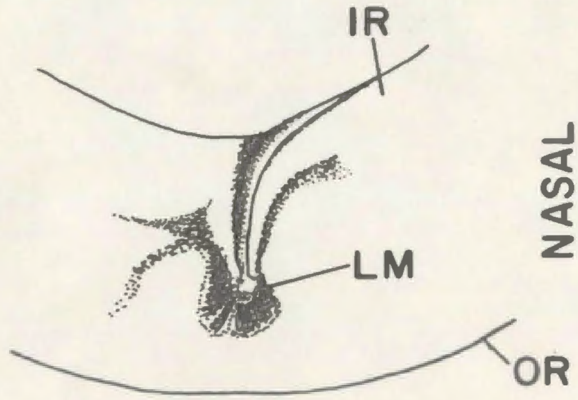
In Rana, the system of vitreal vessels is almost the same as in Bufo. To mention a minor difference, the venous trunk takes on a 'Y' shape more clearly. The ciliary folds are more numerous and better developed than in Bufo.

2. Order Urodela

In Necturus maculosus (Proteidae), no vessel was found in the vitreous cavity or on the retina. As in the case of Axolotl described by Virchow (1901), the ophthalmic artery is seen to proceed along the ventro-temporal meridian of the choroid to the most ventral part of the iris. Near this part, a poorly developed lens muscle is found as a very small swelling on the iris. From the apex of the lens muscle a narrow ridge passes dorsally to the pupillary margin, probably indicating the closed line of the embryonic fissure. (Fig. 13). Ciliary folds are indistinct.

Fig. 13. The lens muscle of Necturus maculosus, viewed from the fundus. The lens muscle (LM) is a very small swelling on the iris without ciliary folds and is accompanied by a low ridge proceeding dorsally.

IR, iris; OR, ora terminalis.


IR
LM
OR
NASAL

DISCUSSION

It is reasonable to assume that all the intraocular blood vessels described above, occurring either in the vitreous cavity or on the retina, originate from the embryonic vascular loop which emerges through the embryonic fissure (Virchow, 1901; de Waele, 1902; Jokl, 1927; Franz, 1934). The falciform process of some of the Teleosts and the various instances of vitreal vessels as seen in both fishes and Anurans are considered to be of the same origin. Further, Nelsen (1953) suggested that intraocular vascularized structures in the Amniotes, such as the papillary cone of lizards and the pecten of birds may also be homologous with the falciform process of fishes.

However, the variation of the intraocular vascularization in the definitive stage is far greater in Class Osteichthyes than in any other class of vertebrates. Teleosts and Holosteans in north-eastern America, represented by the species examined in this investigation, also show considerable variation ranging from the typical falciform process to the so called vitreal vessels. They include some other unusual instances as well. In dealing with these various instances as a whole, it would be of prime importance to ascertain as to how successfully they have been classified. If all or some of them should be classified improperly, no consistent understanding concerning their interrelationship in terms of both morphological and functional differentiation could be expected. With this in mind, the author prefers to dwell upon the classification of intraocular blood vessels in Osteichthyes, especially in Subclass Neopterygii, which embraces the bulk of bony fishes.

According to Virchow (1901), the falciform process, which is defined as a plate of connective tissue projecting along the embryonic fissure, has four basic types (Grundformen). These four are, 1) the very low falciform process as seen in most Acanthopterygii, 2) the distally high falciform process as seen in Salmonidae, Esox and herring, 3) the proximally high falciform process as seen in Thynnus and Auxis, 4) the very short and distally present falciform process in Cyprinidae and Hippocampus. This method of distinction, though it is the only one that has ever been repeatedly cited in literature (Franz, 1934; Walls, 1942; Tamura, 1957b), seems to be unsatisfactory. It neglects the indispensable constituent, viz. vascularization, in the falciform process and does not demonstrate any necessary relationship among these types.

Since the most important constituents of the falciform process are the blood vessels arising from the hyaloid artery which enters the vitreous cavity through the persisting embryonic fissure, the extent of vascularization should first be taken into account in classifying the various instances of falciform process. In many Acanthopterygians or spiny-finned Teleosts, the vascularization confines itself almost within the embryonic fissure, not extending conspicuously into the vitreous cavity, as typically seen in *Gadus callarias*. This less developed or low falciform process type corresponds to the very low type in Virchow's distinction.

More advanced in vascularization than this frequently occurring low falciform process type are the instances in which various degrees of vascular development into the vitreous cavity are encountered. These instances are also often accompanied by pigmentation and connective tissue (Hanyu, 1959a). Among these are;

1) a somewhat high but simple vascular net as in Lateolabrax japonicus (Serranidae) and Scomber tapeinocephalus (Scombridae); 2) a higher, pigmented membranous process as in Zenopsis nebulosa (Zeidae), Salmo salar and Oncorhynchus rhodurus (Salmonidae); 3) an unpigmented, well developed vascular net as in Sphyraena picuda (Sphyraenidae); 4) a large, pigmented vascular net as commonly seen in Scombridae and Priacanthidae ; and 5) a highly pigmented, sickle-shaped membrane as seen in Histiophoridae and Coryphaenidae. For the sake of simplification, however, all of them should be grouped into one category, the higher falciform process type or, at most, two categories, the higher and the highest types, rather than the 2nd and the 3rd types of Virchow (1901) which are represented by Salmonidae and Scombridae, respectively. His method of distinction, distally high or proximally high, would not be quite valid from the point of view of vascularization.

The disadvantage of Virchow's viewpoint which regards the falciform process as a structure of connective tissue is reflected in his 4th type very well. An example of this type, as seen in most Cyprinids, is actually a small membranous part connecting the lens muscle to the ventral retino-iris angle, rather than a distally restricted vascular structure originating from the hyaloid artery (Hanyu, 1959a). Similarly as has been illustrated above in Argentina (Fig. 3), Myoxocephalus (Fig. 5), Tautogolabrus (Fig. 6), Lycodes (Fig. 7) and Lepisosteus (Fig. 11), there is a tendency for a well pigmented membrane to be formed along the most distal part of the embryonic fissure so that it enables the main vessel above to reach the lens muscle and also connects the latter to the retino-iris angle. This membranous part may serve as a support to the lens muscle which is responsible for the accommodative movement of the crystalline lens. But, this part alone would not deserve the term falciform process any longer, if it should be separated from the rest of vascularization. The same criticism may also be applied to Franz's statement that in some species the length of the falciform process is reduced by the partial closing of the embryonic fissure (Franz, 1934).

Besides, no instance in which the falciform process as a vascular structure is restricted by the partial closing of the embryonic fissure has been met with, so far. It seems that in Osteichthyes, the closing of the embryonic fissure does not displace the entry of the hyaloid artery distally. Rather, it simply prevents the main vessel from communicating with the choroid through the fissure. In _Tautogolabrus adspersus_, for example, although the embryonic fissure appears to have closed between the optic disc and "Dreiecke", the arterial entry is still at the optic disc and from here the main vessel proceeds along the entire original course of the embryonic fissure to the lens muscle.

Between the vascularization of the falciform process types discussed above and the so called vitreal vessels covering the inner surface of the retina, there is an intermediate state wherein a low falciform process with branches on the retina is present. This state is not a clear, well demarcated state but is one where considerable degree of transition is observed. In some instances, there are only a few branches running on the retina in addition to a more or less definite part corresponding to the low falciform process. In others, however, the part corresponding to the falciform process is less marked, while the branches on the retina are much more advanced in their distribution, thus warranting the term vitreal vessels. Based on the examination of many species in an earlier investigation (Hanyu, 1959a), the author suggested the presence of this intermediate state or the low falciform process with branches on the retina. The evidence obtained in the present investigation supports this view. It should be stressed that this explanation of the relationship between the falciform process and the vitreal vessels is quite different from the prevalent view (Franz, 1934; Walls, 1942) which assumes that the vitreal vessels may develop when the falciform process becomes restricted distally by the closing of the embryonic fissure.

In the instances of the vitreal vessels or densely developed branches over the retina, the most peripheral branches collecting other smaller branches tend to get thicker (as in Tautogolabrus and Lycodes), until eventually forming a peripheral annular vessel running along or in the neighbourhood of the ora terminalis (as in Opsanus). The annular vessel receives all branches over the retina except the main vessel and goes out at the base of the lens muscle or the ventral ora. There is also evidence to believe that the embryonic fissure is closed partially (as in Tautogolabrus) or totally (as in Opsanus), and the main vessel becomes obliterated (as in Opsanus). Obviously, this line of vascular differentiation results in the "carp type" vitreal vessels of Virchow (1882b), in which the artery enters the eye at the optic disc and sends off branches over the retina, while the vein lying along the ora terminalis goes out downwards.

Both the Holosteans, Lepisosteus and Amia, turned out to have the same situation as that described by Virchow (1882b) in his "bony Ganoid and catfish type" vitreal vessels, which is different from the "carp type" only in that the arterial entry is at the ventral ora, therefore adjacent to the exit of the vein, as seen also in Polypterus, Calamoichthys, Malapterurus and Amiurus. However, it must be suggested that this peculiar entry of the hyaloid artery seems to be associated with a certain deformity in the optic disc. As has been pointed out (Fig. 11), in Lepisosteus there is an extraordinarily elongated optic disc which proceeds ventrally to the medial end of the lens muscle insertion, at which point the artery enters. In Plotosus anguillaris (Plotosidae) and Misgurnus anguillicaudatus (Cyprinidae) which show a similar peculiarity, the optic disc is not single but multiple, consisting of several dotted spots arranged on the line of the closed embryonic fissure (Hanyu, 1959a). Similar dotted optic discs are known to be present in the species examined by Virchow (1882b); Polypterus (Studnicka, 1897) and Calamoichthys, both being Cladistans; Amiurus (Deyl, 1896) and probably Malapterurus, both belonging to Siluridae. It is quite possible that these ventralward deformities in the optic disc have caused the distal entry of the hyaloid artery, which would otherwise enter proximally near the centre of the fundus. Under the circumstances, the "catfish type" should be regarded as a deviation from the common "carp type", rather than as an independent basic type of vitreal vessels.

Special instances of vitreal vessels in Liparidae are quite similar to Virchow's (1882b) "eel type" in that the branches over the retina have their exit through the optic disc, not at the ventral ora. In Neoliparis, fine branches over the retina, being capillary size, gather into a few thicker venous branches which make their exit through the optic disc, while in Liparis there is a peripheral annular vessel resembling that in the "carp type" but having a trunk which unites the nasal and ventral arms of the annular vessel ventrally and leads to the optic disc (Fig. 9). In Crystallias matsushimae, another Liparid, the vitreous body is also vascularized (Hanyu, 1959a). Thus, among species belonging to this particular family, there would be a special variety of vascularization which should be studied further. In the eel like fishes, Apodes, intra-retinal capillaries are also found (Vrichow1882a, Michaelson 1954, Hanyu 1959a).

With the available information, these special instances of the "eel type" vitreal vessels cannot be definitely related to any ordinary instances mentioned above. An interesting observation is that the total closing of the embryonic fissure is always associated with the presence of the "eel type" vitreal vessels. A possible interpretation is that the closing of the fissure might have restricted the exit of the embryonic intraocular blood vessels proximally, instead of distally as, for example, in the "carp type".

Other unusual instances which are found occasionally in some families and species can usually be understood as being deviations from the proposed types of the falciform process and the vitreal vessels. The deviations are ascribed to either partial vascular development or vascular degeneration, always accompanied by the closing of the embryonic fissure (Hanyu, 1959a). Here, in *Lophius americanus*, only the main vessel is considered to be remaining from an instance of the low falciform process after the total closing of the embryonic fissure (Figs. 2 and 10), while in *Macrourus bairdii*, the vessel itself is lost. This avascular instance in *Macrourus* is one of the few exceptions in Neopterygii.

In order to establish the interrelationship decisively, it is essential both to follow the intraocular vessels outwards through the choroid and to trace the vascular development in the embryonic stages.

In addition to the discussion concerning the classification, it should be recalled that in the majority of Teleosts the intraocular vascularization is given its position somewhere along the series of types ranging from the higher falciform process, through the low falciform process and the low falciform process with branches on the retina, to the vitreal vessels (including the "carp type" and the "catfish type" of Virchow). Generally speaking, the vitreal vessels are found more often in primitive Teleosts such as Isospondyli and its derivatives than in higher Teleosts such as Percomorphi and groups related to it (Hanyu, 1960). In Holosteans or the most primitive Teleosts, only the vitreal vessels are encountered. In this connection, it is interesting to note that in Salmo trutta (von Kittlitz, 1907) and Salmo irideus (Hanyu, 1961), the falciform process is preceded by a transient intraocular vascular net quite similar to the vitreal vessels, while in Channa argus (Hanyu, 1961) there occurs no vascular degeneration throughout the development of the "carp type" vitreal vessels in the definitive stage. These facts suggest that the vitreal vessels may represent a more primitive stage of intra-ocular vascularization in Subclass Neopterygii.

In not many fishes belonging to the other sub-classes of Osteichthyes, or Palaeopterygii and Choanichthyes, the situations appear to be much simpler, although no information is available concerning some of them. In Palaeopterygii, Cladistans such as Polypterus and Calamoichthys (Virchow, 1882b) have a system of vitreal vessels of so called "catfish type", while a Chondrostean, Acipenser (Virchow, 1882b) altogether lacks intraocular vessels. In Choanoichthyes, two

Dipnoans show different instances. Ceratodus (Virchow, 1882b) has an avascular situation, while Protopterus (Hosch, 1904) possesses vitreal vessels with arterial entry at the optic disc. As for Crossopterygii, no information is available at present. Thus, the avascular instance is rather common in these groups of bony fishes, which are considered to have been conservative in the evolutionary process of ichthyization which gave rise to the flourishing group, Neopterygii (Matsubara, 1955).

During the observation of various instances of intraocular vascularization, attention was naturally drawn to the diversity of the associated structure, the lens muscle, or campanula Halleri. The lens muscle is originally formed by an inward growth of a part of the ventral rim of the eye cup, where the embryonic fissure becomes fused a bit (Nussbaum, 1901). In adult fishes, the lens muscle is believed to pull the crystalline lens backwards for accommodation, therefore is also called the retractor lentis muscle. According to Franz (1934), the lens muscle is rudimentary or lacking in fishes belonging to groups other than Neopterygii. Walls (1942) also doubted the ability of these fishes for active accommodation. In some Teleosts, accommodation has actually been measured (Beer, 1894; Tamura, 1957a). In Neopterygii, as has been described, the lens muscle usually receives a particular branch of the hyaloid artery which is the main vessel. A large muscle (relative to the eye) is always supplied by a prominent main vessel, as seen in the case of the higher falciform process type and some other instances. It is possible that the thick main vessel with many fine branches communicating with the choroid, or with many effective bypasses of the blood flow, is most efficient in nourishing the strong, contractile lens muscle. On the other hand, wherever the main vessel is obliterated or missing, as commonly seen in instances of vitreal vessels and other unusual instances, only a poorly developed lens muscle is present. Consequently it would follow that the intraocular vascularization in Neopterygii has been significantly affected by the development of the accommodative lens muscle, in other words, by the development of the accommodative ability which is a characteristic event during the course of ichthyization, possibly in such a way that a well developed lens muscle requires the falciform process type vascularization.

In Class Chondrichthyes, the situation is very simple and uniform, but quite different from that in Osteichthyes. In adult stage, as observed in four species from both the orders, Selachii and Batoidei, there are no vessels either in the vitreous cavity or on the retina. The same situation is known in Chimaera of Holocephali (Virchow, 1882b). de Waele (1902) demonstrated how this avascularity is brought about in the embryo of Mustelus. In Mustelus, as the embryonic fissure closes in the proximal to distal direction, the embryonic vascular loop along the fissure becomes restricted distally, eventually leaving no branches inside. Franz (1934) believes that the afferent limb of the vascular loop is represented by the iris artery running along the ventral meridian of the choroid in the adult fish. From the iris artery which supplies the iris, as confirmed in Squalus, a small branch is also sent to the lens muscle papilla originally formed by the fusion of the distal part of the embryonic fissure.

According to Franz (1931), the lens muscle papilla, though small, is responsible for accommodation to a small extent in the Elasmobranchs by serving as the protractor lentis muscle which pulls the lens forwards. But this function of the lens muscle papilla was doubted by Rochon-Duvigneaud (1943). Along with the less developed lens muscle papilla, it is worthwhile noticing that the ciliary folds tend to develop in the Elasmobranchs, while they are not found in the Neopterygians.

In the two subclasses of Amphibia examined it was observed that the Anuran eye has a well developed system of vitreal vessels while the vitreous cavity of the Urodelean eye is completely avascular. These observations on the north American species correspond to the descriptions given by Virchow (1901), Tretjakoff (1906) and Michaelson (1954) mainly in the case of European species.

The system of vitreal vessels in Anura is different from the common "carp type" vitreal vessels of fishes in that the artery enters at the ventral ora, divides into two main branches running along the ora, and the venous trunk proceeds from the fundus near the optic disc to the exit at the ventral ora. This kind of vascular system has never been found in fishes. The arterial entry is determined when the embryonic vascular loop becomes restricted distally by the closing of the embryonic fissure (de Waele, 1902). This process of restriction is somewhat similar to that in Mustelus (de Waele, 1902), an Elasmobranch, except for the subsequent development of vascularization in Anura which gives rise to the vitreal vessels.

Franz (1934) pointed out the similarity between Amphibia and Crossopterygians such as _Polypterus_ and _Calamoichthys_ in the entry and the exit of the vitreal vessels and considered it to be an evidence for the Crossopterygian origin of the Amphibians. However, there are two weak points in this opinion. One is that _Polypterus_ and _Calamoichthys_ are grouped into Cladista, a group considerably different from Crossopterygii which consists of only the true lobe-fins. It is generally agreed at present that the Crossopterygii were the ancesters of Amphibia. The other is that in these fishes, as discussed above, the arterial entry at the ventral ora is rather associated with the particular, ventralward deformity of the optic disc, than caused by the closing of the embryonic fissure. In this respect, a living Crossopterygian or a Coelacanth such as _Latimeria_ should be examined before any assertions can be made. Until then, the author would like to look upon this system of vitreal vessels as a unique formation found only in Amphibia.

The lens muscle of Amphibia, or protractor lentis muscle is said to be of mesodermal origin (Franz, 1934; Rochon-Duvigneaud, 1943), unlike that of fishes where it is of ectodermal origin. As described in both Bufo and Necturus, it is a small elevation at the ventral ciliary region. It appears to be supplied by a small branch of the terminal portion of the ophthalmic artery, although this could not be confirmed due to the small size of the lens muscle. It would appear reasonable to assume that the development of the lens muscle has no significant effect on the intraocular vascularization in Amphibia, unlike in Osteichthyes.

There would be no doubt about that the intraocular blood vessels emerging through the embryonic fissure, which may either be temporary or persisting, do supply the neighbouring parts of the eye cup in the embryonic stages. In these stages, they would certainly contribute to the growth of the lens, the production of the vitreous humor and the proliferation of the retinal layer. Subsequently, however, the intraocular vessels are bound for a number of destinations, depending upon the group of vertebrates, as has been partly described before. This raises a number of questions; Why does the morphological diversity come into being? What are the functional differences in the definitive stage as long as the vessels persist as marked structures?

In this regard, only a few interpretations are available in the literature concerning the Anamniotes. Virchow (1901) suggested that the falciform process or "Leiste" serves as the path for both the artery and the nerve for the lens muscle, while the vitreal vessels, being an intraocular complexity, have been discarded by active, voracious fishes, for whom the visual sense is most important. Somewhat coincident with this suggestion is the view discussed above namely, that the falciform process type vascularization may be favourable for the strong, contractile lens muscle, which is well developed only in the Neopterygii, phylogenetically. Walls (1942), from a much wider but rather different viewpoint, was of the opinion that any of the conspicuous intraocular structures such as the papillary cone of lizards and the pecten of birds as well as the falciform process of fishes would primarily serve as a nutrient supplying device for the retina, as the vitreal vessels also do.

In order to answer these questions more clearly, two lines of research appear to be essential. One line should deal with a comparative study of the retinal structure and the choroidal vascularization, in addition to the study of intraocular vascularization. The other line should deal with direct physiological studies on the function of well developed structures such as the typical falciform process and the vitreal vessels.
As for the latter approach particularly, no information is yet available in the Anamniotes.

SUMMARY AND CONCLUSIONS

1) Retinal circulation and, vascularization originating from the embryonic hyaloid vessels were examined in 4 Elasmobranchs, 23 Teleosts, 2 Holosteans, 1 Urodele and 2 Anurans representing the Anamniotes inhabiting the north-eastern part of North America. Attention was also given to the associated structures such as the lens muscle, the ciliary folds, the persisting embryonic fissure, etc.

2) With some important species, an indirect method of ophthalmoscopy was performed in order to confirm the direction of the blood flow in the vessels examined by injection.

3) In Elasmobranchs such as *Squalus*, *Centroscyllium* and *Raja*, the avascular condition where no vessel is present either in the vitreous cavity or on the retina, was confirmed. The poorly developed lens muscle papilla which is apparently a continuation of the ciliary folds is supplied by a branch of the iris artery which proceeds along the ventral meridian of the choroid.

4) In Teleosts, various instances were encountered and grouped into 4 recognisable types and other unusual categories. Depending upon the degree of vascular development from the hyaloid artery into the

vitreous cavity along the persisting embryonic fissure, there are the higher (Salmo) and the low (Gadidae, Argentina, Eumicrotremus) falciform process types. The third type is the low falciform process with branches on the retina (Myoxocephalus, Sebastes, Anarhichas, Cyclopterus). The branches on the retina are developed both densely and extensively in the fourth type viz. vitreal vessels (Pleuronectidae, Tautogolabrus, Lycodes).

5) A constant constituent of the falciform process types, the main vessel which proceeds from the optic disc to the lens muscle, tends to be obliterated in the vitreal vessels (Opsanus) where the embryonic fissure is closed. Herein the branches, which would otherwise join the choroid through the fissure, are received by a peripheral annular vessel which has its exit near the underdeveloped lens muscle.

6) The system of vitreal vessels in Liparidae is unique because of its exit through the optic disc. In Lophius, only one vessel is left. Macrourus shows an avascular condition. In all these instances, the embryonic fissure is lacking and the lens muscle is rudimentary.

7) In the vitreal vessels of Holostei, both Lepisosteus and Amia, the arterial entry near the

ventral ora was confirmed. But the optic disc proved to be particularly elongated ventrally, reaching the arterial entry.

8) Avascularity in Urodela (Necturus) and the well developed vitreal vessels in Anura (Bufo and Rana) were also confirmed. In the Anuran vitreal vessels, both the entry and the exit are at the ventral margin of the lens muscle, a small swelling of the ciliary folds near the ventral ora. The hyaloid artery which divides into the vitreal vessels is a branch of the ophthalmic artery. In Anura as well as Urodela the ophthalmic artery runs along the ventro-temporal meridian of the eye-ball to supply the cilio-iris region.

9) The validity of the above mentioned classification of the falciform process and the vitreal vessels is discussed in comparison with Virchow's (1882b, 1901) classification and the bases and categories of the latter one are criticized. Possible relationships with the other categories are suggested.

10) Having reviewed the situations in all major groups of Class Osteichthyes, it is pointed out that the avascularity is rather common in the groups other than Neopterygii. The falciform process type vascularization may have arisen due to the vitreal

vessels having been influenced by the development of the accommodative lens muscle, which is functional only in Neopterygii.

11) In Classes Chondrichthyes and Amphibia, it appears that the less marked lens muscle has not had any significant effect on intraocular vascularization.

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