

Julian D. Corrington:

Morphology of the anterior  
arteries of sharks



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# MORPHOLOGY OF THE ANTERIOR ARTERIES OF SHARKS

BY

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## CONTENTS:

Introduction . . . . .	185
Historical . . . . .	186
Variations encountered . . . . .	187
The region discussed . . . . .	189
Synopsis of the anterior arteries in sharks . . . . .	190
Morphologic history of the arteries:	
Afferent branchial . . . . .	191
Efferent branchial . . . . .	194
Hypobranchial . . . . .	205
Coronary . . . . .	223
Carotid . . . . .	225
Cerebral . . . . .	251
Summary . . . . .	254
Method . . . . .	256
Literature cited . . . . .	258

## INTRODUCTION.

Since the time when the circulatory system of fishes was first comprehensively investigated by JOHANNES MÜLLER, a great deal of attention has been paid to this subject, resulting in a voluminous and scattered literature. Consequent to the amount and diversity of the work performed, much confusion and mis-statement of fact occurs both in texts, laboratory manuals, and special papers, and it has therefore seemed desirable to revise that portion of the field in which the greatest difficulty has been encountered, — the arteries of the head. Sharks, of all living chordates, will most clearly elucidate the ancestral conditions, and since it would seem that we already have sufficient developmental data, the writer has approached the subject from the point of view of comparative anatomy. An endeavor has been made to bring together and harmonize the results of all known morphological and embryological investigations, controlling and augmenting by means of additional studies.

## JULIAN D. CORRINGTON

Specimens of suitable size and in proper variety are becoming increasingly difficult to secure of late, and the writer is especially indebted to two firms for their coöperation in the matter of supply. MR. ALFRED EHRENREICH, President of the Ocean Leather Company, courteously invited a visit to that one of the firm's plants located at Morehead City, N. C., and the General Biological Supply House, of Chicago, succeeded in getting some Pacific types. Thanks are also due BECTON, DICKINSON, and Company for providing a cut of the syringe used in injection (fig. 24), as described later under method.

Grateful acknowledgment is made of the helpful advice and suggestions of Dr. H. D. REED, under whose direction this investigation was performed.

## HISTORICAL.

Twelve milestones designate the more important acquisitions to our knowledge in this field:

1. In 1839 JOHANNES MÜLLER published the fourth chapter, dealing with the vascular system, in his classical *Vergleichende Anatomie der Myxinoiden*, and in which numerous references attested his exhaustive knowledge of the blood vessels of elasmobranchs. His dissections included: Alopias, Carcharias, Centrophorus, Catulus, Galeorhinus, Galeus, Hexanchus, Lamna, Notorynchus, Rhina, Spinax, Scymnus, Myliobatis, Raja, Rhinobatus, Torpedo, and Trygon.
2. MÜLLER and HENLE (1841), *Systematische Beschreibung der Plagiostomen*.
3. Detailed descriptions and figures of the head arteries in sharks were first offered by HYRTL (1872) in *Die Kopfarterien der Haifische*. As a pioneer worker in this field, HYRTL published some ten papers between the years 1838 and 1872, and engaged in numerous controversies with MÜLLER, RATHKE, and others upon the homologies of various vessels.
4. The cornerstone embryological treatise is that of BALFOUR, who began his *Development of Elasmobranch Fishes* in 1876. The separate papers were collected as a monograph two years later.
5. From 1882 to 1906, DOHRN issued the many parts of his *Studien zur Urgeschichte des Wirbelthierkörpers*, in which was included the first comprehensive account of the ontogeny of selachian head arteries.
6. The initial complete description of the blood-vascular system of any species of shark was that of T. J. PARKER, *On the Blood-Vessels of Mustelus Antarcticus*, in 1886. Excellent on the whole, it contained several homologies since rejected.
7. RAFFAELE (1892), *Ricerche sullo sviluppo del sistema vascolare nei Selacci*, added further embryological data.

## MORPHOLOGY OF THE ANTERIOR ARTERIES OF SHARKS

8. ALLIS, in 1897, published the first of a long series of morphological papers on the branchial and cranial anatomy, and especially the arteries, in many fish forms.
9. Anatomical: CARAZZI (1905), *Sul sistema arterioso di Selache maxima e di altri Squalidi*.
10. Embryological: SCAMMON (1911), *Normal Plates of the Development of Squalus acanthias*.
11. Systematic: GARMAN (1913), *The Plagiostoma*.
12. Finally, *The Elasmobranch Fishes* by DANIEL in 1922 is a complete and most excellent comparative anatomy of this group.

This brief survey would hardly be complete without mention of that monumental aid to all ichthyologists, the *Bibliography of Fishes*, issued in three parts by DEAN, in 1916, 1917, and 1923. For other exhaustive bibliographies the reader is referred to the above listed works of DANIEL, SCAMMON, MÜLLER and HENLE, and GARMAN, in the order named.

## VARIATIONS ENCOUNTERED.

The importance of individual variation as a factor in the alteration of the ancestral pattern is usually not adequately stressed in morphological studies. Most investigators have limited themselves to one or two specimens in their dissections and where these have differed from whatever average condition might be considered as normal for the species, have been apt to assign improper values. No organs of the body appear to be more susceptible to variation than those of the vascular system. The following synopsis of variations noted in the present study will explain references to such conditions in the principal chapters:

1. *Anastomoses* between subsidiaries of primarily independent trunk lines, as that between the subclavian and hypobranchial. Sprouts from different sources frequently encroach upon the same territory and may link up into a continuous vessel.
2. *Captures*.
  - A. *Of territory*. An artery originally foreign to a given region may expand so as to occupy this site contemporaneously with the native vessel, or may even displace, wholly or in part, the indigenous member. An example is the invasion of the spiracular retia by a branchial commissure at the expense of the primary afferent branchial, which atrophies later in development, an alteration correlated with a change in function of the pseudobranch.
  - B. *Of vessels*, as a result of an anastomosis. Such a diversion profoundly modifies the size, direction, position, number, and relationships of the parts concerned, and effects a reversal of current. This type of

variation may be observed during the later embryological history of the collector arteries of the demibranchs, where the ellipse around each gill is altered to a loop around each cleft, due to capture by commissures.

3. *Shifting*: a change in
  - A. *Source*, as occurs in the origin of the external carotid.
  - B. *Derivatives*; minor branches never have quite the same relationships in different specimens.
  - C. *Trajectory*; a vessel never follows exactly the same route in any two examples.
  - D. *Terminus*. By expansion or by capture, an artery may supply a part not originally included within its precinct. Thus a segmental twig became the subclavian during acquisition of pectoral fins.

One type of shifting produces

4. *Fusion*.
  - A. *Axial*. Paired vessels may fuse to form a single median structure, as in the dorsal aorta.
  - B. *Paraxial*. Bilateral fusing of vessels which are not members of a pair, shown by the formation of certain afferent branchials; or unilateral fusion, producing asymmetry. Either fusions or capture may lead to
5. *Convergence*; illustrated by the symmetrical confluence of the commissures which build up the median hypobranchial artery.
6. *Divergence*: the coracoid artery may split into paired epicoracoids.
7. *Interpolations*; the presence of abnormal or supernumerary elements, such as the "unpaired head aorta" of HYRTL.
8. *Heterochromia*.
  - A. *Precocious*: the ophthalmic artery is one of the earliest vessels to form in the embryo, appearing long before its ultimate terminus, the choroid coat of the eye.
  - B. *Retarded*: the coronary vessels cannot be established until the entire hypobranchial system, — of which they are derivatives, — is well formed. This takes place late in development, subsequent to the completion of the heart.
9. *Alterations of*
  - A. *Function*, as in the spiracular retia of some sharks, where the change has been from aëration to pressure regulation.
  - B. *Extent*.
    - a. *Increase*: the efferent pseudobranchial artery is folded upon itself many times and has far greater length than the distance to be traversed in certain sharks.
    - b. *Decrease*: in higher forms the branches of the orbitals reach the eye muscles more directly than is the case in lower types.

C. *Caliber.*

- a. *Augmented*: the dorsal lateral artery frequently assumes a diameter and importance far greater than usual.
  - b. *Diminished*: occurring in posterior vessels of the hypobranchial circulation in higher groups. This condition may lead to
10. *Elision*; complete atrophy of once functional units. The caudal section of the lateral hypobranchial suffers this fate in many forms. Diminished caliber may also be expressed as
11. *Asymmetry* of
- A. *Development*. The pericardial arteries illustrate a graded series of this type of variation, from symmetrical pairs through unequal mates to complete loss of one member, wherein the other captures the territory involved. Shifts account for inequality of
  - B. *Relationship*. Segmentals are seldom precisely paired.

## THE REGION DISCUSSED.

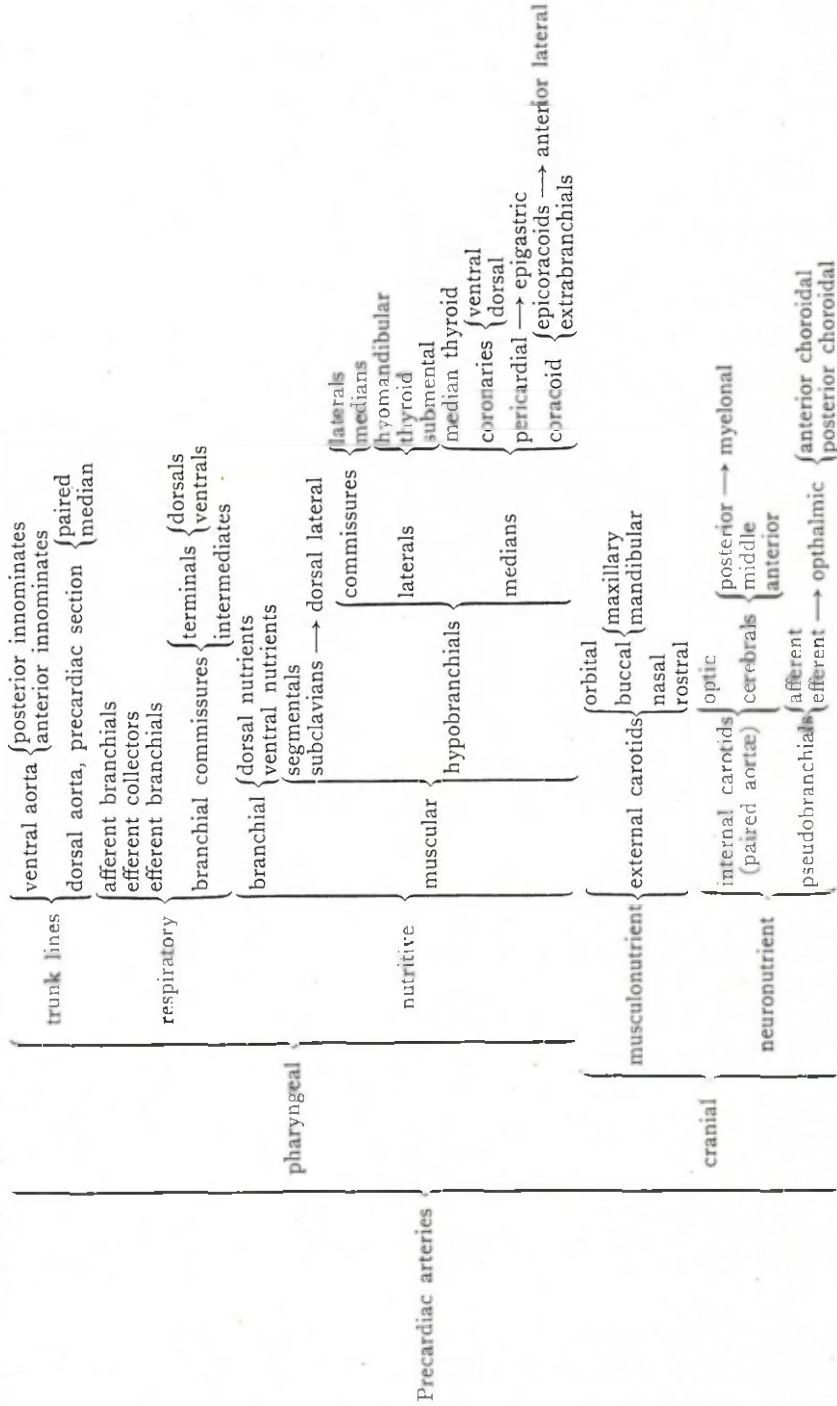
All arteries originating within the head are considered in this paper. All of these are intimately bound up with the branchial circulation, even those most remote in the adult arising in development as sprouts from the aortic arches. Six regional divisions, of no morphological significance, but of great convenience in description may be recognized and delimited as follows:

1. The *afferent branchial* arteries extend from the ventral aorta, carrying impure blood into the gills. Capillaries from these reunite to form the
2. *Efferent branchial* arteries, conveying the now oxygenated blood to the following four divisions:
3. The *hypobranchial* arteries supply the ventral pharyngeal region, thyroid, gill septa, pericardial walls, esophagus, and form the
4. *Coronary* arteries for the heart.
5. The *carotid* arteries continue the dorsal aorta forward, nourishing all dorsal structures cephalad of the gill region, and give rise to
6. The *cerebral* arteries for the brain, and for those paired lateral sense organs which represent extensions of the brain.

A set of original figures accompanies the descriptive matter of each of these subdivisions. For this purpose *Galeus glaucus* (*Prionace glauca*) was selected as presenting the greatest complexity and most interesting conditions of any form so far investigated, and also because it has not been previously illustrated. In addition, several of HYRTL's well known plates have been reproduced and relabelled to conform with the homologies herein advocated.

A complete synopsis of the head arteries follows:

SYNOPSIS OF THE ANTERIOR ARTERIES IN SHARKS.



MORPHOLOGY OF THE ANTERIOR ARTERIES OF SHARKS<sup>191</sup>  
MORPHOLOGIC HISTORY OF THE ARTERIES.

I. THE AFFERENT BRANCHIAL SYSTEM.

VENTRAL AORTA — Balfour, T. J. Parker, Kingsley, Daniel.

Aorta — Claus.

Aorta ascendens — Claus, Kingsley.

Artère branchiale — Milne Edwards, Cuvier & Valenciennes.

Arteria branchiale — Carazzi.

Arteria branchialis — Müller.

Branchial artery — Balfour, Allen, Monro, Owen, Gegenbaur.

Cardiac aorta — Claus, Huxley.

Gemeinsame Kiemenarterie — Vogt & Yung.

Hauptstamm der Kiemenarterie — Wiedersheim.

Kiemenarterienstamm — Stannius.

Tronco dell'aorta — Emery.

Truncus arteriosus — Hochstetter, McKenzie.

Figs. 1—9, 12, 15—17; *VA*.

Running forward in the deep musculature of the floor of the interbranchial region, this median trunk sends an afferent branchial artery into each gill septum, and these derivatives are always paired symmetrically. Caudad of the mandibular symphysis the aorta divides right and left to form either the first or the first two pairs of afferents. It is a very uniform structure in all selachians, inherited from lower groups.

AFFERENT BRANCHIAL ARTERIES — T. J. Parker, Allen, Allis, Kingsley, Daniel.

Artères branchiales propres — Milne Edwards.

Arteria branchiales — McKenzie.

Arterie branchiali — Emery.

Arterie afferenti — Carazzi.

Branches of branchial artery — Monro, Rameau, Cuvier & Valenciennes.

Branchial arteries — Claus.

Kiemenarterien — Müller, Hyrtl, Stannius, Vogt & Yung.

Figs. 2—10, 12, 15—17; *ABA*.

Each of these vessels courses through the deep mesal portion of its gill, lying just ectad of the gill arch (fig. 10, *ABA*) and gives off branches (*ABAr*) right and left to the two demibranchs. The main stem constantly diminishes until it is exhausted at the upper extremity of the septum. The hyal afferent differs from the remainder only in that it supplies arterioles to but a single demibranch, the posterior hyoidean.

The bases of the first two and last two afferents frequently fuse during development into anterior and posterior innominate arteries (*AYERS*) (figs. 12, 15, *AIA*; 16, *PIA*). The third afferent always





arises separately in sharks, but has fused with the last two in rays. The number of afferent branchials depends on the number of gills: 7 in *Notorynchus* and *Heptranchias*; 6 in *Chlamydoselachus*, *Hexanchus*, and *Pliotrema*; and 5 in all others. *Heptranchias* (*Heptanchus*) is the only known species to date in which the base of each afferent is separate (ALLIS, 1912. 2) there being accordingly no innominate arteries. This is the case also in *Chimæra* (ALLIS, 1912. 4). *Notorynchus*, *Chlamydoselachus*, and *Galeus* have an anterior but no posterior innominate, while other known species have both. The writer observed no variations in the innominates and few are to be expected, though ALLIS (1923) records an example in *Chlamydoselachus*. In some forms, as *Galeorhinus* (*Mustelus*) *canis* (FERGUSON, 1911) the last two afferents may arise side by side so that it is difficult to say whether they have a common stem or not. Other species of this genus have been figured as possessing a posterior innominate.

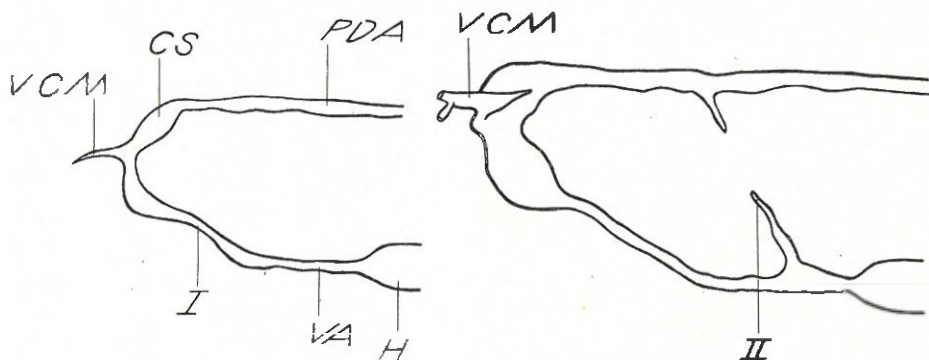
A more interesting and important variation in this system is recorded by ALLIS (1911. 2) in *Chlamydoselachus*, where each of the six afferent arteries was united with its neighbors both dorsally and ventrally by commissural loops, forming a complete venous circulation around each gill cleft, exactly as is the case with the arterial ellipses of the efferent collectors. Wishing to see if there was any trace of this unique arrangement in a related form, he next (1912. 2) investigated *Heptranchias perlo* (*Heptanchus cinereus*) and found the ventral ends of the first two and last two afferents so connected; slender vessels arising from the ventral ends, forward surface, of the remainder, but failing to establish connection; and each afferent turning back dorsally part way around the upper end of the cleft in rear, but not completing a commissure. Other genera have not been investigated in this particular, or show no traces of such a system. AYERS's (1889) paper on *Chlamydoselachus* overlooked these commissures entirely, and DANIEL (1922) gives the complete anatomy of *Notorynchus platycephalus*, a closely related form, but does not record them, nor does he cite the above paper by ALLIS in his excellent sets of bibliographies. However, DANIEL was aware of the conditions in *Chlamydoselachus* and we must presume he sought for but did not find any trace of such construction in *Notorynchus*.

The questions then arise, is *Chlamydoselachus* primitive or specialized in this particular, and is *Heptranchias* undergoing development or reduction? The basic position of these sharks would incline one to accept the idea of ALLIS, that *Chlamydoselachus* shows the ancient condition and that *Heptranchias* is in the intermediate stage of reduction of these loops, which in all other forms have entirely aborted. This is the first of many excellent examples encountered in this study which demonstrate the futility and grave danger of arguing from the evidence of dissection without recourse to observations of development.

193

MORPHOLOGY OF THE ANTERIOR ARTERIES OF SHARKS

A glance at figures 1—9 will acquaint the reader with the method of formation, growth, and modification of the primary aortic arches. It will be noted that the efferent vessels are produced from the afferent by a process of budding and that they later capture the territory of the latter and supplant them, so that the afferents are no longer connected with the dorsal aorta. Not only is there no indication of the transient existence of afferent commissures, but it is also clear that they could not form until a considerably later stage, and therefore in *Chlamydoselachus* they, like all anastomoses, are among the most recent acquisitions of the branchial arches. They are hence a secondary and specialized condition — an interpolation — in *Chlamydoselachus*, and probably incipient in *Heptranchias*. Their utility



Figs. 1—9. Development of the head arteries in sharks; semi-diagrammatic lateral aspects.

Fig. 1. *Squalus acanthias*, embryo of 4.9 mm., 26 somites. From SCAMMON.  
 CS cephalic sinus; H heart; PDA paired dorsal aorta; VA ventral aorta; VCM vena capitis medialis; I mandibular aortic arch.

Fig. 2. *Squalus acanthias*, embryo of 5.2 mm., 35 somites. From SCAMMON.  
 VCM vena capitis medialis; II hyoidean aortic arch.

would seem to be slight and a high degree of variability should be met with when a greater number of examples have been explored. That these loops are by no means as valuable to the animal as are the efferent ellipses may be inferred from (1) the almost total absence of the former and universal presence of the latter, and (2) the fact that efferent loops produce several important non-respiratory stems while the afferents naturally do not.

AFFERENT BRANCHIAL ARTERIOLE — Daniel.

Afferent filament artery — Allen.

Ast der Kiemenarterie — Müller.

Branches of the afferent artery — T. J. Parker.

Une branche à chacun de ces feuilletts — Cuvier & Valenciennes.

Figs. 10, 12; *ABAr.*



## JULIAN D. CORRINGTON

These are the twigs which convey blood from the afferent stem, one to each branchial filament, and end in respiratory capillaries. Venous blood courses up the inner (septal) face of the filament, and after purification returns down the outer (gill cleft) border via the efferent arteriole. Afferent arterioles for the anterior demibranch of a gill are three times as numerous but only one third the size of those for the posterior. This is because they are free to deploy at any and all points along the path of the afferent trunk, while the posterior twigs can pass out only between the interstices of the branchial rays. In *Triakis semifasciata* each of these larger posterior arterioles supplies seven filaments. To demonstrate this arrangement and the distribution of these fine vessels it is best to slit open an afferent artery from its mesal surface and inspect the lateral half of the lumen.

## II. THE EFFERENT BRANCHIAL SYSTEM.

EFFERENT BRANCHIAL ARTERIOLE — Daniel.

Ast der Kiemenvene — Müller.

Branches of the efferent arteries — T. J. Parker.

Efferent filament artery — Allen.

Une veine branchiale — Cuvier & Valenciennes.

Figs. 10, 12; *EBAr*.

There are two sets of these tiny twigs for each series of afferent arterioles. For this reason, and inasmuch as each filament has its own efferent vessel, the efferents are much smaller and more numerous than the afferents. At the base of each demibranch the efferent arterioles are received by an

EFFERENT COLLECTOR ARTERY — Daniel.

Artères epibranchiales — Milne Edwards (in part).

Arteria efferente — Carazzi (in part).

Branchial vein — Balfour, Monro, Owen, Huxley, Gegenbaur, Claus, Rolleston, Macalister.

Efferent branchial artery — T. J. Parker, Allen, Allis (in part), Kingsley (in part).

Epibranchial artery — Claus (in part).

Kiemenvene — Müller, Hyrtl, Stannius, Vogt & Yung.

La grande veine de la branchie — Cuvier & Valenciennes.

Vene branchiali — Emery.

Figs. 5—10, 12—16, 18; *AECA*, *PECA*.

These vessels run at right angles to the arterioles which build them up and conform to the semicircular curve of the adjacent skeletal arch. There is always a collector for each demibranch in sharks, and though PARKER (1886) figured but one to the gill in *Callorhynchus*, ALLIS (1912.4) finds two in *Chimæra* except in the last gill, where the posterior collector, small

in sharks, has aborted. In the absence of an anterior hyoidean demibranch, what is probably a vestige of its former collector has shifted its attachment to the hypobranchial system, with a corresponding change in function, and will there be discussed under the name of hyomandibular artery (p. 214).

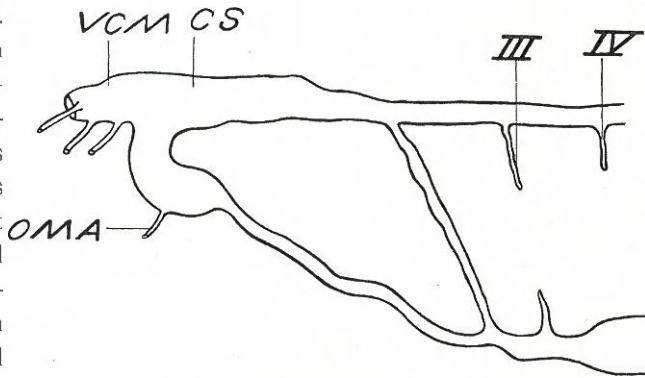


Fig. 3. *Squalus acanthias*, embryo of 7.5 mm., 53 somites. From SCAMMON.

CS cephalic sinus; OMA ophthalmic artery (ophthalmica magna); VCM vena capitis medialis; III, IV aortic arches.

As can be seen in figures 1—9, any aortic arch except the first is formed by the coalescence of sprouts from the dorsal and ventral aortæ. A bud then appears near the upper end; posteriorly in the hyoidean, anteriorly in the others (SCAMMON, 1911, on *Squalus*), or posteriorly in all (DOHRN, 1884, 1886, with *Pristiurus*). The bud forks, grows both dorsally and ventrally, and the upper division unites with the dorsal aorta, captures the role of transporting the blood stream to that trunk line, and becomes the definitive efferent branchial artery. The upper section of the primary arch is thus supplanted. The lower division of this growing fork, in the second arch, becomes the efferent collector of the hyoidean demibranch. In other gills, it sends out sprouts which pass mesad of the afferent trunk and expand and coalesce into another collector. The connection between afferent and efferent vessels at the site of the original bud is then ruptured and a capillary network developed between the two systems. Thus the afferent components are primary, the efferent secondary in their morphology. Some of the collectors may transiently unite with the ventral aorta, a fact of doubtful phylogenetic value.

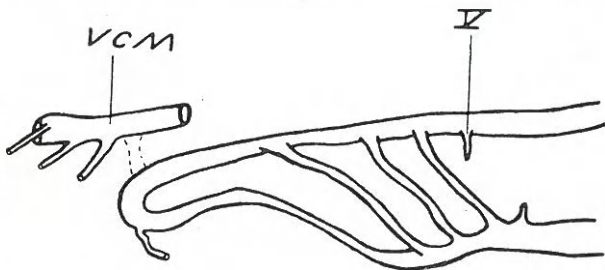


Fig. 4. *Squalus acanthias*, embryo of 11.5 mm., 65 somites. Modified from SCAMMON.

VCM vena capitis medialis; V fifth aortic arch.

Soon (fig. 7) the two collectors of a gill unite dorsally establishing an arterial loop around the upper branchial pole, but shortly thereafter this connection is broken and

the posterior collector of arches 3, 4, and 5 swings back above the succeeding gill cleft and unites with the anterior collector of the following arch (fig. 8), thus establishing an arterial loop around the cleft instead of around the gill.

This new development, which is of a fourth order of sequence, may be termed a dorsal branchial commissural artery (figs. 8, 9, 18, 22; *DBCA*). Toward the end of the prenatal period, as shown by DOHRN (1890), such a connective is also formed between the second and third arches (figs. 8, 9) by the union of reciprocal sprouts, but only this later and different method of origin reveals this vessel as not serially homologous with other dorsal commissures, since all appear uniform in the adult. But the last

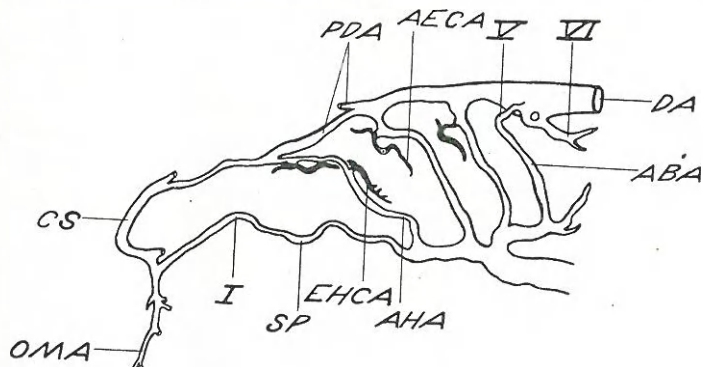


Fig. 5. *Squalus acanthias*, embryo of 15 mm., 86 somites.  
From SCAMMON.

*ABA* afferent branchial artery; *AECA* anterior efferent collector artery; *AHA* afferent hyal artery; *CS* cephalic sinus; *DA* dorsal aorta; *EHCA* efferent hyal collector artery; *OMA* ophthalmic artery; *PDA* paired dorsal aorta; *SP* site of pseudobranch; *I, V, VI* aortic arches.

with that of the arch next in rear, so that there is a perfectly continuous dorsal commissural chain.

The sprouts by which one collector artery of a gill produces the other (fig. 6) persist in the adult as the intermediate branchial commissural arteries (figs. 7-10, 12; *IBCA*). The number of these short vessels varies widely in different species, and doubtless individual variation will also be found to obtain when a greater number of specimens will have been examined. DANIEL (1922) figures 16-14-11-11-11-11 for the six complete gills of *Notorynchus*. ALLIS shows 3-7-7-7-7 in *Chlamydoselachus* (1911.2), 6-6-6-0 in *Chimæra* (1912.4), and 1-1-1-1 in *Raja* (1912.3). *Squalus* has usually 4 to 5 in each arch, *Galeus* 2 throughout, and *Triakis* 1-1-1-2. In all cases (1) these stems are the only means by which the last demibranch is drained, the last collector having no other connections; (2) these commissures pass mesad of the afferent trunk; and (3) the flow

cleft remains without such a loop, for there is no vessel on its posterior, gill-less wall with which the posterior fourth collector might so unite. *Chlamydoselachus* is the only shark (ALLIS, 1911.2) and *Chimæra* (ALLIS, 1912.4) the only other described elasmobranch in which the first embryonic construction of commissures is retained and in addition to the later change. Here each posterior collector is united with the anterior collector of its own arch and also

197

MORPHOLOGY OF THE ANTERIOR ARTERIES OF SHARKS

of blood through them is forward. The evolutionary tendency in these vessels is to concentrate them into a small number of large commissures located at the distal apex of the gill.

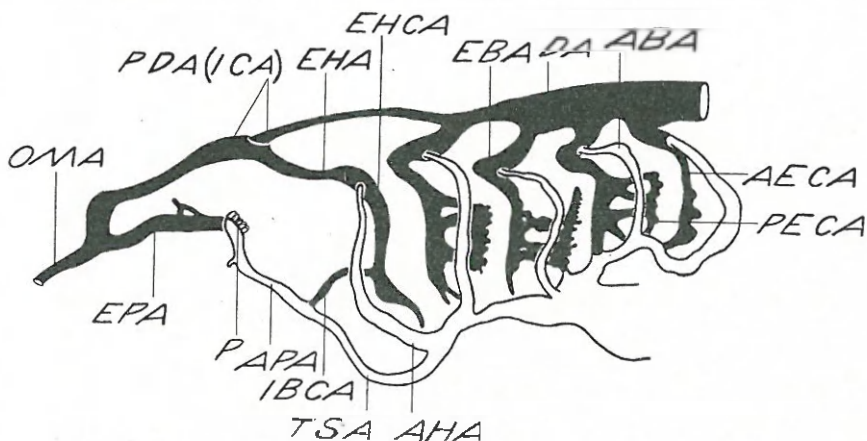


Fig. 6. *Squalus acanthias*, embryo of 20.6 mm. From SCAMMON.

ABA afferent branchial artery; AECA anterior efferent collector artery; AHA afferent hyal artery; APA afferent pseudobranchial artery; EBA efferent branchial artery; DA dorsal aorta; EHA efferent hyal artery; EHCA efferent hyal collector artery; EPA efferent pseudobranchial artery; IBCA intermediate branchial commissural artery; ICA internal carotid artery; OMA ophthalmic artery; P pseudobranch; PDA paired dorsal aorta; PECA posterior efferent collector artery; TSA thyro-spiracular artery.

No matter how many are present in other arches, the hyoid has but a single much enlarged intermediate commissure, except in the isolated case of *Galeorhinus (Mustelus) plebejus*, where HVRTL (1872) shows two large trunks. This commissure, first both in location and appearance, taps the mandibular aortic arch at the site of the future spiracle (fig. 6) and becomes the afferent pseudobranchial artery of the adult.

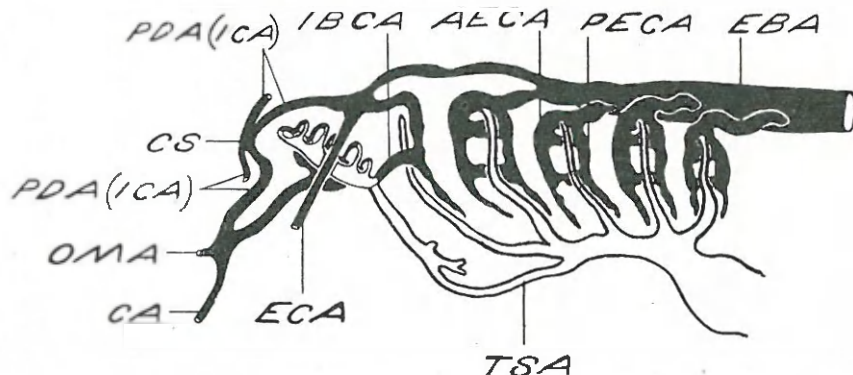


Fig. 7. *Pristiurus*, embryo of about 25 mm. Modified from DOHRN.

AECA anterior efferent collector artery; CA cerebral artery; CS cephalic sinus; EBA efferent branchial artery; ECA external carotid artery; IBCA intermediate branchial commissural artery; ICA internal carotid artery; OMA ophthalmic artery; PDA paired dorsal aorta; PECA posterior efferent collector artery; TSA thyro-spiracular artery.

As a final development in this complex branchial apparatus, there is established a series of ventral branchial commissural arteries (figs. 9, 12—16; *VBCA*). Their formation proceeds from anterior to posterior by means of reciprocal sprouts (figs. 8, 9), and ultimately the first four clefts become ringed by a complete arterial ellipse. As was the case with the dorsal commissures, the last cleft is unprovided with a ventral connective also.

EFFERENT BRANCHIAL ARTERY — Daniel, Kingsley (in part).

Aortenwurzeln — Hyrtl, Dohrn.

Artères epibranchiales — Milne Edwards (in part).

Arteria efferente — Carazzi (in part).

Epibranchial artery — T. J. Parker, Allen.

Epibranchial portion — Allis.

Radices aortæ — Wiedersheim.

Venæ branchiales communes — Müller.

Figs. 6—9, 18—22; *EBA*.

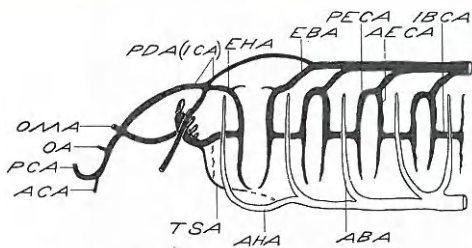


Fig. 8. Later stage, generalized diagram. *ABA* afferent branchial artery; *ACA* anterior cerebral artery; *AECA* anterior efferent collector artery; *AHA* afferent hyal artery; *EBA* efferent branchial artery; *EHA* efferent hyal artery; *IBCA* intermediate branchial commissural artery; *ICA* internal carotid artery; *OA* optic artery; *OMA* ophthalmic artery; *PCA* posterior cerebral artery; *PDA* paired dorsal aorta; *PECA* posterior efferent collector artery; *TSA* thyro-spiracular artery.

6 efferent branchials, depending on the species, and conforming to the number of gills and of afferents, as previously noted. Usually these are all separate, but in *Notorynchus*, *Heptranchias*, *Chlamydoselachus*, and doubtless in other notidanids, the last efferent joins the penultimate midway of its course so that the two have a common stem thence to the aorta. This condition indicates the approaching loss of the last gill in each case, and is a parallel circumstance

Epibranchial was a conveniently descriptive term, since these vessels run from the upper portion of each gill in to the dorsal aorta, a practically horizontal course, and lying upon the gill region. But now that DANIEL has given us the apt designation of efferent collector artery for the lower forks which actually gather up the purified blood, we may restrict the use of the name efferent branchial to the upper and single trunk and in that way best express its revehent correspondence to the afferent branchial in their relationships to a gill.

The first of the series is the efferent hyal artery (figs. 6—8; *EHA*) which courses forward and has been so long identified with the carotid system that its discussion has been deferred to that section. There follow 4, 5, or

to the fusion of the pharyngobranchials of the last two skeletal arches, so commonly seen in sharks. The first two efferent branchials appear united for half of their extent in rays, but the single section is really paired dorsal aorta. In *Chimæra* the first two efferents form one common trunk and the last two another, giving the dorsal aorta but two pairs of roots.

In each of the three types of commissure between the two collectors of a gill, or of adjacent gills, the direction of current is such that the anterior collectors are considerably larger than the posterior. The efferent branchials are direct continuations of these anterior collectors instead of taking their departure from the extreme dorsal pole of the gill cleft. The cephalic efferents swing around caudally in a wide curve, the posterior efferents course more nearly in a straight line to the meson. Here each efferent meets its mate symmetrically, the two uniting and at the same time entering the ventral surface of the dorsal aorta, running at that point directly caudad so that the blood stream slips into the major trunk without disturbance.

From either the dorsal commissures or the bases of the efferent branchials, or both, numerous small twigs come off, the dorsal nutrient branchial arteries (fig. 18; *DNBA*), supplying the dorsal superficial constrictors of the gills, and other muscles of the region. From the evidence of dissection, and especially well shown by the example illustrated (fig. 18), these would seem to have been primarily derived from the first set of embryonic dorsal commissures, — those connecting the two collectors of a gill. Sometimes each nutrient artery confines its distribution to its own branchiomere, but more often one or two become exceptionally developed, and capturing territory originally supplied by serial neighbours, may attain greater size and extent. In *Galeus* (fig. 18) these vessels link up into a complex longitudinal chain, with contributions from each arch; in *Heptanchias* only those nutrients from efferents 1 and 3 are developed; while in *Squalus* there is a decided tendency so to specialize the nutrient of arch 2 that others become obsolete. This hypertrophied vessel is a fairly large artery which extends caudally quite a bit beyond the branchial region. CARAZZI (1905. 1) described such an enlarged pair in *Catulus* (*Scyllium*) as superior

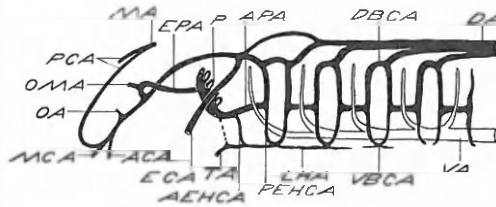


Fig. 9. Stage just previous to assumption of definitive estate; generalized diagram.

*ACA* anterior cerebral artery; *AEHCA* anterior efferent hyal collector artery; *APA* afferent pseudobranchial artery; *DA* dorsal aorta; *DBCA* dorsal branchial commissural artery; *ECA* external carotid artery; *EPA* efferent pseudobranchial artery; *LHA* lateral hypobranchial artery; *MA* myelonal artery; *MCA* middle cerebral artery; *OA* optic artery; *OMA* ophthalmic artery; *P* pseudobranch; *PCA* posterior cerebral artery; *PEHCA* posterior efferent hyal collector artery; *TA* thyroid artery; *VA* ventral aorta; *VBCA* ventral branchial commissural artery.



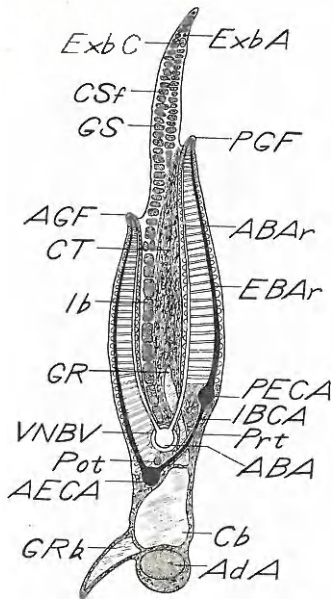


Fig. 10. Frontal section of a shark-gill, semi-diagrammatic.

*ABAr* afferent branchial artery; *ABAr* afferent branchial arteriole; *AdA* adductor arcuus; *AECA* anterior efferent collector artery; *AGF* anterior gill filament; *Cb* ceratobranchial; *CSf* constrictor superficialis; *CT* connective tissue; *EBAr* efferent branchial arteriole; *ExbA* extrabranchial artery; *ExbC* extrabranchial cartilage; *GR* gill ray, distal portion not shown; *GRk* gill raker; *GS* gill septum; *Ib* intrabranchialis; *IBCA* intermediate branchial commissural artery; *PECA* posterior efferent collector artery; *PGF* posterior gill filament; *Pot* post-trematic ramus, branchial nerve; *Prt* pretrematic ramus, branchial nerve; *VNBV* ventral nutrient branchial vein.

Aorta abdominalis — Wiedersheim.

Aorta descendens — Müller, Claus, McKenzie.

Aorta dorsale — Milne Edwards.

Aorte — Cuvier & Valenciennes.

Trunk of descending aorta — Monroe.

Figs. 1—9, 14, 18—23; *DA*, *PDA*.

esophageal arteries and stated that they form an anastomosis with branches of the anterior gastric artery in a situation between mucosa and muscularis in the dorsal wall of the esophagus. A continuation of this type of variation in the future may effect some profound alterations in the angiology of this region.

The ventral branchial commissures or their longitudinal connective trunk, — the lateral hypobranchial, — or both, also produce similar twigs, the ventral nutrient branchial arteries (figs. 12, 13; *VNBA*) for the ventral superficial constrictors and hypobranchial musculature. They do not join up or produce larger vessels as do the dorsal nutrients, since the necessity of so doing is obviated by the presence here of the lateral hypobranchials. The nutrients, collectively, have the following synonymy:

Arteria bronchialis — Stannius.

Arteriæ nutritiæ — Owen.

Bronchialarterien — Müller.

Nutrient arteries — Daniel.

Nutrient branchial arteries — T. J. Parker, Allen.

Nutrient hyoidean arteries (in second arch) — T. J. Parker.

The use of the word *branchial* by older investigators is curious in this connection, as is also their designation of the efferents as *veins*, for they did not possess the technical distinction of the capillary system in the gills as forming a *retia*.

DORSAL AORTA — Huxley, Claus, T. J. Parker, Allen, Allis, Kingsley, Daniel.

Aorta — Müller, Hyrtl, Stannius, Owen, Emery, Carazzi, Vogt & Yung.

201

MORPHOLOGY OF THE ANTERIOR ARTERIES OF SHARKS

In most sharks this trunk is virtually formed by the mesal union of the first pair of efferent branchial arteries, as the paired dorsal aortæ ahead are greatly reduced and not usually as large in caliber as an efferent collector. In *Squalus* (fig. 22) it is the second pair of efferents which first join in the midline.

It is interesting to note the number of names applied to the paired and unpaired portions of the dorsal aorta in its course throughout the body from tail to head. Beginning caudally, these include the following: caudal artery, dorsal aorta, paired dorsal aorta (the hyoidean efferent or first epibranchial of many authors), internal carotid, cerebral artery, middle cerebral artery; six names for different sections of the same vessel. The forward portions are considered later.

Both paired and median divisions of the dorsal aorta give off

SEGMENTAL ARTERIES — T. J. Parker, Daniel.

- Arteria renales — McKenzie.
- Arteria segmentale — Carazzi.
- Arteria spinales — Hyrtl.
- Arteriæ intercostales — Müller, Hyrtl, Stannius.
- Dorso-lumbar arteries — T. J. Parker.
- Intercostal arteries — Owen, McKenzie, Allen, Kingsley.
- Intervertebrale Äste — Vogt & Yung.
- Neural arteries — McKenzie, Allen.
- Nierenarterienzweige — Vogt & Yung.
- Rami musculi-spinales — Hyrtl.
- Renal arteries — T. J. Parker, Allen, Kingsley.
- Musculospinals — Daniel.
- Spinal arteries — T. J. Parker.
- Vertebral arteries — Allis, Kingsley.

Figs. 18, 21, 22; SA.

This lengthy synonymy is caused by varying aspects as to the distribution of these vessels in (1) the same, and (2) different parts of the body, the observations of older workers being incomplete. The divisions of a trunk segmental are given in admirable detail by DANIEL (1922) and may be outlined as follows:

Leaving the dorsal aorta each segmental divides at once into three branches; dorsal, lateral, and ventral.

I. Vertebromuscular; dorsal branch; turning up around vertebra and thence up dorsal septum to mid-dorsal line.

A. Muscular.

- a. central muscle bundle artery;
- b. neural muscle bundle artery;

## JULIAN D. CORRINGTON

- c. dorsal septal artery, to dorsal septal muscle bundle;
- d. dorsomedial septal artery, to dorsomedial septal muscle bundle.
- B. Neural; vertebrospinal artery; passes mesad through neural arch to spinal cord.
  - a. ramus dorsalis; smaller; passes fore and aft on cord, entering to form tractus arteriosus lateralis, terminating in gray matter (STERZI, 1904);
  - b. ramus ventralis; larger; anastomoses midventrally with myelonal artery.
- 2. Intercostal; lateral branch; supplying muscles encircling peritoneum; often very long.
- 3. Renal; ventral branch; enters mesonephros; especially strong caudad; specialized renals form oviducals. This branch is absent in the head.

The primordial arrangement of these ancient arteries was doubtless strictly paired and metameric, as in present day embryos (HOCHSTETTER, 1906), a condition since considerably disturbed and now in a fairly advanced stage of reduction. *Squalus* is fairly regular but *Galeus* (fig. 18) shows great alterations in size, symmetry, and metamerism. The tendencies exhibited in the plagiostoma are (1) reduction to fewer and larger (specialized) trunks, effected by capture of territory and subsequent elision of the displaced segmentals; (2) asymmetry, and as a further consequence (3) ametamerism.

SUBCLAVIAN ARTERY — Monro, Owen, McKenzie, T. J. Parker, Allen, Allis, Kingsley, Daniel.

Artère claviculaire — Milne Edwards.

Arteria ascellare — Emery.

Arteria subclavia — Müller, Hyrtl, Stannius.

Arteria succlavia — Carazzi, Pitzorno.

Schulterarterie — Vogt & Yung.

Figs. 14, 18, 21; *ScA*.

While distributed to a part of the body extraneous to the subject of this paper, the origin of the subclavian lies within the head, and so it should be included here. It arises usually from the dorso-lateral wall of the aorta between the points of entrance of the third and fourth efferent branchials, as in *Galeus* (fig. 18) or *Catulus* (fig. 21). In *Cestracion* and the ray *Pristis*, they depart at the third efferent confluence, and in certain rays, as *Dasyatis* (DANIEL, 1922), opposite the fourth pair. PITZORNO (1905) says the subclavians never arise ahead of the third nor behind the fourth efferents. In rays the two subclavians are frequently unsymmetrical, and in sharks may be so, as in *Galeus* (fig. 18).

As sharks were the first vertebrates to possess paired fins, so this structure is a vessel *de novem*, and arose either by (1) fusion of several

MORPHOLOGY OF THE ANTERIOR ARTERIES OF SHARKS<sup>203</sup>

adjacent segmentals, or more likely (2) specialization of a single one of those belonging to segments which contributed fin materials, others aborting. The intercostal (lateral branch) is the only one of the three divisions of a typical segmental here developed. From the varying attachment to the dorsal aorta in different groups of selachians, it is evident that the base of the subclavian has shifted along the aorta, or that segmentals of different somites have fused or become specialized so that this artery is possibly not an equivalent vessel in all members of the order. A careful study of comparative development would be required to clear up these points.

DANIEL (1922) calls attention to the fact that in *Notorynchus* (fig. 14) the subclavians are so poorly developed that they are smaller than ordinary intercostal branches of the segmentals, and sometimes twigs given off would indicate that blood is flowing toward the dorsal aorta. This form, in common with many but not all sharks, has developed a secondary anastomosis between the subclavian and the epicoracoid, an artery belonging to the hypobranchial circulation, and illustrates an unstable condition in which the dorsal and ventral trunks are competing for the supply of the pectoral fin. If such a struggle has been the rule in the past history of selachians, than the subclavian has clearly been the victor in all higher forms, and has managed to maintain the role for which it was originally developed in the face of this encroachment on the part of a foreign artery.

The subclavian furnishes numerous small twigs for adjacent muscles while curving around ventrally, and especially the

DORSAL LATERAL ARTERY.

Arteria dorsale — Carazzi.

Arteria dorsale longitudinale — Carazzi.

Arteria laterale dorsale — Carazzi.

Dorsolateral artery — Daniel.

Arteria thoracica-dorsalis — Pitzorno.

Figs. 14, 18, 21; *DLA*.

As described by DANIEL (1922) in *Notorynchus* (fig. 14) this vessel sends an anterior and posterior ramus, both larger than the proximal portion of the subclavian, to nourish the musculature of the region. In *Selache* and *Squatina* (*Rhina*) CARAZZI (1905. 2) figures only the posterior branch, which is well developed; PARKER (1886) figures but does not name such a posterior extent for *Galeorhinus* as better developed than the anterior lateral artery, which (CARAZZI) is unusual. The dorsal lateral artery of *Pristis* comes off from the anterior wall of the subclavian, but bends back, passing dorsad of the latter, and runs caudally; in *Galeus* (fig. 18) it extends forward, ramifying widely over adjacent tissues and forming anastomoses with segmentals

and dorsal nutrients, and has also a posterior branch. This artery is absent in some forms, as *Cestracion*.

The dorsal lateral artery is an excellent example of the manner in which a new trunk line may be formed. During progress of the subclavian numerous slender twigs pass both fore and aft to supply nearby muscular tissues, and the dorsal lateral has arisen by the enlargement and specialization of one of these at the expense of its neighbours. It has no especial significance, but is detailed here to show the method by which functional demand for nutrition may cause the development of a fairly large stem, and to point out, then, the absurdity of attempting to identify such a vessel as the modification, rudiment, or vestige of another structure, and of the fallacy and utter lack of necessity of homologizing it with the supposed altered arterial supply of some other organ. Such a practice has been widespread in the past and has seriously impeded correct morphological interpretations. These arteries could well have become more and more highly developed in the evolution of later forms, so that in mammals, for example, there might have been a pair of large and important dorsal lateral trunks, acting as subsidiary distributing arteries to the dorsal aorta; yet structures of such considerable import would have had just so simple an explanation of phyletic origin in elasmobranchs. From the material used in the present investigation, the writer believes a history of this same nature accounts for the development in sharks of the entire hypobranchial and coronary systems and for the external carotid and certain cerebral arteries.

Continuing ventrally, the subclavian gives off the brachial artery to the ventral side of the pectoral fin, and then in many forms anastomoses insensibly with the epicoracoid. One may judge where the anastomosis takes place and therefore in which direction the blood is flowing, only by inclination of the angle made with derivative vessels, and by relative size of different portions of the trunk, neither of which criteria is any too dependable. The next branch on the main stem is the anterior lateral artery, which is evidently a product of the epicoracoid, and so the anastomosis takes place somewhere along the brief course of the subclavian between anterior lateral and brachial.

The branchial region of sharks presents few morphological problems, providing the developmental stages are thoroughly understood. These fishes have inherited a common ground plan of ventral and dorsal aortæ, primary afferent and secondary efferent branchials, and paired segmentals, and have added the subclavian, dorsal lateral, nutrients, branchial commissures, and innominates.

## III. THE HYPOBRANCHIAL SYSTEM.

These are the last arteries of the head to be formed before assumption of the adult condition. This lateness of development and also absence in lower groups argue that this system was one of the last vascular acquisitions of the immediate shark ancestor. Increased bulk and muscular specialization of the subpharyngeal, interbranchial area demanded an extra mechanism for

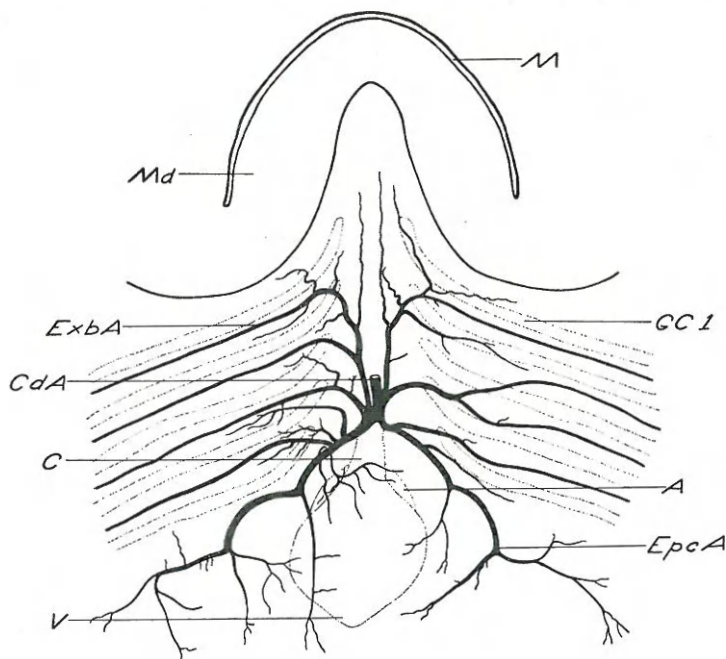


Fig. 11. Coracoid artery, *Galeus glaucus*, ventral aspect.

*A* auricle, *C* conus arteriosus; *CdA* coracoid artery; *EpcA* epicoracoid artery; *ExbA* extrabranchial artery; *GC* gill cleft; *M* mouth; *Md* mandible; *V* ventricle. Dotted structures lie beneath the arteries.

nutritive supply, and this was hence derived from the nearest source. No homologies involving the alteration of any elements previously present are necessary or possible, and none have been suggested as far as I am aware.

HYRTL was the first author to describe and figure this complex system in detail for rays (1858) and for sharks (1872); PARKER (1886) worked it out in *Galeorhinus*, and CARAZZI (1905. 1—2) has been the first to investigate its comparative anatomy and variation and to stress the proper importance of this group of vessels. As CARAZZI emphasizes, there is no type arrangement for these arteries in either the Class or Order, or even in various species, so that description must be of a somewhat general nature.

## LATERAL HYPOBRANCHIAL ARTERY — G. H. Parker &amp; Davis, Daniel.

External lateral hypobranchial — Allis.

Grosse branche anastomotique — Milne Edwards.

Hypobranchial artery — Allen.

Longitudinal commissures (1) — T. J. Parker.

Ventrale Verlängerungen der Venen des zweiten Kiemensackes — Hyrtl.

Described by McKenzie.

Figured by Monro.

Figs. 9, 12—16; *LHA*.

This trunk line is built up during late embryonic stages from the ventral branchial commissural arteries, after these have completed the formation of arterial loops around the ventral ends of the gill clefts. In cephalo-caudal progression, sprouts are sent out fore and aft from these commissures

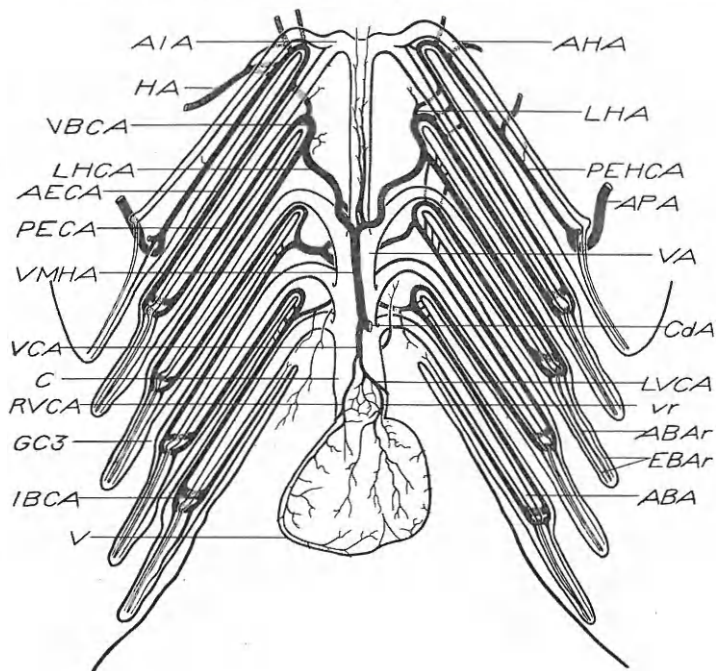


Fig. 12. Branchial and ventral hypobranchial systems, *Galeus glaucus*, ventral aspect. Vessels shown in fig. 11 have been removed.

*ABA* afferent branchial artery; *ABAr* afferent branchial arteriole; *AECA* anterior efferent collector artery; *AHA* afferent hyal artery; *AIA* anterior innominate artery; *APA* afferent pseudobranchial artery; *C* conus arteriosus; *CdA* coracoid artery; *EBAr* efferent branchial arteriole; *GC* gill cleft; *HA* hyomandibular artery; *IBCA* intermediate branchial commissural artery; *LHA* lateral hypobranchial artery; *LHCA* lateral hypobranchial commissural artery; *LVCA* left ventral coronary artery; *PECA* posterior efferent collector artery; *PEHCA* posterior efferent hyal collector artery; *RVCA* right ventral coronary artery; *V* ventricle; *VA* ventral aorta; *VBCA* ventral branchial commissural artery; *VCA* ventral coronary artery; *VMHA* ventral median hypobranchial artery; *vr* ventral ramus, left ventral coronary artery.

(fig. 9) which soon unite end-to-end and thus produce a longitudinal artery. This lateral hypobranchial in turn gives off mesially directed buds which become transverse commissural vessels of two types and sometimes of several sets, all of which were formerly ignored, but which have more recently been collectively termed commissures and individually designated with numerals applying to specific conditions. This renders a comparison between species well nigh impossible, and so the writer has thought best to distinguish these anastomotic or formative units by definite names. It is hoped that the terminology here advocated will be adaptable to future descriptions.

Running mesad from the lateral hypobranchial at the ventral union of two efferent collectors, i.e. from the ventral branchial commissure (*Notorynchus*, *Catulus*), or at a point between two efferent loops (*Galeorhinus*, *Squalus*), or from both sites (*Cestracion*) are one or more

#### LATERAL HYPOBRANCHIAL COMMISSURAL ARTERIES.

Arteria cardio-cardiaca — Hyrtl.

Commissural arteries — Daniel.

Commissures — T. J. Parker, G. H. Parker & Davis.

Vasi commissurali — Carazzi.

Figs. 12—16; *LHCA*.

After a very brief course, the inner ends of these arteries are connected, on each side of the meson, by another pair of longitudinal trunks, the

#### MEDIAN HYPOBRANCHIAL ARTERIES — T. J. Parker, G. H. Parker & Davis, Daniel.

Arteria ipobranchiale — Carazzi.

Internal lateral hypobranchial — Allis.

Figs. 12—15; *DMHA*, *VMHA*.

If there is thus formed a pair of median hypobranchials, the two may be connected by another set of transverse vessels, the

#### MEDIAN HYPOBRANCHIAL COMMISSURAL ARTERIES.

Connectives — Daniel.

Fig. 14; *MHCA*.

These may arise from the median hypobranchial at a site opposite to and in regard to the blood stream, continuous with the lateral commissures, or they may begin at points displaced from the ends of the lateral commissures. Nomenclature is further complicated by the fact that either paired or single median hypobranchials may lie dorsally or ventrally in respect to the ventral aorta, and hence the commissures of both kinds may also be of



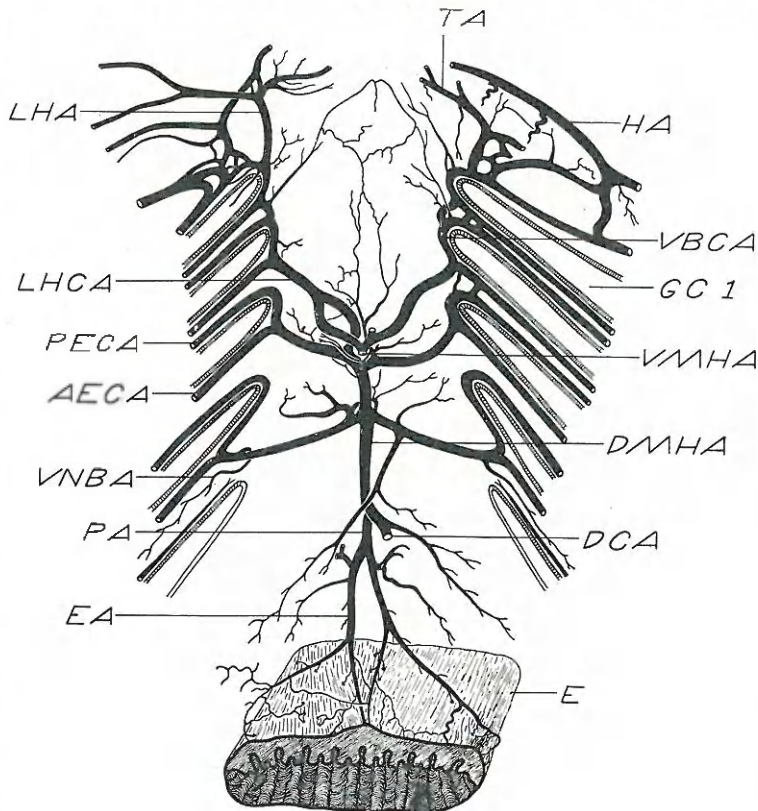


Fig. 13. Dorsal and lateral hypobranchial arteries, *Galeus glaucus*, ventral aspect. Vessels shown in fig. 12 have been removed.

*AECA* anterior efferent collector artery; *DCA* dorsal coronary artery; *DMHA* dorsal median hypobranchial artery; *E* esophagus; *EA* epigastric artery; *GC* gill cleft; *HA* hyomandibular artery; *LHA* lateral hypobranchial artery; *LHCA* lateral hypobranchial commissural artery; *PECA* posterior efferent collector artery; *TA* thyroid artery; *VBCA* ventral branchial commissural artery; *VMHA* ventral median hypobranchial artery; *VNBA* ventral nutrient branchial artery.

either type, and in all of these vessels the prefix dorsal or ventral is frequently necessary to secure an exact designation. There is never, however, a *single* median hypobranchial on the same side of the ventral aorta with a *pair* of median hypobranchials and hence, by applying the terms dorsal and ventral we may obviate the need of still another name for one of these two types. It may appear odd to employ the adjective *median* for one of a *pair* of arteries, but the writer believes that such usage is not only convenient as well as conservative as to terminology in the present case, but also is expressive of the morphology involved, since the single median vessel has doubtless arisen by fusion of closely parallel trunks, — the paired medians. Justification for this statement derives mainly from the fact above mentioned, — that both types are never encountered on the same side of the ventral

aorta, — and also from the evolutionary tendencies shown in dissections of this system, in which it appears that in higher sharks the paired plan of median hypobranchials is giving way to development of larger, single trunks. In most sharks, in fact, many of the parts enumerated in this system are reduced or lacking.

The complete ground plan of the hypobranchial complex is like a lattice-work, successive rows of longitudinal trunks being connected by an alternating series of transverse arteries. Their order of occurrence, from the lateron mesad is:

1. Efferent collector artery; transverse.
2. Ventral branchial commissural plus lateral hypobranchial artery; longitudinal.
3. Lateral hypobranchial commissural artery; transverse.
4. Paired median hypobranchial artery; longitudinal.
5. Median hypobranchial commissural artery; transverse.
6. Single median hypobranchial artery; longitudinal.

Such a complete set has been thus far described only for *Notorynchus* (DANIEL, 1922: fig. 14, this paper). This complicated array may now be most conveniently surveyed as to estate in different species by means of a table (p. 210).

The same information put in reverse order may prove more convenient for reference purposes:

1. Lateral hypobranchial artery.
  - A. Continuous: *Notorynchus*, *Galeorhinus*, *Carcharias*, *Catulus*, *Cestracion*.
  - B. Forward portion only: *Heptranchias*, *Chlamydoselachus*, *Triakis*, *Galeus*, *Catulus*.
2. Lateral hypobranchial commissural arteries.
  - A. All dorsal: *Notorynchus* (5 or 6), *Heptranchias* (6), *Catulus* (2).
  - B. All ventral: *Galeorhinus antarcticus* (2 or 3), *Galeorhinus stellatus* (2), *Catulus* (2).
  - C. Mixed: *Chlamydoselachus* (2 each), *Triakis* (1 each), *Galeus* (1 ventral, 2 dorsal), *Galeorhinus canis* (2 ventral, 1 dorsal), *Carcharias* (1 ventral, 1 or 2 dorsal), *Catulus* (1 each), *Cestracion* (2 ventral, 1 dorsal), *Selache* (1 ventral, 3 or 4 dorsal).
3. Median hypobranchial artery.
  - A. Paired.
    - a. Dorsal: *Notorynchus*, *Heptranchias*, *Galeorhinus*, *Catulus*, *Cestracion* (?).
    - b. Ventral: *Galeorhinus*, *Catulus*.
  - B. Single.
    - a. Dorsal: *Chlamydoselachus*, *Triakis*, *Galeus*, *Carcharias*, *Selache*.

## ESTATE OF HYPOBRANCHIAL ARTERIES.

SPECIES.	LATERAL HYPOBRANCHIAL	LATERAL COMMISSURES	MEDIAN HYPOBRANCHIAL
<i>Notorynchus platycephalus</i> (DANIEL, 1922) Fig. 14	contiguous; from 1st to 5th or 6th efferent loops; sometimes incomplete	5, from 2nd to 5th loops; or 6, from 2nd to 6th: dorsal	paired dorsal; 7 dorsal median commissures; 1 pair ventral commissures forming single median ventral hypobranchial artery
<i>Heterobranchius perlo</i> (ALLIS, 1912.2)	forward portion only; loop	from 1st 6, from 2nd to 6th loops: dorsal	paired dorsal; 3 dorsal median commissures opposite lateral commissures 2, 5, and 6.
<i>Citamyndoselechnus anguineus</i> (ALLIS, 1911.2)	forward portion only; and 2nd loops	from 1st 2 ventral from 2nd and 3rd loops; 2 dorsal from 4th and 5th loops	1 dorsal; 1 ventral, with 1 dorsal median commissure across two roots of origin
<i>Triakis semifasciata</i> (This study)	forward portion only; and 2nd loops	from 1st 1 paired ventral from 2nd loop; 1 dorsal from right 3rd loop, its mate aborted	1 dorsal; 1 ventral; no median commissures (as a matter of course)
<i>Galeus glaucus</i> (This study) Figs. 12, 13	forward portion only; and 2nd loops, sometimes also from 3rd	from 1st 1 ventral from 2nd loop; 2 dorsal from 3rd and 4th loops; branch from right ventral aids 1st dorsal	1 dorsal; 1 ventral; no median commissures
<i>Galeorhinus arcticus</i> (T. J. PARKER, 1886)	continuous; from 1st to 4th loops	2 or 3 ventral, from ahead of 3rd and 4th loops	paired plexiform ventral; paired dorsals represented by pericardial arteries
<i>Galeorhinus canis</i> (FERGUSON, 1911)	continuous; from 1st to 4th loops	2 ventral from ahead of 3rd and 4th loops; 1 dorsal from the 2nd ventral	paired plexiform dorsal; paired plexiform ventral
<i>Galeorhinus stellatus</i> (HYRTL, 1872) Fig. 16	continuous; from 1st to 5th loops; plexiform	2 ventral, from 2nd and 3rd loops	paired plexiform ventral; paired dorsal built up from ventral plexus
<i>Carcharias littoralis</i> (G. H. PARKER & DAVIS, 1901)	continuous; from 1st to 3rd or 4th loops	1 ventral from 2nd loop; 1 or 2 dorsal from 3rd and sometimes from 4th loops	1 dorsal; 1 ventral; no median commissures
<i>Catulus catalus</i> & <i>C. canaliculus</i> (HYRTL, 1872)	forward portion only; loop	from 1st 1 from 2nd loop, dividing into dorsal and ventral rami	paired ventral with 2 median commissures; 1 dorsal, becoming plexiform
<i>Catulus catalus</i> (CARAZZI, 1905.2)	continuous; from 1st to 3rd or even to 5th loops	2 dorsal from 2nd and 3rd loops; or 2 ventral from same; or 1st ventral and 2nd dorsal	paired dorsal with 1 dorsal commissure, or represented only by pericardials; 1 ventral or none
<i>Cestacion sygena</i> (HYRTL, 1872) Fig. 15	continuous; from 1st to 4th loops	2 ventral from ahead of 2nd and 3rd loops, — splitting; 1 dorsal from 4th loop	1 ventral; condition of dorsal not stated; — probably paired
<i>Selache maxima</i> (CARAZZI, 1905.2)	not stated	1 ventral from 2nd loop; 3 or 4 dorsal, from 3rd, 4th, and ahead of 5th loops	1 dorsal; 1 ventral; no median commissures

## MORPHOLOGY OF THE ANTERIOR ARTERIES OF SHARKS

- b. Ventral: Notorynchus, Chlamydoselachus, Triakis, Galeus, Carcharias, Catulus, Cestracion, Selache.
4. Median hypobranchial commissural arteries.
- A. Paired.
- a. Dorsal: none.
- b. Ventral: Notorynchus (1 pr.).
- B. Single (intramedian).
- a. Dorsal: Notorynchus (7), Heptarhynchias (3), Chlamydoselachus (1), Catulus (1).
- b. Ventral: Catulus (2).
- C. Plexiform: Galeorhinus, Catulus.
- D. Absent, because of absence of paired median hypobranchial arteries: Triakis, Galeus, Carcharias, Selache.

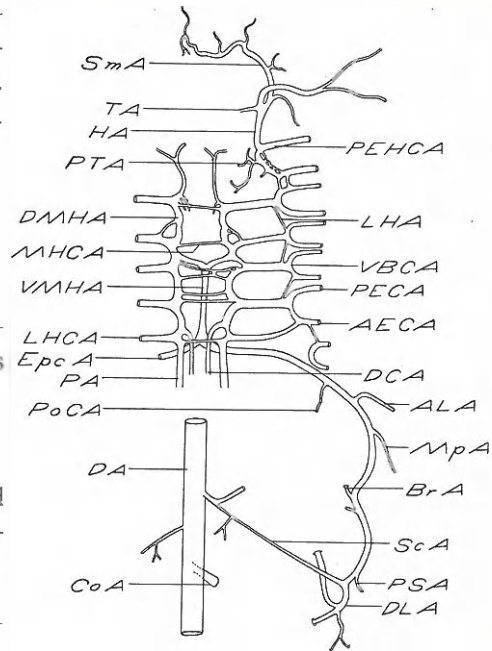


Fig. 14. Hypobranchial system, *Notorynchus platycephalus*, dorsal aspect. From DANIEL.

The only species in which a considerable number of individuals have been examined is *Catulus catulus*, where CARAZZI (1905.2), as may be seen in the above synopses, found differences as great as those existing between any of the other species investigated, individual variations equalling those of family rank. It is then to be expected that when several specimens of other sharks will have been examined, they also will be found to vary within possibly the widest limits to which this system may be expanded, and the above tables will be of little value as specific descriptions. It is hence futile to depict typical conditions from a single specimen, and a very large number of examples will have to be dissected in order to establish even an average case. This instability is further evidence of the recent development of the hypobranchial system, and examples may here be found of all of the types of variation listed on pages 187—189.

AECA anterior efferent collector artery; ALA anterior lateral artery; BrA brachial artery; CoA coeliac axis; DA dorsal aorta; DCA dorsal coronary artery; DLA dorsal lateral artery; DMHA dorsal median hypobranchial artery; EpcA epicoracoid artery; HA hyomandibular artery; LHA lateral hypobranchial artery; LHCA lateral hypobranchial commissural artery; MHCA median hypobranchial commissural artery; MPA metapterygial artery; PA pericardial artery; PECA posterior efferent collector artery; PEHCA posterior efferent collector artery; PoCA posterior coronary artery; PSA posterior scapular artery; PTA posterior thyroid artery; ScA subclavian artery; SmA submental artery; TA thyroid artery; VBCA ventral branchial commissural artery; VMHA ventral median hypobranchial artery.

Analysis of the foregoing tables does reveal certain general tendencies, however, despite scant data, which seem to be looking toward a specialized,

stable, and efficient system. The notidanids, as our lowest existing forms, have the most complex set of definite vessels, and *Notorynchus*, with a complete series of both lateral and median hypobranchials, and abundant commissures of both types, may be taken as most primitive. Heptranchias and *Chlamydoselachus* show a reduction of the posterior portion of the lateral hypobranchial; *Galeorhinus* is in an intermediate condition, exhibiting a plexiform arrangement; *Carcharias* and *Cestracion* have a complete lateral hypobranchial, but have decreased the lateral commissures and perfected a single dorsal and single ventral median hypobranchial. Finally, *Triakis* has a posteriorly suppressed lateral hypobranchial, a single dorsal and single ventral lateral commissure, and a single dorsal and single ventral median hypobranchial, seemingly the most compact and independent arrangement which could possibly be devised.

The lateral commissure most favored is that from the second efferent loop, and the one present in all sharks. Next in utility is that from the third loop, found in most, and lastly the one from the fourth, occurring only in the minority of forms. It appears likely that eventually all blood sent to this system will come from the second loop only, one side of the body forming a single dorsal and the other a single ventral median hypobranchial. The first loop always produces the persistent forward portion of the lateral hypobranchial, which has become specialized in connection with nutrient supply for parts cephalad of the first branchial cleft, just as the median hypobranchials usually concentrate on regions posterior to the last cleft. The numerous and important derivatives of the hypobranchial system may now be considered.

#### Anterior hypobranchial derivatives.

##### 1. *From the median hypobranchial:*

#### MEDIAN THYROID ARTERY.

Arteria thyroidea impar — Hyrtl.

Arteria tiroidea — Carazzi.

Median hypobranchial artery — T. J. Parker (in part).

Fig. 15; *MTA*.

Of unusual and irregular occurrence, this vessel has been generally overlooked in recent work. It was first described by HYRTL (1872) in *Cestracion* (*Zygæna*), where it appears as a forward continuation of the single median ventral hypobranchial artery, running along the bottom of the ventral aorta and supplying the thyroid gland (fig. 15; *MTA*). PARKER (1886) figured the same condition in *Galeorhinus antarcticus*, without the application of a special name, but stated that the terminal branches break up in the coraco-

MORPHOLOGY OF THE ANTERIOR ARTERIES OF SHARKS<sup>213</sup>

mandibular muscle. Since he also said that collaterals from the hyomandibular (his mandibular artery) which are now known as the paired thyroid arteries, similarly supply the same muscle, and since he neither figured nor mentioned a thyroid gland, we may presume that he entirely overlooked this gland and that the terminus of the median thyroid artery is the same here as elsewhere. All of the thyroid arteries have muscular twigs. Lastly, CARAZZI (1905: 2) figures the median thyroid as (1) present, (2) reduced and plexi-

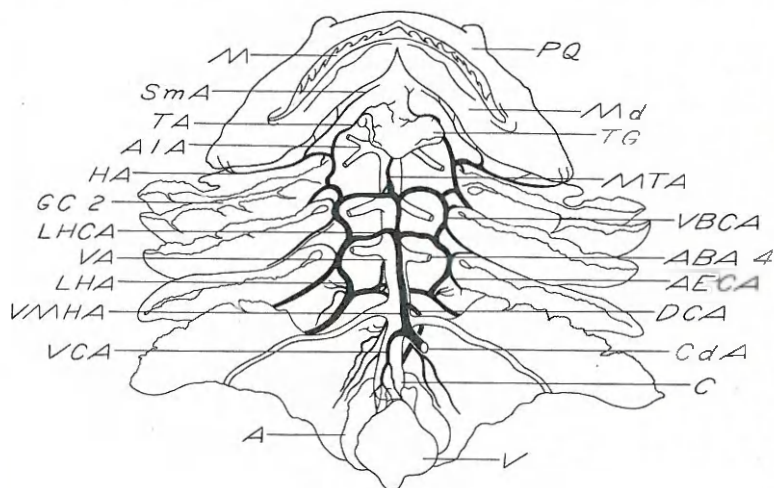


Fig. 15. Hypobranchial system, *Cestracion zygaena*, ventral aspect. From HYRTL.

A auricle; ABA afferent branchial artery; AECA anterior efferent collector artery; AIA anterior innominate artery; C conus arteriosus; CdA coracoid artery; DCA dorsal coronary artery; GC gill cleft; HA hyomandibular artery; LHA lateral hypobranchial artery; LHCA lateral hypobranchial commissural artery; M mouth; Md mandible; MTA median thyroid artery; PQ palatoquadrate; SmA submental artery; TA thyroid artery; TG thyroid gland; V ventricle; VA ventral aorta; VBCA ventral branchial commissural artery; VCA ventral coronary artery; VMHA ventral median hypobranchial artery.

form, or (3) absent in *Catulus*. FERGUSON (1911) found a small median and unpaired vessel in *Galeorhinus canis* arising from the left thyroid artery (from lateral hypobranchial; see later), less frequently from the right, which entered the thyroid, divided, and sent twigs to the coraco-hyoideus muscle. He thought this artery was probably homologous with the median thyroid, but its origin would seem to be against such a view, and it no doubt merely represents an unimportant variation, — an example of asymmetrical interpolation. The true median thyroid is a cephalic continuation of the single median ventral hypobranchial artery and is in the nature of a secondary forward growth. It is absent in all other described forms.

## 2. From the lateral hypobranchial:

## HYOMANDIBULAR ARTERY.

- Afferent mandibular artery — Allis.  
 Anterior hyal efferent — Allis (in part).  
 Arteria mandibolare — Carazzi.  
 Arteria submentalis — Hyrtl.  
 Arteria thyro-maxillaris — Hyrtl.  
 External carotid artery — de Beer.  
 External lateral hypobranchial artery — Allis (in part).  
 Hyoideomandibular artery — Daniel.  
 Mandibular artery — T. J. Parker, Ferguson.

Figs. 12—16; HA.

In the majority of sharks this is a fairly large vessel arising from the ventral branchial commissural artery below the first gill cleft. Sometimes it continues the lateral hypobranchial directly forward, and sometimes takes

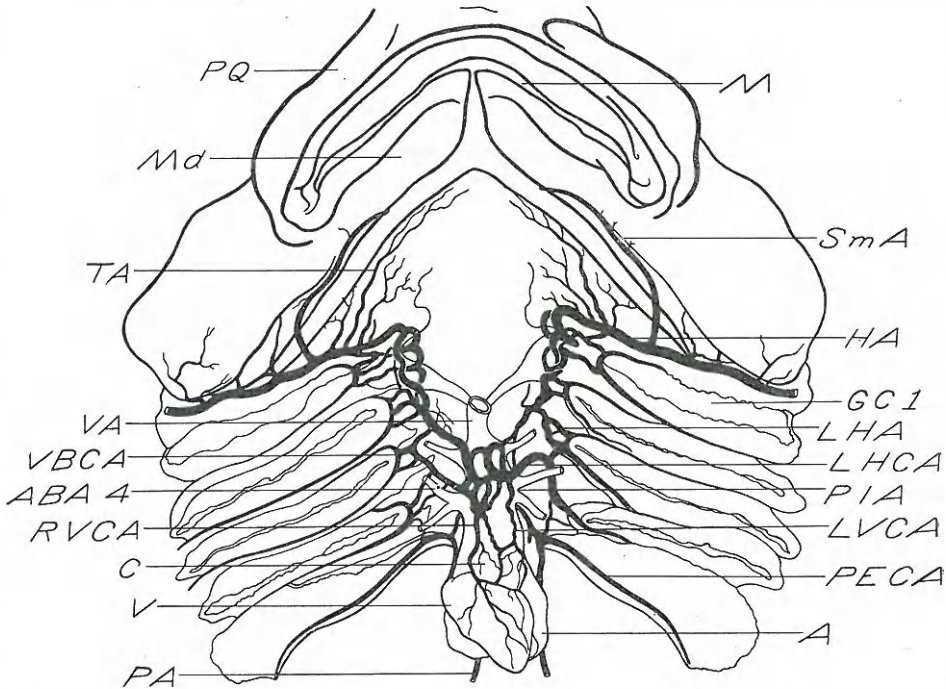


Fig. 16. Hypobranchial system, *Galeorhinus stellatus*, ventral aspect. From HYRTL.  
 A auricle; ABA afferent branchial artery; C conus arteriosus; GC gill cleft; HA hyo-  
 mandibular artery; LHA lateral hypobranchial artery; LHCA lateral hypobranchial  
 commissural artery; LVCA left ventral coronary artery; M mouth; Md mandible;  
 PA pericardial artery; PECA posterior efferent collector artery; PIA posterior in-  
 nominate artery; PQ palatoquadrate; RVCA right ventral coronary artery; SmA sub-  
 mental artery; TA thyroid artery; V ventricle; VA ventral aorta; VBCA ventral  
 branchial commissural artery.

## MORPHOLOGY OF THE ANTERIOR ARTERIES OF SHARKS

origin from the posterior efferent hyal collector a short distance up from the ventral pole of the arterial loop. This variation is probably a simple case of shifting of source, and the vessel the same in all. While running forward, the hyomandibular gives off in succession, cephalo-mesially, the thyroid and submental arteries, then turns up the anterior face of the hyoid arch to follow a course strictly parallel with the efferent collectors of the gills, and continues to the dorsal surface of the body, supplying twigs to all of the neighboring muscular tissues.

The morphology of this vessel is the most intricate of any with which we have to deal. There are a number of possibilities as to its homology:

1. It may represent the primary afferent portion of the mandibular aortic arch. This was the first conclusion of ALLIS (1911.2), who subsequently changed his opinion. WRIGHT (1885), in well advanced embryos of Galeorhinus, found this hyomandibular to arise from the ventral end of the first efferent branchial artery, and thought it difficult to conceive of an aortic arch losing its connection with the ventral aorta and taking up with the efferent vessel of the second arch behind. Yet this is exactly the condition DOHRN (1886) found to obtain in the trout embryo, the two attachments even existing contemporaneously for awhile.

That part of the primary mandibular arch which lies below its commissure with the posterior efferent hyal was called by DOHRN at various times the *arteria thyroidea*, *a. thyro-mandibularis*, and *a. thyro-spiracularis* (figs. 6—8; *TSA*). He found that it dwindled as development proceeded, but thought it persisted as the definitive hyomandibular artery. PARKER (1886) adopted the same idea. RAFFAELE (1892) found this vessel to abort entirely in rays; SCAMMON (1911) figures the same fate in *Squalus*; and DE BEER (1924) states that it disappears in *Catulus* and *Centracion*. No one has ever followed through a series of the later developmental stages of selachians and claimed to have seen the lower part of the first aortic arch thus persist as the hyomandibular artery, so far as an exhaustive literary search has determined. From all available evidence, this first supposition appears highly improbable.

2. The vertical portion of the hyomandibular artery may represent the anterior efferent hyal collector artery, as was first proposed by ALLIS (1916). DOHRN (1886) described the formation of lacunæ on the site of this collector (figs. 8, 9; *AHCA*) at a considerably later period than the proliferation of the posterior hyal collector, but RAFFAELE (1892) explained this sequence as normal, as he found all posterior collectors to develop before anterior ones. The pseudobranchial commissure taps some of these lacunæ on its way to the spiracle, good evidence that this homology is the correct one. But still stronger proof is presented by the fact that in several forms, the hyomandibular taps this commissure (afferent pseudobranchial artery) in the



adult. HYRTL (1872) figured and described the extra large hyomandibular of *Galeorhinus plebejus* and described the same in *Squatina* as anastomosing with the afferent pseudobranchial, a paragraph overlooked by ALLIS, who would have found therein good confirmation of his theory. The latter author worked out the distribution of all vessels connected with the hyomandibular trunk in great detail in *Chlamydoselachus* (1916, 1923) and here also, and the only other recorded case, the main stem anastomoses with the pseudobranchial commissure.

3. It may represent an especially developed nutrient branchial artery, as proposed by WRIGHT (1885). The location and regularity of its course, which is usually strictly parallel to and like that of an efferent collector, and the anastomosis in some with the afferent pseudobranchial are rather against this idea.

4. It may represent an anterior prolongation of the ventral aorta, which has shifted its origin to the hypobranchial system, as suggested by DE BEER (1924). This is altogether unlikely, as no such prolongation of the ventral aorta is known in any shark, either embryo or adult; the actual paired continuation forward being, of course, the mandibular aortic arch.

The writer accepts the second supposition, that of ALLIS, identifying the hyomandibular as the anterior efferent hyal collector artery, for a working hypothesis as being the most plausible and convincing. In all specimens personally dissected, the hyomandibular has this appearance, and the same conclusion was reached before reading of this homology in ALLIS. The artery is so depicted in fig. 9, the actual course as represented being taken from the description of the adult *Chlamydoselachus* (ALLIS) or *Galeorhinus plebejus* or *Squatina* (HYRTL). This morphology can only be substantiated by investigating the later stages of development of several examples of each of a number of species of sharks. In the present-day absence of the anterior hyoidean demibranch, the hyomandibular artery has only a nutritive function, and since the same result could be obtained from several sources or over a number of routes, a certain amount of variation is to be expected.

This homology applies only to the vertical extent of the artery. The basal and longitudinal portion is without doubt the forward continuation of the lateral hypobranchial. In the majority of species, where there is no anastomosis with the pseudobranchial commissure, the hyomandibular passes ectad of the commissure and continues dorsally; where the anastomosis is present, the dorsal section is not developed. In *Raja* (ALLIS, 1912. 3) the dorsal part is probably represented by the temporo-maxillary artery from the paired dorsal aorta.

But we are not yet through with the hyomandibular artery. In *Chlamydoselachus*. ALLIS (1916, 1923) describes further complications. After giving off the anterior hyal efferent, the lateral hypobranchial continues forward, next

sending a second branch dorsally, which ALLIS calls the afferent mandibular. The hypobranchial then goes on to an anastomosis with the mandibularis of the external carotid. The afferent mandibular runs dorsally, first anastomoses, then separates, then anastomoses again with the anterior efferent hyal, and their united trunk joins the pseudobranchial commissure. From or near this union, another branch runs to anastomose with the mandibular of the external carotid, and hence may be (ALLIS) a forward continuation of the intermediate branchial commissural system. ALLIS suggests that this afferent mandibular artery can be either (1) a vestige of the primary mandibular aortic arch, or (2) the posterior efferent mandibular collector artery. From previous comments on the identity of the hyomandibular itself, the latter supposition is chosen by the present writer as the more likely, with the same reservations as to positive proof.

ALLIS shows a decided inclination to represent the aborted lower section of the mandibular aortic arch in the adult by one means or another, an unnecessary as well as improbable conception. Also in these papers, as in nearly all of his work, he lays great stress upon the topographic relationship between minute arteries and adjacent cartilages, ligaments, muscles, nerves, and other blood vessels, the opposite emphasis from that exemplified by CARAZZI. Descriptive anatomy of vascular elements, especially in the hypobranchial system, cannot be pressed too closely, the high degree of variability encountered often nullifying fine details of relationships and preconceived homologies. In *Galeus* (fig. 13), for example, there is a great complexity and asymmetry of arteries, even of quite large ones in this region, rendering a complete description well nigh unreadable and certainly of no specific value whatever. Most of the sharks personally dissected exhibited varying traces of a posterior mandibular collector in addition to the well developed anterior hyoidean (hyomandibular artery). These two and the lateral hypobranchial will produce many insignificant and inconstant muscular rami. No anastomoses of any part of this system with the external carotid were observed, and even allowing for the primitive position of *Chlamydoselachus*, such unions as ALLIS described would appear to be secondary and to furnish no reliable evidence that any part of the external carotid once functioned as an efferent artery of a mandibular or premandibular gill.

THYROID ARTERY — McKenzie, Allen, Allis, Ferguson, Daniel.

Arteria tiroidea — Carazzi.

Coraco-mandibular artery — T. J. Parker.

Figs. 13—16; *TA*.

This vessel curves cephalo-mesially from the hyomandibular, — from that longitudinal portion which is morphologically the lateral hypobranchial

artery, and supplies the thyroid gland and nearby muscles. FERGUSON (1911) in *Galeorhinus* and *Squalus*, states that the thyroid artery may (1) have an independent origin from the ventral pole of the first gill cleft, (2) have a common stem with the hyomandibular, or (3) with the submental. He gives the detailed distribution of twigs to various parts of the gland. DANIEL (1922) shows two separate pairs of vessels in *Notorynchus*, anterior and posterior thyroids, the first from the hyomandibular, the second from the base of the first gill cleft (fig. 14; *PTA*). In any of these cases, the thyroid arteries represent merely specialized muscular rami.

SUBMENTAL ARTERY — T. J. Parker, Allis, Daniel.

Arteria submentalis — Hyrtl (in part).

Figs. 14—16; *SmA*.

The most cephalic branch from the hyomandibular, this vessel follows the curve of the mandible, running to the symphysis, where it usually may be traced to a union with its mate of the opposite side. It supplies the coracomandibularis muscle with numerous fine twigs. ALLIS (1916) holds that this artery is sent in a morphologically ventral direction and is serially homologous with the lateral hypobranchial commissural arteries. DANIEL (1922, p. 169) speaking of the posterior thyroid artery in *Notorynchus*, says that it "in general position takes the place of a first commissural." This homology seems plausible for the posterior thyroid, but is not as reasonable for the (anterior) thyroid or submental. The mouth is a terminal structure and is not morphologically ventral to the hypobranchial artery, but cephalad; identifying the mandible as a modified gill arch will not affect this statement, since the arch had to swing into almost a horizontal position in order to function as a jaw. Secondly, commissures were one of the later acquisitions of the hypobranchial system, and may well have arisen subsequently to the need of an arterial supply for the thyroid gland and submental muscles.

#### Posterior hypobranchial derivatives.

Complexity and variations again render description difficult. Perhaps the most typical arrangement is as follows:

- I. From the dorsal median hypobranchial:
  - A. Dorsal coronary.
  - B. Pericardial.
    1. Epigastric.
      - a. Anastomosis with anterior gastric from coeliac.
- II. From the ventral median hypobranchial:
  - A. Ventral coronary.

## B. Coracoid.

## 1. Epicoracoid.

## a. Anastomosis with subclavian from dorsal aorta.

The lateral hypobranchial never contributes any posterior elements. The coronaries and pericardial may be single or paired, depending upon whether the median hypobranchial forming them is single or double. The coracoid is single, the epicoracoids double by definition, — a purely arbitrary convenience. Though receiving different names in various parts of their courses, all of these vessels are to be regarded morphologically as extensions of the related hypobranchial trunk, produced caudally on demand of posterior tissues. Enlargement of the heart, for example, from the simple tube of *Amphioxus* necessitated some arrangement for nourishing its relatively thick and extensive walls, and the ventral aorta provided the requisite highway over which such nutrient arteries might course.

PERICARDIAL ARTERY — T. J. Parker, Daniel.

Arteria pericardiale — Carazzi.

Figs. 13, 14, 16; *PA*.

1. From paired dorsal median hypobranchials; paired:  
Notorynchus (fig. 14), *Squalus*, *Cestracion*, *Galeorhinus* (fig. 16), *Catulus*.
2. From single dorsal median hypobranchial:
  - a. Dividing into paired epigastric arteries:  
*Galeus* (fig. 13), *Triakis* (right aborted).
  - b. Continuing as a single epigastric:  
*Selache*.

Usually a pair of pericardials become distinct from the dorsal hypobranchial(s) at the cephalic apex of the pericardial cavity. This they penetrate and begin then to diverge, running on or just above the ventral surface of the dorsal wall of the cavity and supplying the tissues of the region en route. They continue beyond, taking up a position on the ventral surface of the cardiac stomach, whose thick wall they pierce with many ramifications. This post-pericardial continuation of paired vessels, or the divided portion of a single artery may accordingly be known as the

EPIGASTRIC ARTERY — Daniel.

Arteria cardio-cardiaca — Carazzi.

Fig. 13, *EA*.

An anastomosis between terminal branches of these arteries and those from the anterior gastric was noted by CARAZZI (1905. 1) in *Catulus*. Sub-

## JULIAN D. CORRINGTON

sequently (1905, 2) he found that this union did not occur in *Selache*, but is silent on the question in other species which he investigated. Such a juncture has not been mentioned in the work of others, many specimens probably not having been searched for this concealed particular. Unfortunately, the present writer can add nothing to this interesting observation. Before noting the desirability of further research on this point, all of my sharks had been secured, and for convenience of storage or shipment had been transected just behind the pectoral fins, destroying any such anastomoses that may have been present.

Frequently both pericardials are equally developed and produce equivalent epigastrics. But various descriptions as well as my own dissections indicate that this character is specifically highly variable, and sometimes the right, sometimes the left pericardial artery is so reduced that it remains confined to the pericardial cavity, and its mate then has the entire function of gastric supply, and continues (1) dividing into more or less symmetrically paired epigastrics (*Galeorhinus*), or (2) trifurcates, with long lateral and a short median stem, as in *Selache* (CARAZZI) and *Triakis*. This condition is to be explained as one of capture of territory, and if stabilized and selected would result in the future perfection of a single azygos trunk, since persistence of the dorsal mesocardium would prevent a mesal course, at least through the pericardial cavity.

CARAZZI records an irregular origin in *Catulus* (1905, 1), where the pericardial is given off by the third lateral hypobranchial commissure, which goes to build up the *ventral* median hypobranchial artery; and PARKER figured a single pericardial in *Galeorhinus*, arising from the third left commissure and later dividing.

CORACOID ARTERY — Daniel (in part).

Arteria coracoidea — Carazzi.

Arteria epigastrica — Hyrtl (in *Cestracion*).

Epigastric artery — G. H. Parker & Davis.

Hypobranchial artery — T. J. Parker (in part).

Figs. 11, 12, 15; *CdA*.

This name has usually been applied alike to the single stem and to its forked continuations, but CARAZZI restricted it to the median trunk, terming the paired continuations the epicoracoid arteries. While the terminology of the hypobranchial components is already quite complex, this addition is both desirable and justified, and has therefore been here adopted. If the median hypobranchial is double, and the vessels merely continue backward, as in *Squatina*, there is no coracoid artery; again, if a single hypobranchial gives off arteries which are paired from their beginning, as in *Notorynchus* (fig. 14)

## MORPHOLOGY OF THE ANTERIOR ARTERIES OF SHARKS

and sometimes in *Catulus*, there is no coracoid. In either case these vessels are properly spoken of as epicoracoids. However, if the single median hypobranchial produces a single stem, which only later divides, as in *Cestracion* (fig. 15), *Galeus* (fig. 12), *Selache*, and sometimes *Catulus*, the definitive coracoid artery is present.

## EPICORACOID ARTERY.

*Arteria coracoidea* — Pitzorno.

*Arteria epicoracoidea* — Carazzi.

*Arteria thoracica ventralis* — Pitzorno.

Coracoid artery — G. H. Parker & Davis, Daniel (in part).

Hypobranchial artery — T. J. Parker (in part).

Figs. 11, 14; *EpcA*.

Arising from any of the above mentioned sources, the epicoracoid artery diverges from the meson, running along the ventro-lateral wall of the pericardial cavity, and crosses the coracoid cartilage ventrally, at or near the glenoid fossa. In this immediate vicinity, but varying somewhat with the species, it gives off the anterior lateral artery and then anastomoses with the subclavian. PITZORNO (1905) describes two types of such a union, an *anastomosi coraco-thoracica* (*Galeorhinus*, *Selache*) and an *anastomosi thoraco-thoracica* (*Squatina*), thinking of the epicoracoid as a different vessel because of the presence in the first case and absence in the second of a median cephalic union of the two. No such difference obtains as a matter of fact. The anastomosis with the subclavian has been determined for *Notorynchus* (fig. 14), *Galeorhinus*, *Squatina*, and *Triakis*; and among other orders of elasmobranchs, in *Chimæra*, *Raja*, and *Pristis*. It is known to be lacking so far only in *Cestracion*, *Catulus*, *Galeus*, and *Squalus*, though it may fail as an individual variation in others.

DANIEL described a posterior coronary artery arising from the epicoracoid in *Notorynchus* (fig. 14; *PoCA*) and passing mesially to supply the sinus venosus. Heretofore this vessel was thought to be restricted in the *Chondropterygia*, to rays.

Among abnormal origins for the epicoracoids may be mentioned (1) that of PARKER (1886) for *Galeorhinus*, where both vessels arise from a stem that is probably to be considered as the left median ventral hypobranchial; (2) that of CARAZZI (1905. 2) in *Catulus*, where the epicoracoid bases have migrated out upon the last lateral hypobranchial commissures for a short distance; (3) that of the same author in another specimen of *Catulus*, and also in *Squatina*, where a pair of epicoracoids come off from the pair of dorsal median hypobranchials; and (4) a personal observation on *Triakis*, where both epicoracoids take origin from a single median dorsal hypobranchial, passing down along the sides of the ventral aorta on their way

out to the pectoral region. Such a change as this last might happen in cases where the hypobranchial commissures split upon approaching the ventral aorta, one branch going to build up the dorsal hypobranchial, and another the ventral. This state of affairs is figured for *Galeorhinus* by HYRTL (1872), PARKER (1886), and FERGUSON (1911), and the first commissure of the right side of *Galeus* (figs. 12, 13) shows a similar condition. Through such transverse loops around the ventral aorta, a ventral vessel like the epicoracoid may be supplied by a dorsal trunk.

T. J. PARKER (1886) had an erroneous conception of the hypobranchial system, in that he supposed the flow of blood to be cephalad through the epicoracoids, the source being the subclavians. This cannot be true, as several authors have noted, because (1) the anastomosis with the subclavian is frequently lacking, (2) the subclavian is not large enough to furnish both the hypobranchial and pectoral fin circulation, and (3) relative calibre and the direction of collaterals of the vessels concerned indicates otherwise.

#### ANTERIOR LATERAL ARTERY — T. J. Parker, Daniel.

Arteria laterale — Carazzi.

Lateral artery — Kingsley.

Fig. 14, *ALA*.

Arising from the epicoracoid, this artery passes caudo-laterally to the side of the body wall where it turns posteriorly, and concealed beneath the lateral vein, runs to an anastomosis with the posterior lateral artery from the iliac. Both laterals doubtless represent hypertrophied muscular rami, approaching along a common channel (inter-fascicular) which formed a line of least resistance, and ultimately meeting and fusing. The entire trajectory of the anterior lateral lies without the region dealt with in this article, but the artery is considered because of its origin from the epicoracoid.

#### EXTRABRANCHIAL ARTERY.

Fig. 11, *ExbA*.

At the point where the coracoid artery divides into epicoracoids, or at a corresponding site in sharks which do not possess a coracoid artery, a number of fine muscular rami depart and extend thence with some degree of regularity to the superficial tissues of the ventral pole of each gill. Each then passes around the periphery of its gill, becoming exhausted upon approaching the dorsal surface. These vessels have not previously been described, yet they were found to be quite distinct in every gill of all specimens dissected, and the writer would propose for them the name of extrabranchial artery, since they follow quite closely the cartilages of the same designation.

IV. THE CORONARY SYSTEM.

A collective synonymy is first presented:

CORONARY ARTERY — Monro, McKenzie, T. J. Parker, G. H. Parker & Davis, Allen, Allis, Kingsley, Daniel.

Arteria coronaria — Pavesi, Carazzi.

Kranzarterie — Müller, Hyrtl.

Figs. 12—17; *DCA*, *VCA*.

While a part of the hypobranchial system, these vessels form a compact and limited group which may conveniently be surveyed in a separate section.

Variation is here at its height and anastomoses run riot. CARAZZI (1905, 1—2) found that in *Catulus* the differences in his several specimens were so great that he could not establish a specific type, and it is to be anticipated that when more individuals of other forms will have been examined, the same condition will be found to obtain. As in other sections of the hypobranchial system then, descriptions are to be understood as taken usually from a single example and cannot be relied upon as typical without further investigation. It is nevertheless well worth while to place such observations on record.

Though the coronaries in some species appear as paired (right and left) vessels, it is evident from their origin that they are really dorsal and ventral, one from each median hypobranchial trunk. Morphologically they are to be regarded as posterior extensions from these primary lines. The writer can see no virtue in the terms anterior and posterior coronaries (KINGSLEY, 1907), as applied respectively to the ventral and dorsal units. In general, the attachment of the coronaries depends on the persisting condition of the median hypobranchials. Thus, in *Notorynchus* (fig. 14) there is one

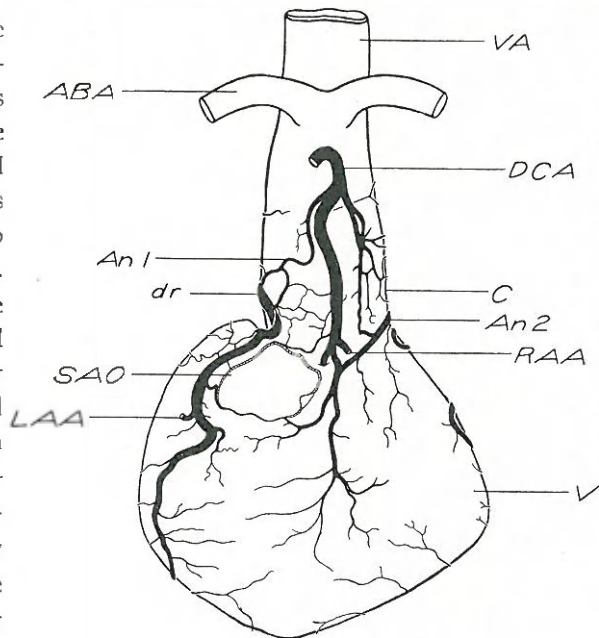


Fig. 17. Coronary arteries, *Galeus glaucus*, dorsal aspect.

*ABA* afferent branchial artery; *An* anastomoses between dorsal and ventral coronary arteries; *C* conus arteriosus; *DCA* dorsal coronary artery; *dr* dorsal ramus, left ventral coronary artery; *LAA* left auricular artery; *RAA* right auricular artery; *SAO* sinu-auricular opening; *V* ventricle; *VA* ventral aorta.



from each of the pair of dorsal median hypobranchials, and none from the single ventral hypobranchial, which produces only the epicoracoids; hence the coronaries are here right and left dorsals. *Cestracion* (fig. 15) has two dorsals and a single ventral; *Galeus* (figs. 12, 17), *Carcharias*, *Triakis*, *Selache*, and sometimes *Catulus* have one of each; and *Galeorhinus* has two ventrals with no dorsals. Finally, *Centracion*, and sometimes *Galeorhinus* and *Catulus* have a full set of two dorsals and two ventrals. The general tendency seems to be strongly favourable toward concentrating the nurture of the heart in a single dorsal and single ventral vessel, each of which divides upon attaining the ventricle.

CARAZZI (1905. 1) describes the following variations in *Catulus*:

1. One dorsal and one ventral.
2. One dorsal and two ventral, the latter
  - a. separate,
  - b. united by anastomosis.
3. Two dorsal and two ventral.

Later (1905. 2), in the same species, he figured:

4. No dorsal and two ventral, regular in origin.
5. No dorsal and two ventral, from third lateral hypobranchial commissure.
6. Two dorsal and no ventral, the dorsals both coming from the left dorsal hypobranchial, and running onto the right and left sides of the ventral surface of the conus and ventricle.

In the further course of the coronaries, each branches repeatedly and sends anastomosing twigs to the other or others. If the coronaries approach the ventricle as right and left vessels, each divides to supply the dorsal and ventral surfaces of their respective sides; if they arrive as dorsal and ventral, each forks to provide both sides of their surface. The usual tendency in all cases is for the production of four secondary trunks, a right and left dorsal and a right and left ventral.

The conus is supplied en route and the main stems continue to the ventricle, which receives about nine-tenths of all coronary blood. Many twigs disappear from the surface while yet of relatively large calibre, penetrating to the deeper layers of the myocardium and there continuing onward. The auricle receives proportionally a small volume of blood, due to the thinness of its wall, and there are usually no vessels of a size visible to the unaided eye upon the sinus venosus.

PAVESI (1874) and PARKER and DAVIS (1899, 1901) worked on the coronary circulation of sharks, but added little to the accounts of HYRTL. The only detailed studies are those of CARAZZI.

These vessels bring to a close the long and involved description of the hypobranchial system, a group of arteries which were more or less neglected

by all the earlier writers save HYRTL. CARAZZI, who has performed the sole intensive and valuable research in this system, stresses its independence and importance. It is not, he says, a subsidiary of the dorsal aorta, but is primarily separate and like a smaller, shorter, ventral mate of the aorta. The efferent branchial system may then be divided into dorsal and ventral portions, each with its longitudinal distributing trunk. These sections become secondarily connected through a possible development of three anastomoses:

1. Epicoracoid—subclavian.
2. Anterior lateral—posterior lateral.
3. Epigastric—anterior gastric.

When to these are added the regular communications through the efferent collectors and efferent branchial arteries, it is seen that the hypobranchials and dorsal aorta may be connected through four sets of channels. The developmental cause of each of the above three anastomoses is evident, but their physiological importance is not so clear. The fact that they are, in the main, present in some forms and not in others, and that they vary markedly in different individuals, would indicate that their value is slight and that the utility of circulation in these regions is not greatly affected in either case. Each anastomosis is due to the gradual expansion into the same territory of branches from two opposed sources. In none of these cases has there been a capture of one system or part by the other, though possibilities are not lacking for such an event in the future. Perhaps the hypobranchials, through the epicoracoid, will eventually supply the pectoral fin, while the subclavian, robbed of its major and original function, becomes a degenerate muscular ramus of the dorsal aorta. This anastomosis is the only one of the three whose components are not in equal balance; either the epicoracoid or the subclavian is dominant in supplying the brachial circulation.

#### V. THE CAROTID SYSTEM.

Under this convenient heading may be described all of those dorsally disposed arteries which nourish parts of the head anterior to the first gill cleft. The only vessel of a ventral origin which invades any part of this territory is the hyomandibular, from the lateral hypobranchial. The vessels concerned in this chapter arise as follows:

1. Dorsal aorta continued forward as paired dorsal aortæ, sections of which are known as:
  - A. Internal carotid, usually giving origin to the
    - a. External carotid artery.
  - B. Cerebral artery, with subdivisions, and originating the
    - a. Optic artery.

2. From the posterior efferent hyal collector artery:
  - A. Efferent hyal artery, generally termed the common carotid and sometimes giving off the
    - a. External carotid artery.
  - B. Afferent pseudobranchial artery, through the first intermediate commissure, running to the spiracular retia and thence continuing as the
  - C. Efferent pseudobranchial artery, the anterior carotid or ramus anastomoticus of authors, which forms the
    - a. Ophthalmic artery, and then unites with the paired aorta.

A review of developmental stages (figs. 1—9) will serve to recall the morphological relationships of these vessels. For convenience of description

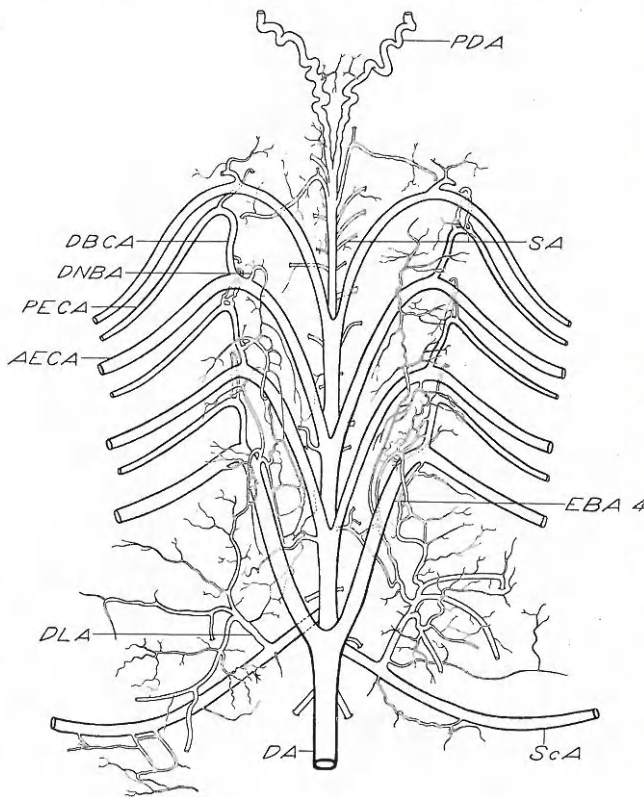


Fig. 18. Efferent branchial system, *Galeus glaucus*, ventral aspect.

*AECA* anterior efferent collector artery; *DA* dorsal aorta; *DBCA* dorsal branchial commissural artery; *DLA* dorsal lateral artery; *DNBA* dorsal nutrient branchial artery; *EBA* efferent branchial artery; *PDA* paired dorsal aorta; *PECA* posterior efferent collector artery; *SA* segmental artery; *ScA* subclavian artery.

it is customary to divide the dorsal aorta into sections, and each writer has his own ideas on this subject, based usually on the conditions presented in a single species. The present author here suggests three divisions for anatomical treatment of the paired dorsal aorta, applicable in all selachians. These are, from rear to front: branchial, pseudobranchial, and medullary.

*EBA* 4 PAIRED DORSAL AORTA, BRANCHIAL SECTION.

Arteria vertebralis — Carazzi.

Erste Aortenwurzel — Hyrtl.

Hyoidean epibranchial — T. J. Parker.

Lateral dorsal aorta — Allis.

Paired dorsal aorta — Daniel.

Part of the internal (or posterior) carotid of many authors.

Figs. 18—22; *PDA*.

This section begins at the posterior origin of the paired aortæ and ends at the confluence of the efferent hyal artery, coming from the

posterior collector of the hyoid gill. The paired trunks diverge from the median dorsal aorta some little distance cephalad of the entrance of the first branchial efferents in most sharks, as *Galeus* (fig. 19) or *Catulus* (fig. 21); while in a few, as *Squalus* (fig. 22), they arise just in front of the union of the second efferents, and themselves receive the first pair. Though usually pursuing a straight course, the paired aortæ are quite tortuous in *Galeus* (fig. 19).

Apparently the idea of twin aortæ was not easily assimilated by earlier writers, and owing to its course, small size, and relationships, this section was long considered to be the efferent hyoidean, following HYRTL and PARKER. DOHRN (1886) depicted the true state of affairs, though he seemed not to grasp its full significance until later, and then came the familiar plate of BOAS (1887) on the morphology of the aortic arches, which is well constructed with an eye to emphasizing the correct interpretation. Such a major error should have become obvious long before it did, and this case furnishes a striking example of the futility of attempting homologies upon the basis of comparative anatomy alone, and without a thorough grounding in the developmental history of the region considered.

In size, this part of the paired dorsal aorta may be quite well developed, as in *Galeus* (fig. 19), where it is very nearly as large as an efferent branchial artery. HYRTL's figure of *Catulus* (fig. 21, this paper) gives this vessel an exceptional calibre, much larger than was found in the same species by CARAZZI. Usually (as *Galeorhinus*, PARKER) it is no larger than the main stem of a coronary artery, and CARAZZI (1905, 2) has figured a practically vestigial condition in *Selache*, *Squatina*, and *Catulus*, where a forward continuation may fail, the slender vessel ending in a few terminal threads. In rays (HYRTL, 1858) the failure is complete. CARAZZI terms this section the vertebral artery, "per comodità e senza occuparsi di omologie" (p. 91), though he fully recognized its identity as the paired aorta. Like the median aorta, this paired division gives off segmentals (vertebrals), one of the most reliable criteria for the identification of any part of the adult aorta, and as he found that nearly all blood transported in these species was expended in actual vertebrals, and the aorta continuing as a slender thread or even network, he chose the name vertebral for the entire section. Needless to say, there can be no justification for such an unnecessary confusion of terms with the attendant danger of wrongly interpreting the true morphological estate.

#### UNPAIRED HEAD AORTA.

Cranial aorta — Ayers.

Kopfaorta — Hyrtl.

Fig. 21, *UHA*.

This imaginary artery has been one of the causes operating to delay recognition of the paired dorsal aortæ. First described by HYRTL (1872)

in *Catulus*, its status and importance were established by the author's prestige. Later AYERS (1889) reported the same vessel in *Chlamydoselachus*, seemingly to place this artery on a firm basis. But many other workers have since been unable to find any trace of it whatever in any species, either in embryo or adult. DOHRN attempted to explain AYERS's paper but only confused matters the more, and it remained for ALLIS (1911, 2) to reexamine the same species and to expose so many other glaring errors in the previous work that AYERS's description has been entirely discredited.

With an accurate investigator like HYRTL, however, the case is different. DOHRN supposed the paragraph and figure on the unpaired head aorta to be due to mistaken observation, but CARAZZI declared such a mistake to be impossible. I am inclined to agree with CARAZZI, as no doubt will the reader also after a glance at fig. 21. In foregoing descriptions of all anterior arteries of the head it will have been noted that *Catulus* provides far more exceptions and abnormalities, if indeed there is any normal type at all for this genus,

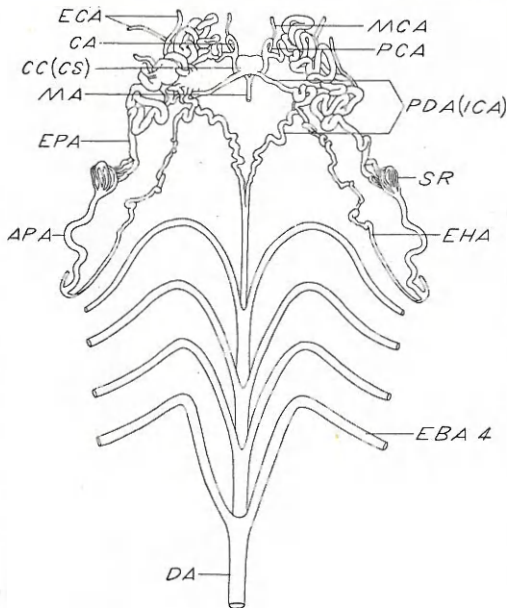


Fig. 19. Carotid system, *Galeus glaucus*, ventral aspect.

APA afferent pseudobranchial artery; CA cerebral artery; CC carotid crossing; CS cephalic sinus; DA dorsal aorta; EBA efferent branchial artery; ECA external carotid artery; EHA efferent hyal artery; EPA efferent pseudobranchial artery; ICA internal carotid artery; MA myelonal artery; MCA middle cerebral artery; PCA posterior cerebral artery; PDA paired dorsal aorta; SR spiracular retia.

than any other described form, and in this fact lies a possible explanation. What HYRTL saw was probably a fused and cephalically directed pair of segmentals, such as I have myself observed in a specimen of *Cestracion tiburo*, where a slender twig proceeded forward from between the forked origins of the paired aortæ, later to divide, pass up along each side of and to pierce the vertebral column, therein to anastomose with the myelonal artery. In any case HYRTL's vessel is certainly not genuine aorta, since the paired aortæ are shown as well developed.

These paragraphs furnish the most striking case encountered in this investigation illustrating the danger of (1) erecting specific types from the dissection of a single specimen; (2) not making adequate allowance for a possible high degree of variability; and (3) attempting to establish adult homologies without thorough embryological prepara-

## MORPHOLOGY OF THE ANTERIOR ARTERIES OF SHARKS

tion. AYERS followed his incomplete and erroneous description of the head arteries in *Chlamydoselachus* with a scheme purporting to explain the morphology of the carotid and related vessels in the entire vertebrate series. The results of this paper were adopted without question for some time, though it rendered the Frilled Shark unconfomable with other species in many respects and otherwise caused considerable confusion, until ALLIS straightened out the matter, brought *Chlamydoselachus* into line with other plagiostomes, and demonstrated the entire fallacy of homologies established twenty-two years previously.

PAIRED DORSAL AORTA,  
PSEUDOBRANCHIAL  
SECTION.

Carotide interne — Milne Edwards.  
Carotide posteriore — Carazzi.  
Carotis interna — Hyrtl, McKenzie.  
Carotis posterior — Müller, Dohrn.  
Internal carotid artery — Allen,  
Allis, Kingsley, Daniel.  
Part of posterior carotid plus com-  
missure "w" — T. J. Parker.

Figs. 19—22; *PDA*.

Resuming the course of the paired dorsal aorta: from the point of admission of the hyoid-ean efferent the aorta makes practically a right-angled turn from a cephalo-lateral to a cephalo-mesal direction, pierces the chondrocranium, and embedded deeply within cartilage, unites with its mate of the opposite side. This section is the one commonly known as the internal carotid, which term is admissable descriptively, but which is unnecessary and has no morphological existence.

Reinforced by the confluence of the large efferent hyal, the aorta now takes on a

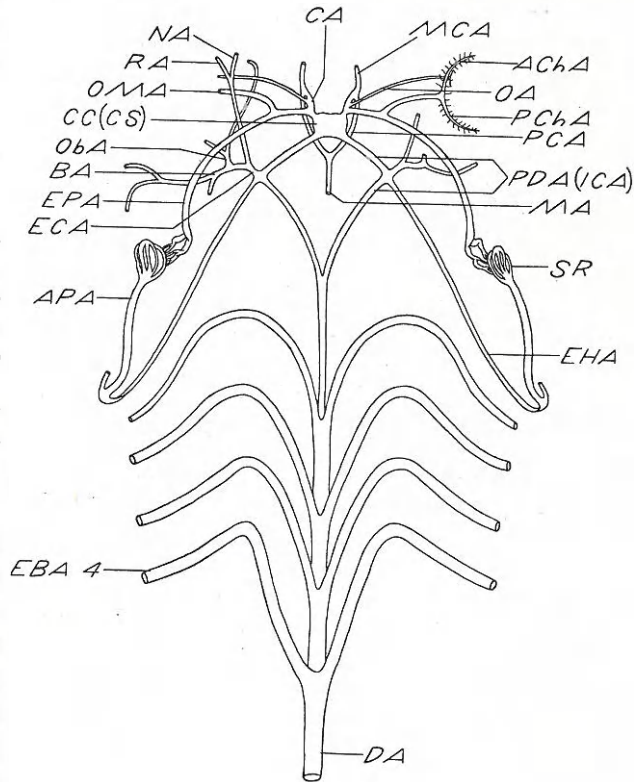


Fig. 20. Carotid system, *Galeus glaucus*, ventral aspect, diagrammed to explain fig. 19 and to reveal vessels otherwise hidden.

*AChA* anterior choroidal artery; *APA* afferent pseudobranchial artery; *BA* buccal artery; *CA* cerebral artery; *CC* carotid crossing; *CS* cephalic sinus; *DA* dorsal aorta; *EBA* efferent branchial artery; *ECA* external carotid artery; *EHA* efferent hyal artery; *EPA* efferent pseudobranchial artery; *ICA* internal carotid artery; *MA* myelonal artery; *MCA* middle cerebral artery; *NA* nasal artery; *OA* optic artery; *ObA* orbital artery; *OMA* ophthalmic artery; *PCA* posterior cerebral artery; *PChA* posterior choroidal artery; *PDA* paired dorsal aorta; *RA* rostral artery; *SR* spiracular retina.

## JULIAN D. CORRINGTON

diameter commensurate with the work which it has yet to do. Considering (1) the usual reduced calibre of the branchial part of the paired aorta, and (2) the uniformly larger size and straight continuation of the efferent hyal with the pseudobranchial section, the mistake of anatomists in regarding the two larger and continuous vessels as one and the same trunk is pardonable. These conditions provide a second reason for the delayed recognition of the true nature of the paired aorta and again emphasize the danger of a one-sided investigation. The efferent hyal thus is also commonly identified as the internal carotid. When, however, a writer is aware of the real morphology, as CARAZZI, and still persists in labelling drawings in this obsolete fashion it is time to complain and to urge that for the sake of future stability such terms be dropped; the efferent hyal can at least be designated as such consistently.

At or near the confluence of the efferent hyal with the paired dorsal aorta, the external carotid is given off.

COMMON CAROTID ARTERY — T. J. Parker, Allen, Allis, Kingsley, Daniel.

Carotis communis — Stannius, Hyrtl.

Kopfarternen — Vogt & Yung.

Les artères de la tête — Cuvier & Valenciennes.

Fig. 21, 22; *CCA*.

This is another term for which there is no real application. Its usage depends upon the particular author's interpretation of the two carotids, external and internal, to which it gives origin by implication. Two figures have here been so labelled as to give an idea of the artificiality of such a designation: in *Catulus* (fig. 21; *EHA*, *CCA*) the hyoidean efferent apparently produces the two carotids, while in *Squalus* (fig. 22; *PDA*, *CCA*) it is the paired aorta which so functions.

CAROTID CROSSING.

Figs. 19—23; *CC* (*CS*).

This anglication of HYRTL's description applies to the union of the two pseudobranchial sections of the paired aortæ (internal carotids) within the basis cranii. The actual morphological condition is a limited persistence of an embryonic structure known as the

CEPHALIC SINUS — Allis, Scammon.

Kopfsinus — Rückert.

Sinus cephalicus — Raffaele.

Described but not named — Platt.

Figs. 1—9, 19—23; *CS*.

231

MORPHOLOGY OF THE ANTERIOR ARTERIES OF SHARKS

This large space (fig. 1; CS) is a common chamber formed by the mesal fusion of the two mandibular aortic arches and two dorsal aortæ, superimposed upon the gut at the most cephalic point attained by any vascular elements at this early stage of development. In a 23 somite *Pristiurus* embryo, MOLLIER (1906) described the mandibular arch as united with the aorta of its own side, but both rudiments were as yet without a lumen. By the 25 somite stage the two arches had united in the mid-line above the gut, and the first indication of the hæmocœle was visible nearby as a hollowing-out. A few cells indicated the site of the hyoid and third arches. Attainment of 40 somites found the first pair of arches well developed and fusing into a large cephalic sinus over the foregut, and all of the elements present were hollow.

As given by SCAMMON (1911) for *Squalus*, the development of the sinus is here reproduced in figures 1—3. First in evidence at about 25 somites, it enlarges rapidly so that by a 50 somite stage (fig. 3) it attains relatively colossal proportions. Immediately after its first appearance, a sprout begins to grow out forward from the lower anterior margin of the sinus, the vena capitis medialis (fig. 1; *VCM*). This vessel keeps pace with the increase in size of the parent sinus, and soon (fig. 2) sends a branch backward. Other sprouts then appear from the primary one until in all five pairs of good-sized trunks run outward, and were designated by RAFFAELE (1892) as the VI—V5. His VI is situated ventrally, at the peak of the mandibular arch, and becomes the ophthalmic artery (fig. 3; *OMA*), but the V2—V5 are to form veins and remain in connection with the vena capitis medialis, the future jugular or anterior cardinal vein (sinus). In a 65 somite stage these veins have all separated from the cephalic sinus (fig. 4) and henceforth are not concerned in a history of head arteries. The parent blood space is by this means greatly reduced in calibre, but in an 86 somite embryo (fig. 5) still has a considerable fore and aft extent. During the final stages of development it ceases to keep pace with the growth of related vessels, and ultimately there is left only a chamber whose longitudinal measurement is no greater than its diameter.

The cephalic sinus was first designed by RÜCKERT (1888), since when its significance has been discussed by various writers. PLATT (1891. I) with *Squalus* embryos, described a pair of head cavities cephalad of the pre-mandibular, which she termed the anterior. In the development of the mandibular aortic arches she observed the formation of the sinus, which was here pierced by the curved tip of the notochord and nearly severed, while just below and upon each mandibular arch appeared sprouts representing the ophthalmicæ magnæ. Now since DOHRN had considered these arteries as remnants of a premandibular aortic arch, related to the premandibular head cavities, PLATT suggested that the cut-off, anterior portion of the cephalic



sinus involved the last vestiges of a pair of arches still further craniad, and segmentally associated with her anterior head cavities. RAFFAELE (1892) also thought the sinus to represent the remains of one or more pairs of premandibular aortic arches.

In my opinion, these conclusions are untenable for the following reasons:

1. The cephalic sinus, being formed by a coalescence of the mandibular arches and dorsal aortæ at the apex of the loop, appears only after the mandibular arches are fully formed, whereas premandibular arches should precede them in sequence of development.

2. PLATT later (1891. 2) found that the anterior cavities were not serially homologous with the other head cavities, since they originate as cut-off portions of the alimentary canal, isolated by the down growth of the infundibulum.

3. SCAMMON (1911), also with *Squalus*, confirmed the presence of the anterior cavities, but other workers have failed to find them in different species. GOODRICH (1919), for example, could not discover them in *Catulus* (*Scyllium*), and they are now generally thought to be restricted to *Squalus*, or at best to a few forms, and to involve a cœnogenetic adaptation which cannot at present be explained.

4. The bulk of the sinus and its derivative vessels separate from the aorta and become incorporated with the venous system.

5. There is no evidence whatever to support such a conclusion.

6. There is no satisfactory evidence of the former existence of any gills cephalad of the posterior mandibular demibranch, a point to be dealt with more fully later.

To my notion, the cephalic sinus has no especial significance at all and is to be regarded as rudimentary rather than vestigial. We do not understand the cause of fusion of such primarily paired structures as the dorsal aortæ, but once fused into such a sinus it is not difficult to conceive of this site as the most favourable one from which the head veins are to develop; in fact there is no other source available at this early period. The sinus is then merely a formative sac for the cephalic venous system, persisting in a greatly reduced estate after the severance of its derivatives.

In many sharks, as *Heptranchias* and *Galeus* (fig. 19), the two aortæ communicate in the adult by means of a somewhat rectangular chamber; *Chlamydoselachus* and *Spinax* have a commissural anastomosis; and *Notorynchus* and sometimes *Squalus* possess a short common stem. In *Galeorhinus* and *Catulus* the two trunks appear to cross, but HYRTL found that in the latter genus (fig. 21) they are in communication at this chiasma, while PARKER apparently did not investigate this point in *Galeorhinus*. ALLIS (1912. 2) gives a good discussion of this apparent crossing, which in such sharks as the last two mentioned may be a real one functionally. The two

MORPHOLOGY OF THE ANTERIOR ARTERIES OF SHARKS 233

currents set toward each other and must come into sharp collision in species having the common chamber, producing a tendency to shift the union vertically and to allow each of the streams to continue across the mid-line without so much interference. Thus the left paired aorta would supply the right side of the head, and vice versa. One might think of the adult shark as exhibiting a tendency to "outgrow" the functional handicap imposed by this embryonic fusion.

CIRCULUS ARTERIOSUS CEPHALICUS — Hyrtl.

Fore and aft union of the paired aortæ produces a diamond-shaped continuous vascular loop which has received the above name, — one of purely descriptive interest. In the older terminology, this circle is composed of the following elements from rear to front: dorsal aorta, hyoidean epi-branchial, internal carotid, carotid crossing (see any figures of the carotid system). In rays, where the hyo-glossopharyngeal section of the paired aorta is absent, a descent must be made to the dorsal commissural artery between these two gills to complete the circuit. ALLIS (1912. 3) thought that this route traversed the actual paired aorta, an assumption which is impossible if the commissurals are the same in rays as in sharks, as is commonly supposed. RIDWOOD (1899) studied the circulus in a large number of fish groups and constructed several types, but found them artificial and possessing no systematic value.

PAIRED DORSAL AORTA,  
MEDULLARY SECTION.

Released from the carotid crossing, each paired aorta again diverges from the meson and passes into the cranial cavity, running along the base

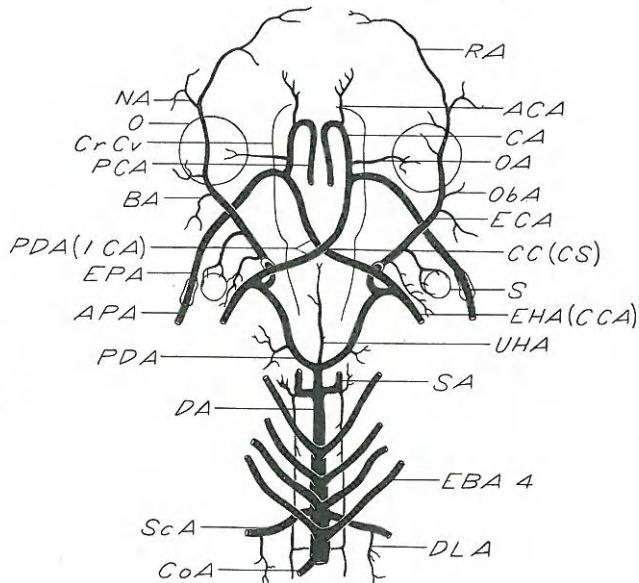


Fig. 21. Carotid system, *Catulus caniculus*, ventral aspect. From HYRTL.

ACA anterior cerebral artery; APA afferent pseudo-branchial artery; BA buccal artery; CA cerebral artery; CC carotid crossing; CCA common carotid artery; CoA coeliac axis; CrCv cranial cavity; CS cephalic sinus; DA dorsal aorta; DLA dorsal lateral artery; EBA efferent branchial artery; ECA external carotid artery; EHA efferent hyal artery; EPA efferent pseudo-branchial artery; ICA internal carotid artery; NA nasal artery; O orbit; OA optic artery; ObA orbital artery; PCA posterior cerebral artery; PDA paired dorsal aorta; RA rostral artery; S spiracle; SA segmental artery; ScA subclavian artery; UHA unpaired head aorta.

and sides of the brain to a confluence with the efferent pseudobranchial, and thereafter becoming known as the cerebral artery, to which a separate section will later be devoted. The medullary division of the paired aorta may be extremely short (*Galeus*, figs. 19, 23 A) or have quite an appreciable extent (*Catulus*, fig. 21; *Squalus*, fig. 22), and in the older nomenclature is still the internal carotid. From this division or from the cerebral artery the optic artery arises.

Sharks have inherited all of these divisions of the carotid system. In *Amphioxus* the paired dorsal aortæ extend forward beyond the first gill cleft, that of the left side remaining small and simple, and we may no doubt add, normal. The right paired aorta gives off an arch-like vessel which MÜLLER supposed was a remnant of a most anterior aortic arch. This branch opens out into a wide vascular expansion at the front end of the pharynx, flanking the velum, and ends blindly below by the right metapleur. Dorsally, the right aorta continues cephalad as a complex of vessels to the groove of

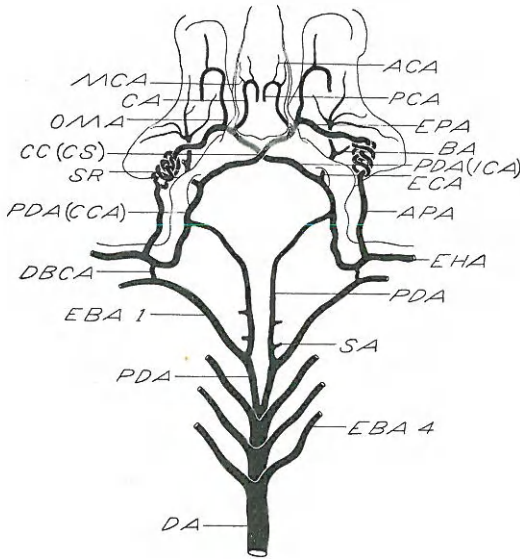


Fig. 22. Carotid system, *Squaius acanthias*, ventral aspect. From HYRTL.

ACA anterior cerebral artery; APA afferent pseudobranchial artery; BA buccal artery; CA cerebral artery; CC carotid crossing; CCA common carotid artery; CS cephalic sinus; DA dorsal aorta; DBCA dorsal branchial commissural artery; EBA efferent branchial artery; ECA external carotid artery; EHA efferent hyal artery; EPA efferent pseudobranchial artery; ICA internal carotid artery; MCA middle cerebral artery; OMA ophthalmic artery; PCA posterior cerebral artery; PDA paired dorsal aorta; SA segmental artery; SR spiracular retia.

HATSCHEK, situated in the roof of the oral hood to the right of the notochord. The complex itself supplies the oral cirri, and there is a cross commissure between right and left aortæ beneath the notochord. All of which involved estate evidently has nothing to do with the conditions in higher forms. The shark embryo presents a clear and convincing picture, but *Amphioxus* has become so highly modified in this respect as to render an understanding very difficult. All that can be said is that the paired dorsal aortæ in each case are homologous structures, and that their extensions into the head beyond the aortic arches are doubtless comparable in general and may if desired be termed internal carotid arteries.

In Cyclostomes there are a few individual differences in the various groups, but on the whole the carotid system in this Class is quite uniform. The efferent arteries from each gill pass upward to the median

dorsal aorta, midway in which course they are serially connected by a longitudinal vessel, usually termed the "common carotid." This trunk is no more than a connector and is entirely similar to and possibly homologous with a chain of dorsal branchial commissures such as persists to-day in *Chlamydoselachus*. Caudally, this trunk arises on each side from the aorta by means of a stem that is morphologically the most posterior efferent branchial. It continues far forward into the head beyond the gill area, but we know from recent work that some three gills have been dropped out here, and the head secondarily lengthened, all in response to the highly specialized feeding habits. The longitudinal commissural artery forks cephalically into a median "internal carotid" and lateral "external carotid." The former joins the aorta and is hence recognizable as the persistent most anterior efferent branchial; the latter functions as an external carotid, but arising as it does from a different aortic arch from that in sharks, cannot be strictly homologous with the selachian external carotid.

The united internal carotids are then said to continue forward as the *arteria vertebralis impar*, but it is really the aorta which so continues, for behind the pituitary sac it divides into two branches, each of which then runs on cephalically, lateral and ventral to the brain, to supply the nasal region. As will be evident, this latter arrangement appeals strictly to the cerebral system of elasmobranchs, and the forking of the aorta is of course its division into paired aortæ, and the section to which the designation of internal carotid should be restricted, if used at all. The internal carotids have no more real existence here than in sharks.

Cyclostomes, then, present a good primitive picture of the ancestral condition of the main vessels of this region in preselachian forms. The dorsal aorta effects the sole internal cranial supply, and the external carotid, from the first efferent branchial, is the principal source for external structures. No such modifications as in sharks have as yet affected the efferents of the first two arches, and hence the arrangement is far simpler.

OPTIC ARTERY — Allen, Allis, Daniel.

*Arteria centralis retinæ* — Dohrn, de Beer.

*Arteria ottalmica* — Emery.

*Arteria ottica* — Carazzi.

*Ophthalmica* — Greil.

*Ophthalmica minor* — Müller.

Figs. 20, 21, 23 A; *OA*.

Usually this vessel originates from the paired aorta just before the latter breaks up into the cerebral arteries, but CARAZZI figures the optic as coming from the anterior cerebral in *Catulus*, probably a good example of shifting

at the base. Always slender, the optic artery is sometimes very fine indeed (Galeus) and difficult to follow. It usually becomes attached to the ventral surface of the optic nerve, with which it penetrates the cranial wall and outer coats of the eye, functioning solely to supply the retina. At the level of the sclera this vessel has to pass very close to the ophthalmic artery, but I have never found any indications of an anastomosis between the two.

While a great many speculations have been made as to the morphology of the ophthalmic, its lesser brother has gone unmentioned. Unquestionably this vessel is but one of the many small branches from the cerebral artery; one which has been carried out along with the extension of the optic stalk. Cerebral branches nourish the brain; hence they would naturally supply the retina. VIRCHOW (1890.1) discusses all blood vessels of the eye, and DENISSENKO (1880) the histology of the vascular supply to the retina. ФРОРИЕВ (1906), in describing the development of the eye of elasmobranchs, states that the first vessels appear therein (Torpedo) at the 14.5 mm. or 71 somite stage.

#### EFFERENT HYAL ARTERY — Allis.

Carotide posteriore — Carazzi (in part).

Carotis communis — Hyrtl.

Hyoidean efferent — Daniel.

Posterior carotid — T. J. Parker (in part).

Figs. 19—22; *EHA*.

The posterior efferent collector artery of the hyoid arch, unlike all other efferent collectors, has retained communication both fore and aft by means of dorsal branchial commissural arteries. Posteriorly a commissure unites it with the anterior first branchial collector, while cephalad the base of the efferent hyal bends around forward as if to unite with an anterior collector. But no such vessel being present at that point, the further course is continued toward the dorsal aorta as the efferent hyal proper. Also unlike the branchial efferents, which turn back to reach the single aorta, this artery runs forward to unite with the paired aorta. Mistaken identities in this connection have already been discussed. An interesting condition was found in Galeus (fig. 19; *EHA*) in which the route of this vessel is quite tortuous, a factor dealt with later under the efferent pseudobranchial.

#### AFFERENT PSEUDOBRANCHIAL ARTERY — Allen, Allis.

Abführendes Gefäß der Spritzlochkieme — Hyrtl.

Arteria carotide anteriore — Carazzi (in part).

Arteria hyoidea — Stannius (in part).

Arteria hyoidea-opercularis — Müller (in part).

## MORPHOLOGY OF THE ANTERIOR ARTERIES OF SHARKS<sup>237</sup>

Arteria ioidea — Emery (in part).

Arterienstamm der Spritzloch-Nebenkieme — Müller.

Pseudobranchial artery — T. J. Parker, Allen, Daniel.

Ramus anastomoticus — Hyrtl (in part).

Figs. 12, 19—22; *APA*.

This artery, the pseudobranchial or anterior carotid (in part) of older terminology, is another product of the posterior efferent hyal collector artery. The importance of this collector in cranial supply can then be scarcely over-emphasized when it is remembered that it gives rise to three main trunks: (1) dorsal, the efferent hyal; (2) intermediate, the afferent pseudobranchial; and (3) ventral, the hyomandibular.

The afferent pseudobranchial is always a large vessel, and runs directly forward from the middle course of the hyal collector, then turns dorso-cephalo-mesially and breaks up (usually) into a retia in the anterior wall of the spiracle. In this fairly short course it gives off no branches whatever and is commonly quite straight, though in *Galeus* (fig. 19; *APA*) the sinuosity characteristic of its efferent continuation is already in evidence.

Morphologically (figs. 6—9; *IBCA*, *APA*) this artery is the first of the series of intermediate branchial commissural arteries as far forward as the point where it either crosses or meets the hyomandibular, that vessel previously identified as the anterior efferent collector of the hyoid arch. This commissure robs the primary afferent mandibular of its mission and finally captures the entire function of arterial supply for the spiracular (now non-respiratory) demibranch, predisposing the abortion of the original trunk from the ventral aorta. In the great majority of species the hyomandibular crosses ectad of the pseudobranchial, but in *Chlamydoselachus* (*ALLIS*, 1912. 4) and *Galeorhinus* and *Squatina* (*HYRTL*, 1872) it unites with the latter trunk. In *Galeorhinus plebejus*, *HYRTL* records the unusual and perhaps individual variation of a double origin of the afferent pseudobranchial from the hyal collector. The two roots unite at the point where they receive an exceptionally strong hyomandibular, and the further continuation is single. Acceptance of the main stem of the hyomandibular as an anterior hyal collector explains this arrangement to a nicety, and in this specimen there are consequently two intermediate commissures connecting the hyal collectors.

In all cases the further pathway of the afferent pseudobranchial crosses space once occupied by the first gill cleft. This slit having become restricted to, at most, a small dorsal opening, its former territory is now available and the commissural trunk is then able to effect union with the former posterior mandibular collector, no part of which remains in this immediate vicinity save the spiracular retia, and even this remnant may become entirely obsolete. The most cephalic portion of the afferent pseudobranchial then represents

a secondary forward growth of the intermediate branchial commissure of the embryo.

In rays (HYRTL, 1858) this artery is especially strong, and divides upon reaching the neighborhood of the large spiracle into (1) one or more muscular rami for the adductor mandibulæ, and (2) the pseudobranchial branch. In *Chimæra* (ALLIS, 1912. 4), the hyomandibular artery is given off by the afferent pseudobranchial, as its ventral connection with the hypobranchial system has aborted, a condition of some significance in view of the morphologies here proposed.

#### SPIRACULAR RETIA.

Rete vascolare dello sfiatatoio — Carazzi.

Wonder net — Daniel.

Wundernetz — Hyrtl.

Figs. 19, 20, 22; *SR*.

HYRTL (1872) described this structure in detail and thought that it represented a bipolar retia, the ends of which had been shoved upon one another to produce an S-curve in all the anastomosing branches. CARAZZI (1905. 2, p. 94) also speaks of "una bellissima rete vascolare bipolare", but this appearance is only secondary and due to degeneration, as the original condition in this demibranch must have been similar to that in an ordinary functional gill, where two parallel vessels, afferent and efferent, are cross-connected by a capillary network. Such a construction is retained by Selache, the rete of which is illustrated by CARAZZI (1905. 2, fig. 18, p. 95). Each of the two main trunks assumes a tortuous course within the pseudobranch, and constantly diminishes by giving off unilaterally a complex series of anastomotic twigs, each main stem then terminating in a small blind pocket. Only a short portion of the former vertical extent of this structure remains.

Sharks with a persistent spiracular opening have the retia well developed, as *Notorynchus*, *Centracion*, and *Squalus* (fig. 22). If some gill filaments are still present, as *Centracion* with eight, the detailed anatomical relationships are the same as those of a normal demibranch. But even in forms where the external aperture is very minute or entirely aborted the retia is nevertheless usually retained, as in *Carcharias*, *Cestracion*, *Isurus* (*Oxyrrhina* or *Lamna*), *Vulpecula* (*Alopecias*), and *Galeus* (fig. 19; *SR*); and in *Squatina* and *Catulus*, HYRTL described the gradual reduction with individual growth, resulting in a final complete obliteration of the retia, so that afferent and efferent sections of the pseudobranchial artery become perfectly continuous (fig. 21) and here form an actual ramus anastomoticus from hyoid gill to paired aorta. This is the case also in *Chimæra*. In rays the spiracle has taken on a new function and the retia is always proportionately much larger than in any shark.

MORPHOLOGY OF THE ANTERIOR ARTERIES OF SHARKS<sup>239</sup>

EFFERENT PSEUDOBRANCHIAL ARTERY — Allis, de Beer.

Anterior carotid — T. J. Parker.

Arteria carotide anteriore — Carazzi (in part).

Carotis interna anterior — Müller, Dohrn.

Ramus anastomoticus — Daniel, Hyrtl (in part).

Zuführendes Gefäß der Spritzlochkieme — Hyrtl.

Figs. 19—22, 23 A; EPA.

Continuing the general forward direction of the afferent pseudobranchial, this vessel swings around through a cephalo-mesal arc, crossing the floor of the orbit ventrad of all other structures, and perforates the cranial wall to unite at a right angle with the paired dorsal aorta below the inferior lobes of the brain. The efferent pseudobranchial may arise from the spiracular retia, or may be perfectly continuous with the afferent trunk in cases where the retia is absent. Its termination is always the same. In this course it may give off several small muscular twigs, perhaps comparable to the dorsal nutrient branchials of other efferents, but the only main collateral originated is the ophthalmic artery. As may be reviewed in figs. 1—9, the efferent pseudobranchial is the entire and actual persistent upper (efferent) section of the first or mandibular aortic arch. It is hence not an anastomotic trunk, but a real efferent branchial artery, whose collector portion is confined to the spiracular retia and perhaps to an isolated tributary of the hyomandibular artery (see p. 216, 217). Choice of a name should then by all means be made from either (1) efferent pseudobranchial, or (2) efferent mandibular artery.

CARAZZI has here strayed from the only safe pathway of morphological interpretation and has reached conclusions which are at variance with the embryological plan and history of the arteries in the immediate region under consideration. At times he does not appear to grasp the real significance of the structures which he so carefully dissects. His figures 16 and 17 (1905, 2, p. 92, 94) show the efferent pseudobranchial (his anterior carotid) entering the carotid crossing in *Selache*, but they are defective and misleading in that they do not show the forward continuations of the paired aortæ as the cerebral arteries. The efferent pseudobranchial is here interrupted by a glomus (gomitolo), a branch continuing on at one side to the carotid crossing. But this branch is obviously the paired aorta *from* and not toward the crossing, and the other trunk from the glomus is really a side branch, arising slightly laterad of the confluence of pseudobranchial and aorta, and consequently representing the ophthalmic artery. CARAZZI speaks of and depicts the four carotids as meeting at the carotid crossing in *Catulus*, and of an anastomosis between the efferent pseudobranchials in *Squatina*, but analysis of his figures shows that all sharks are exactly alike in these particulars, which are as here described in the first paragraph on the efferent pseudobranchial artery.



The trajectory of this vessel supplies some highly interesting details. In *Catulus* (fig. 21), *Squalus* (fig. 22), *Galeorhinus*, *Notorynchus*, *Chlamydoselachus*, and *Squatina*, there is no particular meandering, while in *Selache* the artery courses in undulating fashion. Finally, in *Cestracion*, as noted by MÜLLER and figured and described by HYRTL, and in *Carcharias* (VIRCHOW, 1890. 2), the efferent pseudobranchial and the forward portion of the efferent hyal are thrown into a number of sinuous loops and twists, forming more or less of an arterial ball at either side, between brain and orbit. TROIS observed similar conditions in *Isurus* (1879) and *Vulpecula* (1882).

But these peculiarities, strange as they may be, and which caused considerable speculation on the part of their observers, are now dwarfed by comparison with the wonderful development of this construction in *Galeus* (fig. 19). The exact disposition of the vessels *in situ* has been carefully reproduced, but the outline figure fails completely to give a true notion of the degree of complexity, since the tangled mass of arteries is as deep as wide. Furthermore, the folding process so pronounced in the efferent pseudobranchial, and more strongly marked in the efferent hyal than in any other species heretofore described, extends in *Galeus* even to the paired aortæ. The distance in a straight line from the spiracular retia to paired aorta, — i.e., the morphological course of the efferent pseudobranchial was 65 mm. in the single specimen which could be secured for dissection, whereas the actual length of this vessel when unravelled was no less than 380 mm., — almost six times the required extent! It was necessary to break a great number of fine threads of connective tissue to untangle this trunk. It has also been necessary to construct two figures (19 and 20) of the same set of arteries, as the morphological relationships of the parts concerned are entirely obscured by this complicated folding, and other and more dorsal vessels hidden from view.

VIRCHOW (1890. 2) thought such a meandering course as had been observed by that date was due to an increase in size of the head vessels. But CARAZZI objected on the grounds of the usual absence of such sinuosity in the efferent hyal, and offered the much more plausible explanation that the spiracular retia is retained, and the efferent pseudobranchial coiled up so that the blood pressure of the cerebral and optic circulations may be regulated and sudden changes prevented. This seems the only likely interpretation available in the present state of our knowledge, and will also account for the development of a glomus in the course of any of these arteries.

In rays the efferent pseudobranchial is a much smaller vessel than is the afferent, and HYRTL (1858) supposed that the flow of blood was in the opposite direction from that which he later described in sharks. The spiracular demibranch is relatively so large in rays that he thought it functioned in a

MORPHOLOGY OF THE ANTERIOR ARTERIES OF SHARKS <sup>241</sup>

respiratory capacity, oxygenating venous blood brought from the eye by the efferent pseudobranchial (Zuführendes Gefäss) and transported thence through the afferent pseudobranchial (Abführendes Gefäss) to the hyoidean collector, and then to the dorsal aorta. The actual facts as to the direction of flow of this blood stream, and as to the function of the spiracular demibranch in this highly modified group of elasmobranch fishes have never been determined. The spiracle, and not the mouth, is here the principal incurrent opening for water used in respiration, and it may be that the demibranch located therein has retained a greater degree of its original development because it can serve in freshening still further the arterial blood destined for the eye and brain, assuming the current to flow cephalad. Or the reason for such persistence of a large retina may be the need for regulation of blood pressure, as CARAZZI urged for the meanderings of the selachian efferent pseudobranchial. At any rate, HYRTL's interpretation, while not impossible, is extremely unlikely.

OPHTHALMIC ARTERY — Owen, T. J. Parker, Allen.

Arteria choroidalis — Dohrn.

Arteria ophthalmica magna — Müller, Stannius, Carazzi.

Arteria orbitalis — Greil.

Ophthalmica magna artery — Allis, McKenzie, Daniel, de Beer.  
Described and figured by Emery.

Figs. 20, 22; *OMA*.

As seen in *Galeus* (fig. 20; *OMA*) this vessel arises from the efferent pseudobranchial near the union of the latter with the paired aorta in the mesal central portion of the orbit. It passes thence directly to the eyeball without giving off any collaterals, plunges through the sclerotic coat, and divides upon the outer surface of the choroid as the anterior and posterior choroidal arteries (*AChA*, *PChA*).

The ophthalmic is a uniform structure in all sharks. CARAZZI designates by this term a tiny twig arising from the orbital ramus of the external carotid in *Selache*, and thought this construction a distinctive character of the genus or possibly the family. But as already explained (p. 240), the ophthalmic is represented by a branch from a glomus situated in the usual site of origin of this artery, and CARAZZI's ophthalmic must be merely one of the six regular divisions of the orbital stem, one for each eye muscle. In *Squatina* he found that the ophthalmic bifurcates before reaching the eye.

In his many papers on head circulation in teleosts, ALLIS associates the ophthalmic with the choroid gland, which he considers a vestige of a pre-mandibular gill, and thinks the artery is hence (1) a commissure from the mandibular aortic arch to a gill which has lost its own arch (1908), or (2) a persisting efferent premandibular trunk (1912. I in teleosts; 1914 in Cera-

odus). In 1914 he stated that the dorsal portion of the efferent pseudo-branchial is formed by the fusion of the proximal part of the ophthalmic with the dorsal section of the mandibular aortic arch in the embryo. That this is not the case, at least in sharks, may be seen from a review of figures 3—5, where it is evident that the ophthalmic is always a branch from the most dorsal portion of the first arch.

ALLIS has never at any time mentioned an actual observation of such a structure as a "choroid gland" in elasmobranchs, nor has anyone else as far as I could determine. There is no evidence of any sort of glandular structure throughout the entire course of the ophthalmic in those sharks personally dissected, and a careful search was made to determine the facts of this particular point. Nevertheless, ALLIS represents the choroid gland in all of his diagrams and adheres to this speculative and entirely unconfirmed morphology. Discussion of the possibility of former preoral gills will be deferred until the division of the external carotid have been considered.

The facts upon which any conclusion as to the morphology of the ophthalmic artery may be based are: (1) it is the first to develop of any of the derivatives of the aortic arch system, appearing almost immediately after the hollowing-out of the first arch, strong evidence as to its great phylogenetic age; (2) supplied with branches in the embryo but with none in the adult; (3) arises from the mandibular aortic arch quite near the union of that vessel with the paired aorta; (4) supplies only the choroid layer of the eyeball, running as directly as possible; (5) after it is well formed the paired aorta begins a secondary forward growth as the cerebral artery (figs. 6—9).

Precocity of appearance and the straight, unbranched course of the adult ophthalmic artery favor its interpretation as a former branchial component; transient embryonic collaterals and adult distribution do not. Its site of origin argues neither way since this point may or may not have shifted slightly, and the artery may have been originally connected with either mandibular arch or aorta. In view of the developmental history of this vessel it would seem to possess considerable significance, and if so then we could not regard it as a purely fortuitous sprout. Comparative anatomy fails to throw any light on this problem, but the facts enumerated in the foregoing paragraph lend color to the following speculation.

Presume a simple prechordate form in which the brain is merely a straight expansion of the neural tube and whose sole sense organs are diverticula (optic vesicles) from brain to exterior. The anterior vascular system consists of a tubular, pulsating heart, continued forward as the ventral aorta which passes up around either side of the alimentary canal in the form of mandibular aortic arches, these turning to run caudally as the dorsal aortæ. From the cephalic apex of this loop, on each side, there arises a stem which proceeds forward and has sole charge of nourishing all structures anterior

to its origin, since it is the only artery in the region. It would be provided with a number of branches, among which the most important would be that one supplying the optic vesicle, itself the major structure here present. Did we have such a condition in an existing animal we could speak of this vessel as the cephalic artery. But later, when the brain had increased greatly in size and complexity, and when sense organs had multiplied and the optic vesicle become specialized, a secondary forward growth of the aorta robbed this cephalic artery of its opportunity for greater service and caused its gradual restriction to a single main stem, that one running to the former mesal surface of the optic vesicle, now the choroid. To-day, the cephalic artery begins its career as the great trunk line of the head and has numerous branches, but is supplanted by the aorta and reduced to the straight and unbranched ophthalmic. Thus I read in the ontogenetic pictures of this vessel a profound general significance which does not involve the reduction of a supposed former gill or other element, but which implies a selective competition for cerebral supply in which the paired aorta is the victor.

EXTERNAL CAROTID ARTERY — Allen, Allis, Kingsley, Daniel.

Arteria facialis — Vogt & Yung.

Arteria orbitale — Carazzi.

Arteria orbitalis — de Beer.

Arteria temporalis — Greil.

Arteries sent to jaws — Monro.

Carotid — Owen.

Carotide interne postérieure — Milne Edwards.

Carotide posteriore — Emery.

Carotis externa — Hyrtl, McKenzie.

Carotis facialis — Rathke.

Carotis interna posterior — Müller.

Carotis posterior — Müller, Stannius.

Gesichtsarterie — Vogt & Yung.

Posterior carotid — T. J. Parker (in part).

Figs. 20—22; *ECA*.

The origin of this artery is diverse: (1) it comes from the union of the hyoidean efferent with the paired aorta, so that there appears to be a four-square meeting of the vessels, as in *Notorynchus*, *Selache*, *Galeus* (fig. 20), and sometimes *Catulus*; (2) it may be given off by the paired aorta before the point of entrance of the efferent hyal, as *Catulus* (fig. 21); (3) by the paired aorta after the confluence of the efferent hyal, as *Galeorhinus*, *Chlamydoselachus*, and *Squalus* (fig. 22); or (4) by the efferent hyal before its union with the paired aorta, as in *Cestracion* and *Squatina*.

After its production, the external carotid may traverse the cranial wall along with the hyomandibular nerve (*Centracion*) or may not enter cartilage at all (*Notorynchus*). In either case it attains the orbit,

whose floor it crosses, and where it gives off the orbital artery (figs. 20, 21; *ObA*) for the eye muscles. Continuing forward through the orbito-nasal canal, the external carotid next sends a buccal artery (figs. 20—22; *BA*) with maxillary and mandibular rami backward and downward to the adductor mandibulæ, and the main stem lastly divides into a nasal (figs. 20, 21; *NA*) for the olfactory cup and rostral (figs. 20, 21; *RA*) for the terminal regions of the snout. Such a distribution occurs in *Notorynchus*, *Chlamydoselachus*, *Galeorhinus*, *Squalus*, and others. *Catulus* (fig. 21) may show a different arrangement, and in *Galeus* (fig. 20) the divisions are more centralized, and the orbital appears as a branch from the buccal.

PARKER'S (1886) terms for the divisions of the external carotid are: orbital, buccal, maxillo-nasal, and rostral; CARAZZI'S (1905. 2) are: oculare, mascellare, and mandibolare. This latter nomenclature was given in connection with *Selache*, where the oculare (orbital artery) is very slender and terminates almost immediately in a glomus, from which two branches continue "all'occhio e ai muscoli oculari" (p. 94). He considered one of these to be the ophthalmic, but undoubtedly both must be but branches of the external carotid, two of which seem to be entirely overlooked or omitted.

PARKER described the course of the orbital in *Galeorhinus* as follows (1886, p. 695): "This sends off twigs to the posterior wall of the orbit, and then divides into two branches, a dorsal which supplies the superior rectus, superior oblique, and inferior oblique muscles, and a ventral which supplies the internal and external recti. The inferior rectus apparently receives its blood supply from a special branch of the posterior carotid." In the accompanying figure 11, this special branch passes from the external carotid at a point immediately opposite the origin of the orbital, so that it may be considered as having shifted basally to a more convenient and direct site.

The selachian eye, using the term in its most comprehensive sense, is then supplied with arteries from three different sources: (1) the optic, from cerebral artery (paired aorta) to retina; (2) the ophthalmic, from efferent pseudobranchial to choroid; and (3) the orbital, from the external carotid to the eye muscles. Their order of phylogenetic appearance seems to have been ophthalmic, optic, orbital; they each serve a different type of tissue; but finally they all agree in their morphology, if the writer interprets them correctly, in that they all represent originally simple nutrient rami.

As is well known, there is no correspondence between the external carotid of fishes and the ventral vessel known as such in mammals. Original workers, like HYRTL, employed the terms of human anatomy and may be pardoned for occasionally using a name which implies an impossible homology. DE BEER (1924) apparently aims at correcting this condition when he calls the selachian external carotid the orbital artery, and restricts the

## MORPHOLOGY OF THE ANTERIOR ARTERIES OF SHARKS

designation of external carotid to the ventrally produced hyomandibular artery. Such a change will scarcely be able at this late date to overthrow the time honoured usage in fish groups, and is moreover inappropriate because the piscine external carotid is the actually important muscular nutrient of the facial region, the hyomandibular being a relatively insignificant vessel which does not begin to fulfill this function. Should a revision of names appear advisable, the designation facial artery seems best for the external carotid. Having already noted that the so-called internal carotid is really the paired aorta, it might be well then to drop the use of the term carotid entirely in at least the lower vertebrates.

The morphology of the external carotid has been the subject of considerable research. DOHRN (1890) thought it might represent the remnant of a premandibular aortic arch, as certain of its branches seem to favour such a belief. ALLIS has done a great deal of work on this artery and has formed several conclusions at various times. It "would seem to be an artery developed from the dorsal nutritive or muscle branches of one or more prevagal aortic arches" (1908, p. 130). He here also states that its principal components are derived from the hyoid arch in all fishes except Dipnoans (*Ceratodus*), where they come from the glossopharyngeal arch. Again (1911. 1) in considering the condition of the external carotid in *Polyodon* and *Acipenser*, he says that in fact it arises from the base of the efferent hyal, and if it can be considered as a branch of this artery, it is then either a dorsal muscle branch or a commissure connecting up cephalically with one or more prehyal vessels. Origin of the carotid from the aorta would then be due to a shifting up to that trunk, and thence along it either forward or backward. Next (1912. 1) he thought that the selachian external carotid may equal the dorsal branchial muscle artery of *Amia*, developed in relation with prehyoid efferents and their dorsal commissure, plus possibly the anterior hyal efferent. Lastly (1916) ALLIS said the mandibular of this artery is probably the anterior mandibular efferent, receiving a commissure from the hyomandibular (*Chlamydoselachus*), and the maxillary a forward continuation of this cross-commissure.

But none of these speculations which involves a branchial component will satisfy all conditions. The external carotid arises from the paired aorta in a territory between (usually) the first and second aortic arches, and nearly always in very close proximity to the second. It can then hardly have anything to do with a mandibular or premandibular gill as a respiratory trunk. Furthermore all of its branches are strictly muscular rami, so that its identification by ALLIS as a dorsal nutritive branchial artery is by far a more likely explanation. Such an artery has previously been described (p. 109, this paper) as attaining vastly supernormal proportions in *Squalus* and *Catulus*, and a development of the external carotid in just such a fashion seems to

meet all requirements. It arises late in ontogeny, as it no doubt did in phylogeny, further evidence of its non-respiratory character, and augments with the growth of the head, constantly expanding its territory forward to keep pace with its function. The presence of rami along the jaws is due to the occurrence of muscles there also, which require nourishment, and does not necessarily argue the former presence of demibranchs at these sites. An anastomosis with the hyomandibular in a single described species is also no proof of any forward extension of the intermediate commissural system, as anastomoses are abundant everywhere in the shark body, both among arteries and veins, and are apt to occur where any two contiguous vessel systems approach sufficiently closely.

From the evidence of my dissections I would establish the external carotid as the dorsal nutrient branchial artery of the efferent hyal, — greatly hypertrophied, and whose base may shift upward to arise from the nearby aorta. Another possible conception would interpret this vessel as an overgrown intercostal division of a segmental artery, with a base sometimes shifting downward onto the efferent hyal. A similar morphology was held for the subclavian.

In these discussions of head arteries, mention has several times been made of the so-called evidences for the former occurrence of preoral or intermediate gills, as claimed by the majority of older investigators. This important topic may now be considered.

The chordate branchiomere consists of skeletal, muscular, nervous and vascular components and the problem has frequently been attacked from each of these standpoints, but the conclusions reached by specialists in these several fields have been neither complete nor harmonious. The ancestral number of gills is now thought to be much lower than was once supposed. The adult *Amphioxus* has a large and indefinite series, one hundred or more, as a secondary condition. In development, as summarized by HERDMAN (1904), 14 gill clefts appear midventrally and then shift over to the right side; next 8 occur on the right side dorsally; then the first set migrates to the left, where some are suppressed so that the pairs become equal in number and segmentally arranged. This results in the "critical" stage, of from 7 to 9 clefts, the nearest approach to the condition in craniate embryos, and presents a curious history which certainly cannot be regarded as paligenetic. Later on, tongue bars arise to subdivide the primary gills, which also increase with age so that they become much more numerous than the myotomes, and cross bars develop to further complicate the definitive condition.

Of Cyclostomes, *Bdellostoma* has the largest number of clefts, 14 being frequently attained by mature individuals (JACKSON, 1901). This figure should be increased to 17, since STOCKARD (1906) demonstrated the appearance and subsequent complete atrophy during development of a hyomandibular and

two post-hyomandibular gills. Other forms have considerably fewer clefts, usually 7 as in *Petromyzon*, though the ammocoetes larva has indications of 8 at one stage (CORI, 1906). *Myxine* has 6, but COLE (1913) found vascular evidence of a former greater number.

In detailing the condition in elasmobranchs, the spiracle is to be understood as constituting the first cleft. DEAN (1895) states that of fossil species, a Permian pleuracanthid had 8, and the Lower Carboniferous *Cladoselache* probably the same number. *Hybodus*, a Liassic cestraciont, had 6. Of living forms *Heptranchias* and *Notorynchus* of the *Hexanchoidei* head the list with 8, then comes *Hexanchus* and *Chlamydoselachus* of the same Super-family, and *Pliotrema* of the *Squaloidei* with 7, and finally all other forms have 6 clefts, or 5 if the spiracle disappears.

The case of *Pliotrema*, family *Pristophoridae*, is an aberrant and unexpected one, standing as this shark does at the opposite end of the systematic list from the primitive notidanids. The genus consists of a single species, *P. warreni*, taken from the coast of Natal and the Cape of Good Hope. In this regard GARMAN says (1913, p. 248): "This genus has six gill clefts on each side. Aside from these there appears very little to separate it from *Pristophorus*. Whether this number of clefts has been continuously retained from a six-gilled ancestry or has been secured by specialization, or by reversion, from five-gilled ancestors is not yet determined. It is certain, however, that its possession in connection with the general structure and affinities gives us no reason for placing the family any nearer to the Hexanchoids."

Indications of former gills have been frequently investigated in the plagiostoma. VAN BEMMELLEN (1886) established the variously termed post-branchial, ultimobranchial, or suprapericardial body as a remnant of a seventh cleft in many pentanchid forms. DANIEL (1916) reported the presence of a well developed vestige of an eighth and even traces of a ninth branchial arch in *Notorynchus*; HAWKES (1907) and GOODEY (1910) vestiges of a seventh in *Chlamydoselachus*; and HAWKES (1906) of a sixth in *Centracion* (*Heterodontus*). This raises the maximum number of gill clefts for sharks to a possible limit of 10. 8 to 9 clefts is usually taken as primitive for vertebrates, the condition in *Bdellostoma* being quite exceptional and perhaps retaining the original instability of a recently acquired series of structures. 8 seems to have been the prevalent number for a considerable period, since when a gradual reduction down to the single opening of *Cryptobranchus* is seen among living adults.

The order of reduction appears to the writer to have always been in a cephalic direction, as witness the vestiges just described, all of which are found caudad of the last functional gill. KINGSLEY (1908, p. 185), speaking of the five aortic arches of "typical vertebrates" says, "There is some evidence to show that the number is really six, an arch dropping out between



the fourth and fifth of those recognized here." No further reference to such a loss has been found in any of the many references consulted, nor can I imagine what the nature of the said evidence could be; — there is certainly none from elasmobranch development or adult anatomy. The number of aortic arches depends upon the stage of ontogeny or evolution under consideration, and it can hardly be claimed that there is any characteristic or typical number for the phylum. DOHRN (1887) thought there was a possibility of a cleft having atrophied between the spiracular and glossopharyngeal, and that the thyroid may have been associated with this vanished slit; but that was before the day when the homology of the thyroid with the cephalochordean endostyle was established. Almost every conceivable orifice in the vertebrate body and a great variety of anterior degenerate glandular or vascular masses have been accused of once forming a member of the gill complement. Among structures so allocated are the nose (MARSHALL, 1879), mouth (DOHRN), hypophysis, lens of the eye, and anus. But the invaginations concerned in all of these organs save the thyroid are from the ectoderm, whereas gills develop from the enteric lining, and there is moreover, nothing in embryology to really substantiate these claims.

WYMAN (1864) described a vestigial seventh gill cleft in an embryo of Raja, but VAN BEMMELEN (1886) found the structure concerned to be merely an ectodermal groove or crease, with no corresponding pharyngeal out-pocketing, and having nothing to do with a true cleft. The latter author, studying quite a series of elasmobranch embryos and adults, then went on to make several claims of his own which subsequently met with a like fate at the hands of others. These were (1) a small follicle in the angle of the jaws, underneath the mucosa and without a lumen, which he would have as the vestige of a cleft between the jaws and labial cartilages, (2) the dorsal and (3) ventral cæcum or canal leading from the spiracle. RIDWOOD (1896) studied the spiracle and denied the latter two homologies. MÜLLER's original idea that the dorsal spiracular cæcum was designed to convey sound waves to the inner ear has outlived the thesis of VAN BEMMELEN, who disputed him. ALLIS (1916), with *Chlamydoselachus*, found the jaw-angle follicle and its arterial supply, and thought it might be a remnant of a mandibular or premandibular cleft. GREGORY (1904), working on the skeleton, hypothesized an ancestral form in which the first two visceral arches were primitive, unattached to the cranium, and gill-bearing, and he also assumed the existence of preoral arches. The labial cartilages were long considered to represent one or two such elements, or as branchial remains between the mandibular and hyoid arches, but are now regarded as extravisceral pieces, serially homologous with the extrabranchials, and belonging to the mandibular arch.

PLATT (1891. I) as before mentioned, thought that the forward portion of the embryonic cephalic sinus consisted of vestiges of former aortic arches

segmentally associated with her anterior cavities, though she raised no question as to any possible gills they may once have supplied; and RAFFAELE (1892) also suggested that the sinus may contain the dorsal ends of a certain number of preoral arches, coalesced with each other and with the adjacent aortæ. DOHRN (1890) believed that certain branches of the external carotid indicated a former premandibular arch, and that the so-called choroid gland of the eye represented a former premandibular gill, with which the ophthalmic artery was associated. ALLIS (1908) adopts the latter idea, showing the choroid gland as a vestigial gill in all of his diagrams, and interpreting the ophthalmica magna as a commissure running forward from the mandibular arch. He later (1916) renewed the labial cartilage idea, for in speaking of the maxillary branch of the external carotid of *Chlamydoselachus*, stated (p. 114) that it sends a branch "ventro-posteriorly along dorsal edge of posterior upper labial cartilage, and another toward the corresponding edge of the anterior upper labial, both branches suggesting efferent arteries of a premandibular arch."

DOHRN's hypothesis that the mouth of chordates was a neostoma, arising from the midventral fusion of a pair of gill clefts, necessitated a search for the old mouth possessed by prechordates before the appearance of gills and clefts in phylogenetic descent. Such a paleostoma was then found in a dorsal opening of the alimentary canal to the exterior via the infundibulum, neuro-cœle, and anterior neuropore, and again the earthworm was inverted in order to fit him for the role of our distant progenitor. Some workers have even gone to the extreme of inventing half a dozen different mouths to account for relatively trivial inequalities in morphological detail. But there is a decided tendency of late to reject the gill-slit and all other polystomal theories, and to regard the mouth as a uniformly homologous structure from medusa to man. All of the evidence of embryology and physiology favors such a view. What would be the functional utility of a change of oral openings, and how would countless generations of animals subsist while passing through such a crisis? A mutation so perfect as to produce an effective new mouth in a single generation is inconceivable; likewise the gradual perfection of the new during slow abortion of the old, involving a long period in which two functional mouths would coexist.

PLATT (1891, 2) found that the mouth involution of *Batrachus tau*, a teleost, is double at first and with a median ventral partition, but this condition has since been demonstrated as secondary. Aside from a serial relationship in position, which is none too perfect, there is no embryological evidence for a gill-cleft origin of the mouth, though anatomically the cartilages and muscles have long been established as homodynamous with those of the branchial arches. Now if the mouth has always been a mouth, it could never have represented a fusion of gill-slits, and its arches could never have borne

any gills save a posterior mandibular, which bordered the first cleft in rear. But there appears nothing inconsistent in such a belief with the identifying of the jaws as visceral arches. The endoskeleton being a purely chordate characteristic, the ancestral mouth, like the incipient gills, lacked hardened support. But when increase in bulk and activity necessitated such reinforcement, cartilages would be formed about the mouth for the same reason and in the same manner as those for the branchial units. And the same argument holds good for muscular and other components. The gill clefts arose on either side of the mouth and immediately in rear, but this does not compel the implication of serial homology. The case is one of contiguity rather than of successive sameness.

The mouth of *Amphioxus* is not at all comparable with a pair of gill clefts. In cyclostomes the original conditions have become so altered as to render a correct reading very difficult; a cartilaginous framework is present for the gills but not for the mouth. This branchial basket has never been successfully connected with the visceral arches of sharks, and probably represents a different sort of early attempt at gill support, since highly modified. And the absence of jaws may be primitive, or a secondary adaptation to sanguivory, or STOCKARD (1906) may be right in finding jaw rudiments in *Bdellostoma*, and in homologizing the so-called tongue of this hag with the mandible of gnathostomes.

In view of all of the foregoing arguments the writer cannot subscribe to the gill-cleft or any other polystomal theory, all of which appear to be entirely fanciful and ill-founded. But should the reader be committed to any such hypothesis, the idea of preoral gills is still illogical, for were a pair of clefts selected for prehensile purposes, they would most certainly stand at the front end of the series and not somewhere in the middle.

Finally, in any case, let it be recalled that from the first appearance in the animal kingdom of a complete digestive tube, the mouth is invariably a terminal structure, either actually or morphologically. Such an inferior location as is seen in the shark is due to a huge overgrowth of the upper jaw region into a rostrum, and takes place in the embryo *long after* the appearance of the gill clefts. How then, could there be any preoral gills? Moreover the evidence for such structures is highly speculative and rests upon exceedingly reduced tissues, many of which may not really be vestigial at all. Every glomus in the course of an artery and every nodule of fatty or glandular cells can by no means be considered as satisfactorily demonstrating a former gill. One may also readily accept the idea of a premandibular and mandibular somite without inferring that they once were associated with gills.

The only undisputed cases of cephalic gill reduction in sharks are those of the posterior mandibular and anterior hyoidean demibranchs. As suggested by DOHRN (1887), the enormous growth of the mouth and its skeletal

and muscular components encroached upon the territory of the first gill cleft to such an extent that its ventral portion was compressed, culminating in loss of function and finally in obliteration. The two demibranchs bordering this cleft became reduced and crowded to the point of uselessness, the posterior set (anterior hyoidean) succumbing first. To-day, some sharks retain a few anterior filaments (posterior mandibular demibranch), others none at all. The dorsal part of this cleft remains as the spiracle, the external opening of which is frequently obsolete, and possession of even this vestige has been due to change of function.

### VI. THE CEREBRAL SYSTEM.

CEREBRAL ARTERY — T. J. Parker, Allen, Allis, Kingsley, Daniel.

Arteria cerebrale — Carazzi.

Brain artery — Allen.

Encephalic artery — McKenzie, Allen.

Gehirnarterie — Hofmann.

Hirnarterie — Stannius, Vogt & Yung, Hyrtl.

Zweige zum Hirn — Müller.

Figs. 19—23; CA.

The paired dorsal aorta, medullary section, may be termed the cerebral artery as soon as it has received the efferent pseudobranchial. As already described, it gives off the optic artery to the retina. The cerebral artery then divides fore and aft into apparently two main trunks, the division taking place (fig. 23) at the base of the mesencephalon, between the optic chiasma in front and the inferior lobes in rear. Actually, however, there are three main stems, the cephalic fork again dividing. Upon the breaking up of the common cerebral artery we have attained the cerebral and final section of the paired dorsal aorta. CARAZZI has here confused his morphology again by regarding the cerebral artery as a continuation of the efferent pseudobranchial instead of the paired aorta; this is actually the case in *Chimæra*, where the connection between

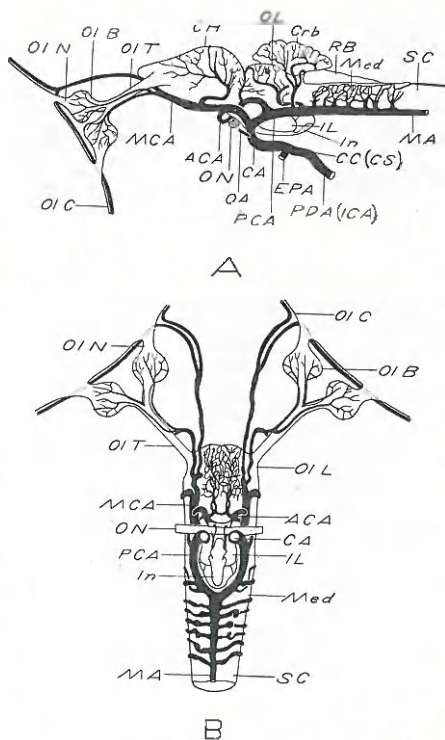


Fig. 23. Cerebral arteries, *Galeus glaucus*. A, lateral aspect. B, ventral aspect.

ACA anterior cerebral artery; CA cerebral artery; CC carotid crossing; CH cerebral hemisphere; Crb cerebellum; CS cephalic sinus; EPA efferent pseudobranchial artery; ICA internal carotid artery; IL inferior lobe; In infundibulum; MA myelonal artery; MCA middle cerebral artery; Med medulla; OA optic artery; OL optic lobe; OIB olfactory bulb; OIC olfactory cup; OIL olfactory lobe; OIN olfactory nerve; OIT olfactory tract; ON optic nerve; PCA posterior cerebral artery; PDA paired dorsal aorta; RB restiform body; SC spinal cord.

## JULIAN D. CORRINGTON

cerebral and aorta has been lost, but no such disposition occurs in any known shark. The caudal division of the cerebral artery is the

## POSTERIOR CEREBRAL ARTERY — T. J. Parker, Allen, Allis, Daniel.

Arteria cerebrale posteriore — Carazzi.

Arteria profunda cerebri — Hyrtl.

Posterior communicating artery — Kingsley.

Figs. 19—23; *PCA*.

This vessel passes backward around the inferior lobes, converging mesially to meet its mate immediately in their rear. In *Selache* and *Squatina* (CARAZZI) they diverge again at once and continue separate and parallel for a short course, only to fuse a second time. This is a specialized condition, as in most species the two posterior cerebrals are united throughout their postinfundibular extent. The resulting common trunk is the

## MYELONAL ARTERY — T. J. Parker, Allen.

Arteria midollare — Carazzi.

Arteria basilaris plus a. spinalis — Daniel.

Arteria spinalis inferior — Hyrtl.

Basilar artery — Kingsley.

Figs. 19, 20, 23; *MA*.

A small but important artery, this vessel courses throughout the length of the spinal cord, whose tissues it supplies. Too slender at its origin to continue far unaided, it is built up segmentally by the ventral rami of the vertebrospinal branches of the segmentals. On the undersurface of the medulla the myelonal artery receives a severe initial loss in calibre by delivering a number of large twigs to this part of the brain (fig. 23 B). The term myelonal has been frequently applied to a pair of relatively large vessels which arise from the united trunk of the first and second efferent branchials in rays (HYRTL, 1858) and join the true myelonal. But this section of the efferent branchials in question represents paired dorsal aorta and the so-called myelonals are actually segmentals and should so be designated.

The forward branch of the cerebral artery (fig. 23) arches up over the optic nerve of its side and attains the ventro-lateral border of the telencephalon. Here it divides in two, the smaller vessel being the

## ANTERIOR CEREBRAL ARTERY — Daniel.

Arteria cerebrale anteriore, ramo esterno — Carazzi.

Anterior cerebral artery (in part) — T. J. Parker, Allen.

Inner cerebral artery — Kingsley.

Figs. 21—23; *ACA*.

## MORPHOLOGY OF THE ANTERIOR ARTERIES OF SHARKS<sup>253</sup>

Leaving the main stem in a ventro-mesial curve (fig. 23) this artery usually then unites with its mate of the opposite side by an anastomotic branch, and continues forward on the ventral surface of the telencephalon. Here it may take the form of (1) a well defined and individual arterial stem and twigs, which may then run up the sides of the forebrain, as in *Squalus*; (2) numerous longitudinal strands, *Centracion*; or (3) it may break up into a complicated network, as in *Galeus* (fig. 23 B). The further continuation of the larger and main trunk at the side of the telencephalon is the

MIDDLE CEREBRAL ARTERY — Kingsley, Daniel.

Arteria cerebrale anteriore, ramo interno — Carazzi.

Anterior cerebral artery (in part) — T. J. Parker, Allen.

Figs. 19, 20, 22, 23; *MCA*.

Passing along on the forebrain, to which it sends no collaterals, this artery is destined to supply the olfactory organ. HOFMANN (1900), in an admirable comparative work on the cerebral arteries of the vertebrate series, and figuring *Squalus* and *Raja* for elasmobranch types, pointed out that certain branches of the middle cerebral run only to the olfactory cup, while others go exclusively to the olfactory tract, bulb, and nerve. This separation of terminus into two groups of structures is very well marked in *Galeus* (fig. 23), and is described by CARAZZI in *Catulus*, *Squatina*, and *Selache*. In the last named there is no definite middle cerebral artery, but instead there are nine equal and slender strands, eight of which go to the olfactory cup and only one to the bulb.

Superficially, this artery appears as the anterior division of the cerebrals, but careful examination (as fig. 23 A) will show that it is actually the middle of three. It is, however, the real continuation of the paired dorsal aorta. ALLIS (1914) found a small artery in *Galeorhinus* which arose from the paired aorta at the point where the optic came off. It ran forward between the cartilage and the lining membrane of the cranial cavity, and upon reaching the foramen olfactorium fell into a larger vessel, the division of the middle cerebral which goes to the olfactory cup. He says (p. 642), "This small artery would thus seem to represent the persisting anterior portion of the primary lateral dorsal aorta." But why so? And where is this vessel in other and in more primitive sharks? And what is wrong with the identity of the middle cerebral itself as the paired aorta? It seems that an excellent opportunity has here been overlooked to establish this tiny artery as the vestige of a pre-pre-pre-mandibular aortic arch, once connected with the gill of the nose!

That portion of the middle cerebral which may be identified as the direct continuation of the paired aorta is that vessel which courses straight

out along the side of the brain, without giving off any branches, and ending in the mucosa of the olfactory cup. Thus the dorsal aorta extends entirely throughout the body from anterior tip to posterior tip. The cerebral section, however, is a secondary cephalic addition, developing at a relatively late date in the embryo, as may be reviewed in figs. 7—9. It does not then possess the phylogenetic significance of the older portions of the aorta but has been produced in response to the ever growing demands of the brain and its outlying extensions, — olfactory bulb and retina of eye. Physiologically, the process of forming a cerebral artery, with its several divisions and many ramifications, is equivalent to that calling for the elaboration of a muscular ramus, such as the dorsal lateral artery, the external carotid, or the coronaries. Cyclostomes explain the true state of affairs, where the paired aorta courses past the brain, which it supplies with twigs, and does not terminate until attainment of that most cephalic structure, the mucous lining of the nasal sac. In sharks the paired aorta provides the brain with a few large dendritic stems instead of with many small twigs. The anterior cerebral is one of the larger and more constant of these main stems.

ALLEN (1905) describes and names the finer divisions of the cephalic trunks, and REX (1891) gives beautiful figures and complete descriptions of the cerebral veins in sharks.

#### CIRCLE OF WILLIS.

Union by anastomosis of the pair of anterior cerebrals ahead of the optic chiasma and infundibulum, and mesal fusion of the posterior cerebrals behind these structures, forms a complete arterial loop known as the circle of WILLIS. There are thus two such rings in the carotid region of sharks, the larger posterior circulus cephalicus and the smaller anterior circle of WILLIS. Both are of purely descriptive interest and without any phylogenetic significance.

#### SUMMARY.

1. An attempt is made to trace the complete history and present day variation in all arterial vessels occurring in the head of sharks, as a basis for a better understanding in this as well as in higher vertebrate groups.

2. Sharks inherited a fundamental ground plan of head arteries, consisting of a single ventral and paired dorsal trunk lines (aortæ), with aortic arch connectives, a secondary forward growth of the paired dorsal aortæ to supply nervous tissue (cerebral arteries), and a branch (external carotid) for muscular nutrition.

3. Amphioxus and Cyclostomes present such a fundamental plan, but the pictures secured through a study of shark embryos are far clearer, and each step is adequately outlined in proceeding from simple to complex.

4. A mastery of the types and significance of variations in this system is highly important for correct morphological interpretations. Those encountered in this study are listed and classified.

5. The primary aortic arches give rise directly to the bulk of head arteries and must be thoroughly understood. Condition of the branchials as found to-day depends upon their past history, which in turn relates to gill evolution. Arguments are presented denying the identity of the mouth as a fused pair of gill-clefts and also the occurrence of premandibular aortic arches or preoral gills.

6. The adult afferent branchial arteries are of primary embryonic derivation, the efferent branchials secondary, and the efferent collectors tertiary. The anterior efferent hyal collector is probably represented by the greater portion of the hyomandibular artery. The posterior hyal collector occupies a role of major importance, giving rise to the hyomandibular, afferent pseudo-branchial, and efferent hyal, — in other words to all of the primary cephalic arteries save the paired aortæ.

7. The complex hypobranchial system of sharks is a new addition to the previous vascular design and arose in accord with demands upon this growing region for a more adequate arterial supply. All subsidiary vessels, including the coronaries, are morphological extensions of either lateral or median hypobranchials.

8. There are no such vessels in actual fact as the common carotid and internal carotid of usual descriptions, though the latter term may be retained for convenience in designating that part of the paired dorsal aorta which lies cephalad of the efferent hyal increment.

9. The so-called posterior carotid is the efferent hyal; the vessel usually termed efferent hyal is the paired dorsal aorta; the pseudobranchial is the afferent artery of the spiracular retia and is developed from the most anterior member of the series of intermediate branchial commissures; the ramus anastomoticus or anterior carotid is the efferent pseudobranchial and represents the upper half of the primary mandibular aortic arch.

10. The external carotid is probably the dorsal nutrient branchial artery of the hyoid arch, and the optic and ophthalmic also modified nutrients.

11. No such vessel exists as the unpaired head aorta of HERTL. His carotid crossing is the reduced but persistent embryonic cephalic sinus.

12. Morphology of the head arteries is intelligible upon a developmental basis alone. The establishing of homologies by the comparative anatomy method, unaided by a thorough knowledge of embryology, is useless and has led time and again to wholly erroneous conceptions.



## METHOD.

The writer employed only the injection method, using a starch mass coloured with chrome yellow, which contrasts with selachian tissues to a higher degree than any other tint. The head arteries were filled from the caudal artery, using a penial syringe (fig. 24) that has (1) a conical soft rubber nipple, (2) a spherical soft rubber compression bulb instead of a plunger, and (3) a glass barrel of medium to large size. After trying various types, this syringe was found to yield by far the most satisfactory results, and in the belief that its employment is new to injection technique, the method is briefly summarized:



Fig. 24. Type of syringe recommended for injecting.

1. As is customary in preparing sharks for injection, partly transect the tail and hang the specimen up to drain, meanwhile cutting a wooden plug for the hæmal canal.

2. Expose the abdominal cavity, spreading out the viscera, and shave off sufficient cartilage from the interorbital region of the top of the head so that the brain may be seen.

3. With the head of the shark braced against some solid object, or the animal held by an assistant, inject through the caudal artery. The barrel of the syringe is held between the third and fourth fingers of the right hand, the bulb resting in the hollow of the palm, and the nipple pressed tightly into the artery. Exert a slow and steady pressure with the base of the right thumb, and if properly done it will be found that not a single drop of the injection mass escapes from around the nipple. Control by observing the steady creep of the solution along the vessels of the mesenteries and viscera. When the smallest cerebral, gastric, and intestinal arterioles have been filled, the operation is successfully completed.

4. Release the shark with the left hand while still holding the syringe firmly in place, and take up the wooden plug. Slide the plug down along the nipple and thrust it into the entire cavity of the hæmal canal, compressing the nipple, which may be withdrawn as the plug replaces it. Drive the plug in tightly. If carefully done, this exchange may be effected without the loss of any starch mass, and hence this method presents the cleanest possible manner of injection. Lastly, the syringe advocated is taken apart and cleaned with the greatest ease, and there are no parts which can corrode.

HYRTL (1872) filled the head arteries from the cœliac, and PARKER (1886) injected a plaster of Paris mixture into the ventral gastric artery. OSBORN (1885) devised an excellent system for the complete injection of all blood vessels, filling any branch of the cœliac with a gelatin and Prussian blue mass, and with the canula still in place, following this with vermilion

plaster of Paris. The gelatin was driven into the veins, while the plaster was held up by the capillaries and restricted to arteries, thus differentially colouring both arteries and veins at a single operation. PARKER stated that only in this way had he ever succeeded in filling the cerebral and myelonal veins.

Other methods of investigation have been frequently employed. PARKER supplemented his dissections with frozen sections, in which the relationship of vessels to their surroundings is often most clearly shown. ALLIS usually found it necessary to study uninjected preserved specimens, sometimes those of long standing, and he then chose ordinary ink, injecting the vessels with which he was especially concerned, repeating as the dissection progressed. He also studied the distribution of anterior arteries by means of serial cross sections, a procedure greatly inferior to the dissection method, and one open to grave errors of interpretation. The most modern technique of all is the preparation of stereoscopic X-ray plates, as given by GAMBLE and HITCHCOCK (1920) for *Necturus*. The vessels to be studied (arteries or veins) are injected with a suspension mixture of barium sulfate and the animal photographed in any aspect desired. Two exposures are made, shifting the position of the tube by two and one-half inches for the second one. The positive preparation, on glass, is a most beautiful object when viewed by transmitted light, such as that from an illuminated ground glass, and is very instructive as to the three-dimensional relations of the various vessels. This method, however, is designed to supplement rather than supplant dissection.

The writer followed several courses of procedure in making his dissections but could improve little on the general method of HYRTL. One specimen was explored entirely from the dorsum, but the removal of the vertebral column without injury to the aorta and segmentals is extremely difficult, and adds nothing to information gained by the far easier ventral approach. The best general plan is to prepare the efferent collectors of the gills of one side, then disclose the entire hypobranchial and coronary systems from the ventral. Transection of all the visceral arches at their lateral apices and appropriate cuts in the pectoral region will next allow the investigator to swing the pharyngeal floor to one side and to expose the roof of the mouth. This will permit a study of the efferent branchials and dorsal aorta from the ventral aspect, after which the preoral arteries must be carefully and separately traced by removing the chondrocranium from the top and one side. Needless to say, a binocular stereo-magnifier or a pair of binocular loupes will be of utmost service.

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259

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