

Resumido por el autor, Edward Phelps Allis, Jr.

El miodomo y la cámara trigémino-facial de los peces y las cavidades correspondientes de los vertebrados superiores.

El miodomo de los peces es completamente externo a la cavidad cerebral del cráneo y en los teleósteos no siluroideos está formado por compartimentos dorsales y ventrales separados por una membrana que puede osificarse como una parte del parasfenoides. El compartimento dorsal aloja los extremos posteriores de los rectos externos y está atravesado por las venas pituitarias. El compartimento ventral aloja los rectos internos y está atravesado por la carótida interna, las arterias pseudobranquiales eferentes y los nervios palatinos. En *Amia* este último compartimento es externo al condrocráneo, situado entre él y el parasfenoides y los rectos internos no le penetran. El compartimento dorsal corresponde en apariencia al canal hemal de la cola, y ha sido invadido secundariamente por los rectos externos. Se presenta más o menos desarrollado en todos los vertebrados excepto en los anfibios; en los mamíferos se transforma en los senos cavernoso e intracavernoso; las venas que los atraviesan son las homólogas de las venas pituitarias de los peces. La cámara trigémino-facial de los peces consta de partes yugular y ganglionar, separadas por una pared ósea en la mayor parte de los teleósteos. La parte ganglionar corresponde a las cavidades epiptérica y supracoclear de los mamíferos. La parte yugular se transforma en la cavidad timpánica; los osículos auditivos son en apariencia partes de su pared lateral. El ala temporal es una barra cartilaginosa formada en la pared lateral de la parte lateral de la porción ganglionar, entre los ramos maxilar y mandibular del trigémino, y por consiguiente, no es la homóloga del proceso ascendente del parasfenoides de los peces o del antipterigoideo (columela) de los reptiles.

Translation by José F. Nonidez  
Columbia University

## THE MYODOME AND TRIGEMINO-FACIALIS CHAMBER OF FISHES AND THE CORRESPONDING CAVITIES IN HIGHER VERTEBRATES

EDWARD PHELPS ALLIS, JR.

*Menton, France*

A functional myodome, or so-called eye-muscle canal, is a structure peculiar to fishes, and even among them it is limited, in the fishes I have examined to *Amia* and the non-siluroid Teleosts. It is such an important organ in those fishes in which it is found that it has necessarily received considerable attention, and various suggestions have been made regarding its origin and development. In my work on the Mail-cheeked Fishes (Allis, '09) it was discussed at considerable length, and I came to the conclusion that it was primarily a subpituitary and intramural space which had been secondarily invaded by certain of the rectus muscles, entrance to it having been acquired, on either side, through a foramen that transmitted a cross-commissural vein which drained the pituitary region and more particularly the hypophysis. That any part of the definitive myodome formed part of the *cavum cerebrale cranii*, that any part of it had been excavated by certain of the rectus muscles in previously solid portions of the basis cranii, simply in order to acquire more favorable points of origin, or that any part of it had been enclosed by the growth of bone or cartilage developed for that special purpose, I did not believe. I accordingly did not, at the time my manuscript was sent to press, accept Swinnerton's ('02) contention that, in *Gasterosteus*, the anterior portion of the myodome was an actual derivative of the *cavum cerebrale cranii*, while its posterior portion was an extramural space secondarily enclosed between the basioccipital and the underlying parsphenoid. I, however, later received Gaupp's ('05 b) work on *Salmo*, and when I found that he had arrived

at practically the same conclusion as Swinnerton, I added the following foot-note to my own work (Allis, '09, p. 195):

Gaupp, in Bd. 3 of Hertwig's *Handbuch der vergleichenden und experimentellen Entwicklungslehre der Wirbeltiere*, a work that I have only seen since this manuscript was sent to press, describes practically similar conditions in *Salmo* [to those described by Swinnerton in *Gasterosteus*], and arrives at practically similar conclusions regarding the homologies of the parts. This would seem to establish the fact that the basioccipital portion of the myodome is extracranial in origin. Regarding the prootic portion of the myodome, Gaupp's descriptions would seem to confirm my contention that it is an intramural space and not an intracranial one.

According to the views set forth in the works above referred to, both Swinnerton and Gaupp maintain that the myodome owes its origin to the fact that certain of the muscles of the eyeball, which primarily had their points of origin on the external surface of the chondrocranium, forced their way into the *cavum cerebrale cranii*, forced the brain upward considerably above the *basis cranii*, and then, after having thus displaced and certainly disturbed the delicate central nervous organ, forced their way out of the chondrocranium to again acquire origin on its external surface, and then became secondarily enclosed there in a canal developed for that special purpose. This has always seemed to me improbable, notwithstanding my provisional and somewhat qualified acceptance of it, and I have long intended investigating the development of this canal whenever I could obtain suitable material, my series of sections of somewhat advanced teleostean embryos not being considered suitable for the purpose.

I, however, recently had occasion, in connection with other work, to examine a series of sections of a 51-mm. specimen of *Hyodon tergisus*, and noticed that the myodome was directly continuous, posteriorly, with a groove on the ventral surface of the basioccipital that lodged the anterior portion of the median dorsal aorta. This at once suggested that the basioccipital portion of the teleostean myodome, and hence possibly the entire myodome, might be a canal of vertebral origin comparable to the haemal canal of the tail, for that canal is not

always limited to the caudal region, as the conditions in *Acipenser* show (Bridge, '04, fig. 115, p. 200).

Accordingly, with this idea definitely in view, I have carefully examined the myodome, not only in this series of sections of *Hyodon* and in a single prepared skull that I have of the adult fish, but also in all other embryos and adults of the *Holostei* and *Teleostei* that I at present have at my disposal that seem to be of interest in this connection, and the result has been not only to strongly favor this interpretation of the conditions, but also to give a conception of the myodome itself and the bones related to it quite different from that I formerly held. The functional myodome, as found in the fishes examined, will first be quite fully described, and then comparison made with the descriptions of the corresponding parts in certain other fishes and in certain of the higher vertebrates.

The preliminary examination of the serial sections used in connection with the work was wholly done by my assistant, Mr. John Henry, camera drawings being made of many sections of each series. The drawings used for the figures are by my assistant, Mr. Jujira Nomura.

#### HYODON TERGISUS

The myodome of *Hyodon* has never been described, so far as I can find, except by Ridewood, ('04), who only says that, in *Hyodon alosoides*: "The parasphenoid underlies but a small portion of the basioccipital, and the eye-muscle canal opens at its posterior end by an oval foramen."

In my skull of the adult *Hyodon tergisus*, the anterior opening of the myodome is triangular and unusually large and tall for the size of the skull. Posterior to this opening the myodome diminishes rapidly in size, and finally becomes continuous with an open groove on the ventral surface of the basioccipital. This groove extends to the hind end of the basioccipital and there cuts through the ventral edge of the vertebra-like hind end of the bone to open upon its posterior surface. This open groove forms no part of the myodome as described by Ridewood, his myodome ending at the oval foramen described by him, which leads from

the myodome directly into the anterior end of the groove. The groove quite unquestionably lodged, in the fresh specimen, the anterior portion of the dorsal aorta, as it does in my 51-mm. specimen, and it may accordingly be called the aortal groove, the term myodome being limited to that canal as described by Ridewood.

The anterior portion of the floor of the myodome, as thus defined and limited, is formed by the parasphenoid, the ascending processes of which form the ventral portions of its side walls. The middle portion of the floor is probably formed by the synchondrosis, in the mid-ventral line, dorsal to the parasphenoid, of the ventral ends of the ventral processes of the prootics, for that is the condition in my 51-mm. specimen, but, as I do not wish to destroy my one skull of the adult of this fish, I cannot definitely say that this is so. A short posterior portion of the floor is probably formed, like its anterior portion, by the parasphenoid, for it is so formed in the 51-mm. specimen. Slightly posterior to the sutural line between the hind edges of the prootics and the anterior end of the basioccipital, the parasphenoid separates into two diverging hind ends which extend posteriorly a certain distance, there resting upon the ventral edges of the bounding walls of the aortal groove.

The dorsal portions of the side walls of the anterior portion of the myodome and the entire side walls of its posterior portion are formed by the ventral processes of the prootics, which are overlapped externally by the lateral edges of the parasphenoid. The roof of the myodome is formed by the horizontal processes of the prootics, the so-called prootic bridge or shelf, but whether these processes suture with each other in the median line or are separated by a median line of cartilage, I cannot tell from my specimen for the reason above given. The prootic bridge is perforated near its anterior edge by a small median foramen, the so-called pituitary opening of the brain case of my descriptions of other fishes, the bridge thus having post-pituitary and prepituitary portions.

The basisphenoid, which, as Ridewood says, has no vertically descending process, suturates posteriorly with the anterior edge of the prepituitary portion of the prootic bridge; later-

ally, on either side, with the related alisphenoid, and anteriorly with the orbitosphenoid. It is perforated by a single median foramen which transmits the two optic nerves, this apparently agreeing with Ridewood's description of this bone, for his statement that it "forms the superior edge of the optic foramen" must mean that the two optic nerves traverse it through a single opening.

As already stated, the groove on the ventral surface of the basioccipital of my 51-mm. specimen lodges the anterior portion of the median dorsal aorta. When, proceeding anteriorly, the aorta begins to widen, preparatory to separating into a lateral dorsal aorta on either side, it recedes from the groove and is replaced by the hind ends of the muscoli recti externi; these muscles soon occupying the entire groove, the aorta lying ventral to them and outside the groove. The lateral edges of the groove give insertion to the tunica externa of the air-bladder, the tissues of the tunica forming, in the posterior, but not the anterior portion of the groove, an arched bridge beneath the aorta and so enclosing it in a canal; this being as described by Bridge ('99) in *Notopterus*. The notochord, enclosed in the basioccipital, lies directly above the bottom of the groove, separated from it by only a thin layer of bone of perichordal origin.

In sections through the extreme hind end of the basioccipital (fig. 12) the aortal groove is shallow and lies directly beneath the notochord, between blocks of cartilage which are unquestionably the homologues of the lower arches, or basiventrals, of current descriptions of the vertebrae, but which I shall refer to as the ventrolateral vertebral processes. On each of these processes there are two slight ridges: a ventromesial one, clothed with perichondrial bone that represents a part of the hind end of the basioccipital, and a dorsolateral one, not clothed with bone, which gives attachment to a ligament running outward in an intermuscular septum and doubtless representing either a dorsal or a ventral rib. In sections slightly farther forward (fig. 11) the ventrolateral cartilaginous processes have entirely disappeared, but are represented by parts of the basioccipital which

are of membrane origin. The dorsolateral ridge of the process of the preceding figure has disappeared, but the ventromesial one is represented by a tall ridge of bone which bounds laterally on either side a deep aortal groove. The dorsolateral vertebral processes (upper arches, basidorsals) are here represented by two large blocks of cartilage in relation to which the exoccipitals are developed.

Each exoccipital is perforated by two occipital nerves, the anterior one represented by a ventral root alone and the posterior one by both dorsal and ventral roots. Anterior to these two nerves a delicate ventral root arises from the medulla, but it does not reach the internal surface of the cranial wall.

On the ventral surface of the first free vertebra there is a slight depression, but no aortal groove, the space between the ventrolateral vertebral processes of opposite sides being completely filled by bony deposits.

Comparing these conditions with those in the adult *Amia*, it is evident that the ventromesial ridges of the ventrolateral cartilaginous processes of *Hyodon*, bounding laterally the aortal groove, are the homologues of the little cartilaginous processes on the ventral surface of the hind end of the basioccipital of *Amia*. There are in *Amia*, as is well known, two pairs of these little cartilaginous processes—called by Hay ('95) aortal supports, by Schauinsland ('05) haemal processes—and Schauinsland says that they are related to certain vertebrae that were said by Sagemehl ('83) to have fused with the hind end of the primordial cranium of this fish. Schauinsland further says that Sagemehl found one pair of these processes, but that he himself finds two; but these two pairs had already been described by both me ('97) and Schreiner ('02). The space between each pair of these processes is almost completely filled by bony deposit, the aortal groove thus being obliterated here, as it is also shown by Hay (95, fig. 1) to be in a transverse section of one of the anterior dorsal (trunk) vertebrae of a 12.5-cm. specimen of this fish. In the last dorsal vertebra of this same specimen, Hay shows (*l.c.*, fig. 6) this space not so completely filled by bony deposit, and in the first caudal vertebra it is even still less so

(l. c., fig. 7). If, in those vertebrae that are known to have fused with the occipital region of the cranium of this fish, the deposit of bone between the aortal supports had been as restricted as it is in the first caudal vertebra, conditions similar to those actually found in *Hyodon* would have arisen. The posterior portion of the aortal groove of *Hyodon* is thus certainly enclosed between processes of vertebral origin, but whether these processes are the exact homologues of the haemal processes of the tail is open to some question, for there is marked want of accord in the descriptions of the formation of the latter.

In *Amia* the aortal supports (haemal processes, Schauinsland) are said by both Hay and Schauinsland to be primarily cartilaginous, and to be simply differentiated parts of the bases of ventrolateral vertebral processes (lower arches). Posterior to the twenty-fourth vertebra, these supports are said by Hay to be developed apparently independently of the main mass of the ventrolateral vertebral processes (lower arches), and in the posterior region of the trunk they are said to be forced away from the notochord by bony deposits, and to each there become attached to the ventral surface of the remaining portion of the related ventrolateral process, which is then called a parapophysis. In the tail region the aortal supports are said by Hay to entirely disappear, and this one statement, together with the several figures given, would lead one to suppose that it is the remaining portions only of the ventrolateral processes, the so-called parapophyses, that form the haemal arches of the tail. The descriptions are, however, not clear as to this. What Hay actually says is ('95, p. 16):

In the vertebrae of the tail the cartilages [aortal supports] are missing. There is, however, in my younger specimen, what seems to be vestiges of them in the first caudal vertebra. Nothing, however, can be more certain than that the lower arches of the trunk are bent down to form the arches of the tail, and that the aortal supports have nothing to do with the formation of the caudal haemal arches.

On a later page he, however, says: "In the tail the halves of each lower arch have united at their distal ends, so as to enclose the blood vessels." It may accordingly be that Hay con-



sidered the haemal arches to be formed by the entire ventrolateral processes, and this is what Schauinsland ('05) says of these arches in all fishes. In *Laemargus*, Schauinsland even shows (*l. c.*, p. 411) the aortal supports (his haemal arches) projecting mesially from the mesial surfaces of the entire ventrolateral processes and partly separating the haemal canal into dorsal and ventral compartments which lodge, respectively, the aorta and the caudal vein.

In *Polypterus* the haemal arches have, as described by Budgett ('02), a totally different origin from that above set forth. In a 30-mm. specimen of this fish Budgett finds three distinctly separate series of cartilaginous vertebral processes, one dorsal, one lateral, and the other ventral. The lateral processes bear the upper ribs, which have the positions of the ribs in the *Selachii*. The ventral processes bear the lower ribs, which have the position of the ribs in the *Teleostei*. It is said that, in the caudal region, "the lateral series of cartilages are not found, while the ventral cartilages, though retaining their position, become the greatly enlarged haemal arches." These latter arches are thus here formed by processes that are certainly not the homologues of the so-called lower arches of the *Selachii*. In the trunk region of specimens of *Polypterus* older than the 30-mm. one, the ventral processes are said to be forced away from the notochord by bony deposits formed in relation to the lateral processes and these bony deposits are shown, in Budgett's figures, forming so-called aortal supports on either side of the aorta. The ventral processes thus forced away from the notochord are then found as blocks of cartilage in the bases of the ventral ribs at some distance from the notochord and loosely attached to the under sides of the lateral processes; these ventral processes of this fish thus strikingly resembling the aortal supports of Hay's descriptions of *Amia*.

The aortal supports and haemal arches, as those terms are employed by English authors, may thus be of different origin in different fishes, but, whatever their origins and homologies may be, the lateral walls of the aortal groove of *Hyodon*, in the posterior basioccipital region here under consideration, are quite

certainly formed by aortal supports, the remainder of each primitive ventrolateral vertebral process being represented in the little cartilaginous ridge that gives attachment to the ligament which runs outward, rib-like, in the related intermuscular septum.

Returning now to the descriptions of Hyodon and proceeding forward in the sections, figure 10 shows that a ridge of bone gradually appears lateral to the tall ridge that bounds on either side the aortal groove, the appearance in these sections somewhat suggesting, excepting in the absence of cartilage, the conditions shown in Hay's figures 5 and 6 of trunk vertebrae of *Amia*, where the aortal supports are attached to the ventromesial surfaces of the lower arches (parapophyses, Hay). Still farther forward, in sections through the hind ends of the parasphenoid (fig. 9), the mesial one of these two processes has disappeared while the lateral one persists as a stout low process, this giving a broad ventral edge to the aortal groove. The lateral walls of the aortal groove are now formed by the entire ventrolateral processes, and not simply by the aortal supports, and the bony deposits on either side that fill the space between these processes and the dorsolateral vertebral processes (upper arches) has been excavated to form the recessus sacculi. Hence the basioccipital is here W-shaped in transverse section, the two grooves on the dorsal surface of this W each forming the ventral portion of the related recessus sacculi, and the grooves of opposite sides being separated from each other by a tall median plate formed by part of the basioccipital. The notochord lies in the ventral end of this median plate, dorsal to the bottom of the aortal groove, but is here represented simply by a notochordal space. The exoccipital of either side has vertical and horizontal plates, the former forming the dorsal portion of the side wall of the related recessus sacculi and the mesial portion of the other the roof of the recessus, the mesial edge of the latter plate resting upon the dorsal end of the tall median plate of the basioccipital and forming, with its fellow of the opposite side, the floor of the *cavum cerebrale cranii*. The median groove on the ventral surface of the W here lodges the hind ends of the

musculi recti externi, with the dorsal aorta lying ventral to them.

Proceeding anteriorly from this point to sections through the bases of the diverging hind ends of the parasphenoid (fig. 8), the bony bounding walls of the aortal groove are gradually replaced by cartilage lined with thin plates of perichondrial bone which form parts of the basioccipital. Angles in this cartilage and bone now replace the two bony ridges, just described, in more posterior sections. The perichondrial bone then disappears, in the region of the hind end of the myodome, leaving the bounding walls of the groove entirely of cartilage, and slightly anterior to that point the remaining portions of the basioccipital also vanish. The notochord extends forward nearly to the hind end of the myodome, its anterior end lying dorsal to the bottom of the aortal groove and hence in the level of the roof of the myodome and not in that of its floor. In this region the aorta has separated into a lateral dorsal aorta on either side.

Anterior to the bases of the diverging hind ends of the parasphenoid, the aortal groove is closed ventrally by the latter bone, and, still lodging the musculi recti externi, becomes the hind end of the myodome. Except that the groove is here closed ventrally by the parasphenoid and that it lies in the prototic region, there is no line of demarcation between it and the open canal in the basioccipital region, and each broad ventral edge of the open groove, lying between the two angles above described, is continued forward as the ventral edge of the lateral bounding wall of the myodomic canal.

Proceeding forward in the sections, there is gradual ventral growth of the cartilaginous side walls of the myodomic canal, this growth taking place between the two little angles above described. This gives rise to a flange of cartilage on either edge of the primitive groove, the flange projecting ventrally and slightly mesially beneath the level of the dorsolaterally projecting basal portion of the lateral wall of the cranium, the base of that portion of the wall lying in the level of the ventral edge of the primitive aortal groove (fig. 7). Proceeding anteriorly, these flanges increase gradually in actual height, and appear to

gain additional height because of the gradual widening of the dorsal portion of the myodomic cavity, cross-sections through which change gradually from oval to pear-shaped and then to triangular. The roof of the myodome thus becomes flat (fig. 6,) instead of being arched (fig. 7). The cartilage forming the top of the arched roof is continued forward as the median portion of the flat roof, and is enclosed between plates of perichondrial bone which do not meet in the median line and which form the distal (mesial) portions of the horizontal processes of the prootics. The lateral portions of these processes and the dorsal portions of the side walls of the myodome are now each formed by two plates of bone, doubtless of perichondrial origin but without enclosed cartilage, this bone replacing the cartilage of the preceding sections and forming the dorsolateral corners of the myodomic cavity. The horizontal portion of each of these angles of bone forms the basal (lateral) portion of the horizontal process of the prootic of its side, and arises from the base of the lateral wall of the *cavum cerebrale cranii*. The vertical portion of the angle of bone forms a wall between the dorsal portion of the myodome and the ventral portion of what is, in the prepared skull of the adult, a large bay on the external surface of the cranium. This bay forms that part of the large auditory fenestra of Ridewood's ('04) descriptions that lies anterior to the so-called vertical lamina of the prootic, and its floor is formed, in my embryo as in the adult, by a laterally projecting, horizontal shelf of the prootic. This bay of this fish corresponds to the facialis part of the trigemino-facialis chamber of my description of Scomber and the mail-cheeked fishes, and occupies a position, relative to the cranial walls, similar to that of the recessus sacculi, the floor of the bay being an anterior continuation of that of the recessus. The *truncus hyomandibularis facialis* enters this bay through a foramen in its mesial, cranial wall, and runs outward above its floor. The *vena jugularis*, traced from behind forward, enters the bay over the posterior edge of its floor, accompanied by a sympathetic nerve, a communicating branch from the *nervus glosso-pharyngeus* to the *nervus facialis*, and the *arteria carotis externa*, this artery lying ventromesial to the other structures.

The foramen faciale perforates the prootic posterior to the postorbital process of the neurocranium, the foramen trigeminum perforating the same bone anterior to that process, the two foramina both leading directly into the cavum cerebrale cranii. Between these two foramina the postorbital process of the cranium is perforated by a short canal, the floor of which lies at the level of the roof of the myodome and hence dorsal to the posterior portion of the floor of the facialis bay. The later bay leads directly into this canal, the canal itself leading into the orbit and transmitting the vena jugularis, the arteria carotis externa, a communicating branch from the nervus facialis to the nervus trigeminus, and a sympathetic nerve. This canal is thus a jugular canal through the prootic bone, and it represents all there is, in this fish, of the trigemino-facialis chamber of my description of others of the Teleostei. There are in this region of the cranium of fishes three distinctly different chambers. One is the trigemino-facialis recess of my descriptions of the Teleostei and Selachii; another is the jugular canal through the prootic, just referred to and which I have heretofore called the teleostean trigemino-facialis chamber; and the third is a chamber formed by the fusion of the other two, and is the trigemino-facialis chamber of my descriptions of *Amia*. It is accordingly necessary to distinguish between these several chambers, and the term trigemino-facialis chamber will hereafter be limited to the chamber as found in *Amia*, the two parts of the chamber being called its pars ganglionaris and pars jugularis.

The ventral edges of the side walls of the myodome of *Hypodon* are nowhere enclosed in perichondrial bone, cartilage always projecting ventrally beyond the related bone and abutting against dense connective tissue that separates it from the parasphenoid. This tissue is apparently all skeletogenous, for there is no definite perichondrial membrane separating it from the cartilage. The parasphenoid develops in the outer layers of this tissue, and the bases of the diverging hind ends of that bone are connected by it across the median line (figs. 8 and 9), the tissue there forming a dense and well-defined band-like layer. Farther posteriorly this transverse band becomes less dense,

and then practically disappears, but there is always a line connecting the two ends of the parasphenoid, and hence also connecting the ventral edges of the aortal groove.

Approximately in the transverse plane of the foramen faciale, a cartilaginous process projects mesially from the ventral end of each cartilaginous side wall of the myodome and meets its fellow of the opposite side in the median line, but it does not completely fuse with it, a slight line of separation always remaining evident. These two processes thus together form a cartilaginous floor to the myodome, the parasphenoid lying against the ventral surface of this floor, but separated from it by the dense skeletogenous tissue above referred to. Immediately posterior to this point, the pharyngobranchial of the first branchial arch articulates with the dorsal portion of the side wall of the myodome, there lying between the vena jugularis and the external and internal carotid arteries; and immediately posterior to that, the pharyngobranchial of the second branchial arch articulates with the ventral surface of the parasphenoid (fig. 7). The external and internal carotid arteries separate from each other slightly anterior to the latter point, both lying along the lateral surface of the lateral wall of the myodome. The external carotid runs forward and upward, ventral to the nervus facialis, and, joining the vena jugularis, traverses, with that vein, the short canal which represents the pars jugularis of the trigemino-facialis chamber. The internal carotid continues forward and downward along the side wall of the myodome until it reaches the hind edge of the ascending process of the parasphenoid, where it traverses a foramen which is, as in the adult, entirely enclosed in that bone.

Beginning immediately posterior to this foramen (fig. 5) for the internal carotid artery and proceeding forward in the sections, the cartilage forming the floor of the myodome, and also the ventral ends of its side walls, gradually disappears and is replaced by the dense skeletogenous tissue already referred to several times, and in it a cavity appears, bounded on all sides by the tissue and lying between the parasphenoid and the myodomic cavity. The floor and side walls of this cavity

form a matrix, in relation to which the body and ascending processes of the parasphenoid are developed, and from here forward for a certain distance teeth are found developed in relation to this bone. The roof of the cavity forms a membrane which extends transversely from the ventral end of one persisting cartilaginous side wall of the myodome to the other, this membrane being horizontal in position in its posterior portion, but arching upward anteriorly to such an extent that, in the subpituitary region, its summit reaches nearly to the middle of the height of the entire myodomic cavity. The parasphenoid has in this region been inclining quite rapidly ventrally, this, and the arching upward of the membrane, leaving a space between the two and separating the myodomic cavity into dorsal and ventral compartments. The ventral compartment, limited to the region of the ascending processes of the parasphenoid, is bounded both laterally and ventrally by that bone. The dorsal portion of the dorsal compartment is bounded laterally by the ventral processes of the prootic bone, its ventral portion being bounded in part by the ventral portions of those processes, overlapped externally by the ascending processes of the parasphenoid, and in part by the latter processes only. The dorsal compartment still lodges the recti externi, the ventral compartment lodging the hind ends of the recti interni and the internal carotid arteries, the two being separated by a delicate line of tissue (fig. 3).

Slightly posterior to the internal carotid foramina in the parasphenoid, the roof of the myodome, formed by the horizontal processes of the prootics, is traversed at each lateral edge by both the nervus abducens and the ramus palatinus facialis, apparently through a single foramen (fig. 4). The abducens goes directly to the mucus rectus externus. The palatinus facialis runs ventrally along the internal surface of the side wall of the dorsal compartment of the myodome, passes through a notch in the anterior edge of the ventral end of the prootic portion of that wall, which is wholly of cartilage, and then, continuing ventrally between that cartilaginous wall and the ascending process of the parasphenoid, enters that portion of the ventral

compartment of the myodome that is occupied by the internal carotids (fig. 3). In its passage along the mesial surface of the lateral wall of the myodome it lies between the wall and a delicate layer of connective tissue which everywhere lines the myodomic cavity, thus apparently not definitely entering the central cavity of the myodome.

Slightly anterior to the point where the prootic bridge is perforated by the *nervi abducens* and *palatinus facialis*, and slightly anterior also to the transverse plane of the internal carotid foramina, the median cartilaginous portion of the prootic bridge ceases, and the roof of the myodome is then perforated by what is, in the prepared cranium of the adult fish, the pituitary opening of the brain case (fig. 1 to 3). This opening is closed, in fresh specimens by a portion of the *dura mater* that projects ventrally into the myodome and so forms a pit-like depression in the floor of the *cavum cerebrale cranii*, in which the pituitary body lies; thus forming the actual pituitary fossa. It will, however, be best to call it the pituitary sac, for the term pituitary fossa, and its equivalent *sella turcica*, has been given to the depression that, in the floor of the cartilaginous or osseous cranial cavity, lodges this pituitary sac, and the two are not always coincident. The sac forms the roof of this part of the myodome of *Hyodon*, and a median vertical membrane descends from its ventral and anteroventral surfaces. Anteriorly this membrane is directly continuous with the membranous interorbital septum; posteroventrally it is continuous with the anterior edge of the median portion of the horizontal myodomic membrane, the lateral portions of the latter membrane here being so broken up and interrupted by the muscles and vessels entering or leaving the myodome that they cannot be followed in the sections. The vertical membrane does not at this point extend ventrally to the floor of the myodome, but in the transverse plane of the hind edge of the basisphenoid (fig. 1) it becomes the interorbital septum, and there its flaring ventral edges are each attached to a ridge on the related lateral edge of the dorsal surface of the parasphenoid. In the triangular space enclosed between the latter bone and the V-shaped ventral end of the septum lies,



on either side, the related *nervus palatinus facialis*, the nerves of opposite sides being separated from each other by a median ridge on the dorsal surface of the parasphenoid, and each accompanied by a small branch of the internal carotid, given off just before that artery enters its foramen in the parasphenoid. This branch does not enter the myodome, but runs forward in a canal in the parasphenoid between what seem to be portions of the bone that are the one of membrane and the other of dental origin.

The rectus inferior muscle of either side has its origin on the dorsal portion of the interorbital septum, near the level of the posterior edge of the basisphenoid. The rectus superior has its origin on the anterior edge of the horizontal myodomic membrane. The pituitary vein of either side enters the dorsal compartment of the myodome in the subpituitary region, and, running posteriorly in it, joins its fellow of the opposite side posterior to the membranous pituitary sac, there forming a large sinus. From this sinus branches are sent to the rectus externus muscles, and from its anterior end a small median branch is sent upward, through the membranous roof of the myodome, into the *cavum cerebrale cranii*, where it immediately breaks up and cannot be followed in the sections.

The pituitary vein of either side is joined by veins from the eyeball and the eye-muscles, these together forming what Allen ('05) has called the internal jugular vein. I have also employed his term in certain of my works, in others calling it simply the jugular vein. This latter term is certainly the only one that can be appropriately employed, for the vein is the definitive *vena jugularis*, and as it is formed in part by the *vena capitis media* and in part by the *vena capitis lateralis*, neither of these terms can be employed excepting to designate certain sections of it.

The internal carotid artery of either side traverses its foramen at the hind edge of the ascending process of the parasphenoid and enters the ventral portion of the ventral compartment of the myodome. There it gives off the orbitonasal artery and then, running forward into the subpituitary portion of the myodome, turns upward in that part of the median vertical myodomic

membrane which forms the anterior wall of the membranous pituitary sac. In this part of its course, and while still enclosed in the median vertical membrane, it anastomoses with its fellow of the opposite side, and then, separating from its fellow, enters the *cavum cerebrale cranii* (fig. 2). There it immediately divides into anterior and posterior divisions. The posterior division sends branches to the hypophysis, and then itself separates into anterior and posterior branches. The anterior branch runs forward along the floor of the *cavum cerebrale cranii* and sends a branch outward in the body of the optic nerve. Other branches are sent to the brain, one of them joining, anterior to the *nervus opticus*, the terminal portion of the anterior division of the entire artery. In one of two specimens examined, the latter division of the artery immediately issued from the cranial cavity by passing ventrally across the posterior edge of the basisphenoid, while in the other specimen it perforated that bone near its hind edge. In each case the artery then ran forward ventral to the horizontal plate of the basisphenoid, enclosed in the dense fibrous tissues that there form the dorsal edge of the interorbital septum. While in this tissue a branch is sent outward to the eyeball, the artery then issuing from the fibrous tissue, passing across the posterodorsal surface of the *nervus opticus*, and entering the cranial cavity through the foramen for that nerve. There it joins and fuses with the anterior branch of the posterior division of the entire artery, just described, the artery so formed then running forward along the floor of the *cavum cerebrale cranii*. The branch sent to the eyeball from the anterior division of the artery, enters it close to the point of entrance of the *nervus opticus*, and there immediately forms a slight enlargement which somewhat resembles a glomus. From this glomus a branch arises and unites with the small artery accompanying the *nervus opticus*, the two together forming the *arteria centralis retinae*.

I cannot recognize the anterior division of the internal carotid artery, above described, in any descriptions that I have of the adults of fishes, and yet it is found in all of the non-siluroid Teleostei that I have examined in serial sections in connection

with the present work. The fact that, in one of my two specimens of *Hyodon*, it perforates the basisphenoid, is peculiar, and it is to be noted that in that specimen this bone has a greater anteroposterior extent than in the other, extending posteriorly beyond the sutural line between the alisphenoid and prootic, instead of ending anterior to that line, as in the other specimen. This, when compared with the conditions in the other fishes examined, to be described later, would seem to indicate that the basisphenoid of *Hyodon* is not strictly comparable to that bone in those other fishes.

On one side of my 51-mm. specimen of *Hyodon* the efferent pseudobranchial artery entered the ventral compartment of the myodome with the internal carotid, through the foramen for that artery. On the other side it perforated the ascending process of the parasphenoid anterior to the internal carotid, separated from it by a narrow column of bone. Having entered the ventral compartment of the myodome, in its subpituitary portion, it passes ventral to the orbitonasal artery and is connected with its fellow of the opposite side by a cross-commissural vessel which passes anteroventral to the internal carotids. The efferent pseudobranchial artery then itself runs outward into the orbit, as the *arteria ophtalmica magna*, to enter the eyeball and there supply the chorioid gland.

In this 51-mm. embryo, as in the adult, the alisphenoid bone has no pedicel (parasphenoid leg), this pedicel being represented by membrane only, as it is, wholly or in part, in many other Teleostei (Allis, '09). The pedicel or so-called vertical descending process (Ridewood) of the basisphenoid is also wanting, as already stated, that bone being represented by its horizontal plate alone. In those Teleosts in which this bone has a pedicel, its hind edge forms the median vertical anterior boundary of the myodome, and the anterior edge of the median vertical myodomic membrane is attached to it. When the pedicel is wanting, as in *Hyodon*, the vertical myodomic membrane runs insensibly into the membranous interorbital septum, and there is nothing to mark definitely its anterior limit.

The myodome of my 51-mm. specimen of *Hyodon* thus lies in part beneath the pituitary opening of the brain case and in part posterior to that opening, a part of it thus being prechordal and the remainder chordal in position, or, in the terminology employed by Froriep ('02 a), the one prespinal and the other spinal. The spinal portion is formed, throughout part of its length, by two distinctly different parts, one dorsal and the other ventral, the two being completely separated from each other in part by cartilage and in part by membrane which forms a direct anterior prolongation of the cartilage. In the prespinal portion these two compartments of the spinal portion are confluent because of the breaking down of the separating wall (the horizontal myodomic membrane) by the structures that here enter or leave the dorsal compartment. The canal traversed by the internal carotid arteries as they run upward in the median vertical myodomic membrane lies in the level, anteriorly prolonged, of the dorsal myodomic compartment, but it forms no part of either compartment of the myodome.

The dorsal compartment of the myodome of *Hyodon* is limited to the subpituitary and postpituitary regions, and although both of these parts lie in the prootic region, the postpituitary portion, which lies beneath the prootic bridge, may be alone referred to as the prootic portion of the compartment. The ventral compartment has prootic, subpituitary, and prepituitary portions. The dorsal compartment is directly continuous posteriorly with the anterior end of the aortal groove, which extends the full length of the basioccipital region. The ventral compartment is not continuous with the groove and it does not extend posteriorly as far as the dorsal compartment. It lies between the floor of that compartment and the parasphenoid, lodges the hind ends of the recti interni, and is traversed by the internal carotid arteries, the palatine branches of the faciales, and the efferent pseudobranchial arteries. The dorsal compartment lodges the pituitary veins and the muscoli recti externi, these muscles entering it from the orbits and leaving it by its posterior opening. The nervus abducens of either side perforates the roof of this compartment to reach and supply the rectus

externus. The ramus palatinus facialis also perforates the roof and traverses the dorsal compartment in order to reach the ventral one, but it is separated from the central cavity of the dorsal compartment by a membrane, apparently of skeletogenous character, the nerve thus probably lying morphologically in the wall of this compartment of the myodome and not actually traversing it.

The recti externi, after issuing through the posterior opening of the dorsal compartment of the myodome, extend posteriorly a certain distance, there lying in a part of the aortal groove which differs slightly in character from the part posterior to it. This anterior part of the groove is, however, so evidently an anterior prolongation of its posterior portion that the two parts must be of similar origin, and as the posterior portion of the groove has certainly not been developed in any relation whatever to any of the muscles of the eyeball, it is certain that the anterior portion also has not been so developed. This is, furthermore, confirmed by the conditions in *Polypterus*, in which there is no functional myodome, but there is both a cavity corresponding to the dorsal compartment of the myodome of *Hyodon* and a closed and wholly separate canal lodging the cranial portion of the aorta and corresponding to the aortal groove of *Hyodon*. This myodomic cavity and aortal canal have both been referred to and discussed in certain of my earlier works (Allis, '08 a, '09), and I now find, on reexamining my sections of a small specimen of this fish, that the enclosing walls of the aortal canal give even more positive evidence of having been formed by vertebral processes than do the walls of the groove of *Hyodon*.

There thus seems little doubt that the bounding walls of the aortal groove of *Hyodon* are formed by processes similar to those which enclose the haemal canal of the tail, and that those bounding walls are formed either by the entire ventrolateral processes of vertebrae which here have been incorporated in the neurocranium, or by aortal supports developed in relation to those processes; and if the walls of this groove are so formed, it would seem as if the side walls of the prootic portion of the dorsal compartment of the myodome, evidently an anterior con-

tinuation of the walls of the aortal groove, must be of similar origin. Why the aorta has been excluded from this prootic portion of the myodome is not apparent, but it would seem as if it might be related to the development of the hypochorda. According to Stöhr ('95), the hypochorda of *Rana*, when first formed, is attached to the dorsal wall of the alimentary canal by a series of tubular bridges, which persist longer in the anterior than in the posterior region of the trunk, and, for a time, there prevent the lateral dorsal aortae from fusing with each other in the median line excepting between the bridges. In the head region the hypochorda is said to develop later than in the trunk, and the related bridges would hence there also, while they persisted, prevent the lateral dorsal aortae from fusing with each other excepting between the bridges. It may then be that, such a bridge persisting in the prootic region, the lateral dorsal aortae could not there fuse with each other, and before this bridge had disappeared they had become fixed in position by the early development of the anterior aortic arches. Anterior to the spinal region of the cranium they, however, fused with each other, in certain fishes, that point either representing an interval between two hypochordal bridges, or lying anterior to the anterior bridge, as the case may be. This would then not only explain the formation of the *circulus cephalicus*, but also account for its position external to the ventral processes of the prootics.

In further support of the assumption that the ventral processes of the prootics are formed by ventrolateral vertebral processes is the fact, possibly significant, that these processes, like the neural processes in the spinal region, enclose a large canal between their proximal portions and a smaller one between their distal ends, the two cavities being separated from each other by a horizontal partition. In my 51-mm. specimen of *Hyodon* this partition is partly of cartilage and partly of membrane. In all the other fishes examined it is wholly of membrane, excepting as that membrane may have undergone ossification as part of the parasphenoid, a median longitudinal opening thus being left, when the parasphenoid is removed, be-

tween the ventral ends of the ventral processes of the prootics. This opening is the hypophysial fenestra of Sagemehl's descriptions of *Amia* and the Teleostei, and I have always employed that term for it in all my works. This fenestra has, however, in a considerable part of its length, no relation whatever to the hypophysis, and it will be later shown that, in all probability, it does not even contain the so-called fenestra hypophyseos of early embryos of these fishes. The term hypophysial fenestra is thus inappropriate, and I shall hereafter refer to it as the fenestra ventralis myodomus. To facilitate the descriptions and comparisons, the ventral processes of the prootics will be considered to be ventrolateral vertebral processes, notwithstanding that this is not definitely established by my present work.

#### SCOMBER SCOMBER

In the adult *Scomber* I found (Allis, '03) the myodome extending nearly to the hind end of the basioccipital but not opening posteriorly; and, doubtless in direct correlation with this, the parasphenoid of this fish does not have diverging hind ends. That part of the myodome that is related to the basioccipital is enclosed between ventral flanges of that bone which closely resemble the ventral processes of the prootics and form a direct posterior continuation of them. Two membranes, one vertical and the other horizontal, were said to extend the full length of the myodome. The horizontal membrane was said to separate the myodome into dorsal and ventral parts which lodged, respectively, the recti externi and interni. The vertical membrane was said to arise from the hind edge of the pedicel of the basisphenoid and, lying between the recti interni, to bisect the ventral part of the myodome. The recti inferiores were said to arise partly from the interorbital septum, between the foramen opticum and the anterior edge of the basisphenoid, and partly from a ligament or tendon which arises from the dorsal end of the pedicel of the basisphenoid. The recti superiores were said to have their origins from the anterior edge of the horizontal membrane.

The above statements all referred only to the adult of this fish, for I at that time had no specimens small enough to be sectioned. I have, however, since prepared a series of transverse sections of a 65-mm. specimen, in which I now find the vertical membrane above referred to descending from the ventral surface of the membranous pituitary sac, as in Hyodon. That part of it which, in the adult, lies beneath the horizontal membrane and extends to the hind end of the myodome is, in this 65-mm. specimen, simply a delicate line of connective tissue, but it would nevertheless seem to represent a remnant of a wall which primarily separated this part of the myodome into two parts, one on either side, as will be later explained. The horizontal membrane is practically as I described it in the adult. In its anterior portion it is not strongly developed, and there arises, on either side, from a layer of tissue which lines the internal surface of the side wall of the myodome cavity and is continued outward around the ventral end of the wall and then upward a certain distance along its external surface. The parasphenoid rests, on either side, upon the ventral surface of this tissue, and a longitudinal ridge on either side of the dorsal surface of the bone projects upward into that part of the tissue which lines the internal surface of the side wall of the cavity; this part of the parasphenoid certainly being an ossification developed in relation to the tissue. Along the line of origin of the horizontal membrane, the cartilage of the side wall of the myodome is slightly constricted and imperfect, suggesting a segmentation line similar to that shown by Schauinsland ('05) where a rib is in process of being segmented from a lower arch in the vertebral region of certain other fishes. Near the hind end of the myodome, beginning slightly anterior to the point where the recti interni terminate, that part of the cartilage of each lateral wall of the myodome that lies ventral to this segmentation line gradually passes, without any line of demarcation, into dense fibrous tissue which forms the ventral end of each lateral wall of the myodome. The parasphenoid here lies against the ventral surface of this tissue, and the longitudinal ridge on either side of the dorsal surface of the bone extends upward along the mesial sur-



face of the tissue. The horizontal membrane is strongly developed here, and extends across the median line between the ventral ends of the persisting portions of the cartilaginous side walls, thus lying at a certain distance dorsal to the parasphenoid. Proceeding posteriorly from here, in the sections, the recti interni disappear, leaving a space between the horizontal membrane and the parasphenoid. The latter bone then shortly disappears, and the myodomic cavity is then closed ventrally by the horizontal membrane only, this condition possibly persisting to the hind end of the myodome, but my sections are here imperfect and I cannot definitely determine this.

The conditions in *Scomber* would thus arise from those in *Hyodon* if the ventral compartment of the myodome of the latter fish were extended posteriorly nearly to the hind end of the aortal groove, and the continuous myodomic-aortal cavity so formed were closed ventrally, to that point, by the parasphenoid.

The internal carotid artery of either side enters, as in *Hyodon*, the ventral compartment of the myodome, runs forward in it into the prespinal portion of the myodome, and there turns upward in the median vertical myodomic membrane, anastomosing, while in the membrane, with its fellow of the opposite side. Leaving its fellow, it separates, as in *Hyodon*, into anterior and posterior divisions both of which run upward, posterior to the basisphenoid, and enter the cavum cerebrale cranii. The posterior division sends branches to the hypophysis and then separates into anterior and posterior branches, the anterior branch running forward along the floor of the cavum cerebrale cranii, sending a branch outward with the nervus opticus, and then joining the anterior division of the artery, this anterior prolongation of this branch of the artery not being found in *Hyodon*. The anterior division of the artery runs forward, dorsal to the basisphenoid, and, anterior to that bone, enters the thick, dense tissues forming the floor of the cavum cerebrale cranii and the dorsal end of the interorbital septum, its course and distribution from there onward being as in *Hyodon*. The fact that this anterior division of the artery runs forward dorsal to the

basisphenoid would seem to show that, as already stated, the anterior portion of the basisphenoid of Hyodon did not primarily form part of this bone.

The cross-commissure connecting the efferent pseudobranchial arteries of opposite sides traverses the ventral part of the prespinal portion of the myodome, there passing ventral to the orbito-nasal artery and anteroventral to the internal carotids. The pituitary veins enter the dorsal compartment of the myodome and there anastomose with each other, a small branch being sent upward into the *cavum cerebrale cranii* and apparently going to the hypophysis.

The *nervus palatinus facialis* of the adult traverses a canal in the prootic which begins in the floor of the *pars jugularis* of the trigemino-facialis chamber and opens on the mesial surface of the ventral process of that bone in the plane of the hind edge of the pituitary opening of the brain case, the nerve thus apparently not traversing the dorsal compartment of the myodome. In the 65-mm. specimen the nerve does not enter the *pars jugularis* of the trigemino-facialis chamber, perforating the roof of the dorsal compartment of the myodome and traversing it, as in Hyodon, but, as also in Hyodon, there lying between the ventral process of the prootic and the lining membrane of the myodomic cavity.

#### MAIL-CHEEKED FISHES (LORICATI)

In the adults of *Scorpaena scrofa*, *Trigla hirundo*, and *Cottus octodecimospinosus*, I found (Allis, '09) the myodome to extend nearly to the hind end of the basioccipital, and there open ventrally. In *Scorpaena* the origins of all the rectus muscles were given, the external and internal ones extending posteriorly in the myodome, the external somewhat farther than the internal. Nothing was said of a horizontal membrane separating the myodome into dorsal and ventral compartments, such as I had previously described in *Scomber* and now find in Hyodon. The orbital opening of the myodome was said to be closed by a strong membrane which the *recti externi* and *interni* perforated to reach their points of origin.

In a 40-mm. specimen of *Scorpaena scrofa* I now find the recti externi and interni as described in my earlier work, but they are separated by a membrane, delicate in places but well developed in others, which corresponds to the horizontal membrane of *Scomber* and *Hyodon* and separates the myodome into dorsal and ventral compartments. The rectus superior of either side arises in part from the anterior edge of this membrane and in part from the dorsal surface of the parasphenoid at or near the line where the lateral edge of the membrane is attached to it, this line being marked by a slight longitudinal ridge on the dorsal surface of the bone. The rectus inferior of either side arises from a median vertical membrane similar to that described in *Hyodon* and *Scomber*.

The internal carotid artery, after traversing its foramen at the hind edge of the ascending process of the parasphenoid, passes across an internal carotid incisure at the antero-ventral corner of the prootic cartilage, as in the adult (Allis, '09, p. 411), and enters the ventral compartment of the myodome, its farther course and distribution being as in *Scomber*. The cross-commissure of the efferent pseudobranchial arteries traverses the subpituitary portion of the myodome, as in *Hyodon* and *Scomber*. The pituitary veins anastomose with each other in the dorsal compartment of the myodome, but they do not there form an important sinus.

In the adult the ramus palatinus facialis traverses a canal in the prootic which begins in the trigemino-facialis recess (pars ganglionaris of the trigemino-facialis chamber) and opens on the internal surface of the ventral process of the prootic. In my 40-mm. embryo this nerve perforates a membranous portion of the prootic bridge, and, running ventrally between the side wall of the dorsal compartment of the myodome and the lining membrane of that cavity, as in *Hyodon* and *Scomber*, enters the ventral compartment in the subpituitary region and then escapes into the orbit.

In a 40-mm. specimen of *Trigla hirundo* the conditions are practically as in *Scorpaena*, excepting that the anterior branch of the posterior division of the internal carotid artery is inter-

rupted, either anterior or posterior to the branch sent out with the nervus opticus, as it is in *Hyodon*, while a branch, not found in either *Hyodon* or *Scorpaena*, is sent outward, anterior to the nervus opticus, to join a branch of the orbitonasal artery and then go to the eyeball.

In a 63-mm. specimen of *Trigla hirundo* the conditions differ in that the depression in the dura mater which lodges the hypophysis has a relatively wide and flat floor from which three membranes arise, one median and one at each lateral edge of the floor. These membranes are each inserted on a corresponding ridge on the dorsal surface of the parasphenoid, and the space enclosed, on either side, between them and the parasphenoid, lodges the rectus internus. Thus the ventral compartment of the myodome here rises to the ventral surface of the pituitary depression, and hence lies between right and left halves of the dorsal compartment. This condition continues posterior to the hypophysis for a certain distance, the roof of the ventral compartment of the myodome there forming the median portion of the floor of the cavum cerebrale cranii; but at the membranous anterior edge of the prootic bridge, the roof of the compartment begins to recede from the floor of the cavum cerebrale cranii, and, the lateral halves of the dorsal compartment uniting with each other above it, the conditions become as in *Scorpaena*. Apparently because of this intercalation of the ventral compartment between the anterior ends of the dorsal compartment, the pituitary veins are greatly reduced, the hypophysis being drained in part by the encephalic veins.

In this embryo of *Trigla* the nervus palatinus facialis perforates the floor of the pars jugularis of the trigemino-facialis chamber and enters the dorsal compartment of the myodome, this apparently being as I found this nerve in the adult Scomber.

In the adult *Cottus octodecimspinosus* I found (Allis, '09) the myodome continued posteriorly a short distance in the basioccipital, and not opening posteriorly on the ventral surface of the cranium. The prootics have perfectly normal horizontal processes, and they are shown, in my figures, preformed in cartilage and forming the roof of the myodome. The parasphenoid has diverging hind ends.

In a 20-mm. specimen of *Cottus scorpeus* I now find the protic portion of the myodome separated from the cavum cerebrale cranii by membrane only, no cartilaginous or osseous protic bridge being as yet developed. In its basioccipital portion the myodome lies in a groove on the ventral surface of the basioccipital (fig. 18), which opens posteriorly between the diverging hind ends of the parasphenoid, but is there closed ventrally by membrane which extends horizontally between those ends. This part of the myodome lodges the hind ends of the recti externi, the two muscles being separated from each other by a delicate vertical membrane. Proceeding anteriorly in the sections, the thin cartilage forming the roof of the myodomic groove runs gradually into membrane (fig. 17), the entire basis cranii thus here being perforated by a longitudinal opening that might be considered to be a fenestra ventralis myodomi. This is, however, not the case, for the recti externi lie definitely in this opening and not above it. The bounding walls of the opening accordingly represent the side walls of the myodomic groove, and the space between the ventral edges of the side walls alone represents the fenestra ventralis myodomi. The space between the dorsal edges of the opening is a perforation of the floor of the primordial cranium, and the membrane extending horizontally between the edges forms part of the floor of the cavum cerebrale cranii and also the roof of the dorsal compartment of this basioccipital portion of the myodome. The recti externi lie between this membrane and the parasphenoid, and they are still separated from each other by a median vertical membrane. The saccus vasculosus is large, lies in the cavum cerebrale cranii, and projects posteriorly slightly beyond this point.

Proceeding anteriorly in the sections to the region between the saccus vasculosus and the hypophysis (fig. 16), the membranous roof of the myodome becomes somewhat arched, and it now has its attachment, on either side, on the dorso-internal surface of the cartilage of the basis cranii, at some distance dorsolateral to the midventral perforation of the cartilage, that perforation now being definitely a fenestra ventralis myodomi.

A second membrane, evident also in the preceding figure, here closes the fenestra ventralis myodomi, the parasphenoid lying directly against its ventral surface. The median vertical membrane still extends between these two membranes, separating the myodome into lateral halves.

Still farther forward in the sections, in the region of the hind end of the hypophysis (fig. 15), the median portion of the membrane that forms the roof of the myodome, and hence also the median portion of the floor of the cavum cerebrale cranii, gradually descends, between the recti externi, on to the membrane forming the floor of the myodome, the two membranes fusing with each other there, and so forming a thick membrane which is both the median portion of the floor of the cavum cerebrale cranii and the median portion of the membrane closing the fenestra ventralis myodomi, the parasphenoid lying directly upon its ventral surface. The myodomic cavity, which here still belongs only to the dorsal compartment of the myodome, is thus separated into lateral halves, the hypophysis projecting ventrally between the two halves of the compartment, and each half lodging the related musculus rectus externus.

Still farther forward in the sections (figs. 13 and 14), the hind ends of the recti interni appear between the parasphenoid and the membrane closing the fenestra ventralis myodomi, that membrane thus being the horizontal myodomic membrane, and the space beneath it the ventral compartment of the myodome. The membrane forming, on either side, the roof of the related lateral half of the dorsal compartment of the myodome, now has its mesial attachment on the dorsal surface of the horizontal myodomic membrane, the latter membrane thus, in its lateral portions, separating the two compartments of the myodome, while its median portion forms part of the roof of the ventral compartment of the myodome and part of the floor of the cavum cerebrale cranii. The conditions here are accordingly similar to those in the 63-mm. specimen of *Trigla hirundo*.

Still farther forward, that lateral part of the horizontal membrane that, on either side, separates the two compartments

of the myodome, breaks down, but its median portion still persists as part of the floor of the cavum cerebrale cranii, and, anterior to the hypophysis, it is perforated by the internal carotids in their passage from the myodome into the cavum cerebrale cranii.

Thus the prootic bridge of this small specimen of *Cottus scorpius* is nowhere formed by cartilage, and if it be of cartilage in the adult, it must be a later chondrification of the membrane that, in this specimen, forms the floor of the cavum cerebrale cranii. That this does take place is probable, for a cartilaginous prootic bridge is developed relatively late in other fishes also, as will be explained later.

In a 37-mm. specimen of *Clinocottus analis* the conditions resemble those in *Cottus scorpeus*, differing only in that the horizontal myodomic membrane takes no direct part in the formation of the floor of the cavum cerebrale cranii, simply arching upward to such an extent that it is in contact with, and partly fused with, the membranous prootic bridge, thus separating the myodome into median and lateral, instead of dorsal and ventral compartments (fig. 19).

The internal carotid arteries of *Cottus* and *Clinocottus* are strictly similar in their course and branches to those of *Trigla*. The cross-commissure of the efferent pseudobranchial arteries has a position strictly similar to that of the latter fish, and the nervus palatinus facialis of *Cottus* is as in *Scorpaena*, while that of *Clinocottus* is as in *Trigla*. An anterior portion of the ascending process of the parasphenoid has the position of, and replaces, the alisphenoid of *Amia*.

In none of these small specimens of the Loricati is either the dorsal or the ventral compartment of the myodome definitely closed toward the orbit by membrane, as, in my earlier work on these fishes, I said was the case in the adults. Both in embryos and the adult the spinal portion of each compartment opens into the prespinal portion, and in embryos this latter portion is largely open toward the orbit. In the adult the myodome is doubtless closed toward the orbits by connective tissues which develop around the rectus muscles as they enter it. In the

adults of these fishes I described a well-developed trigemino-facialis recess. In embryos this recess is not evident, but it must necessarily exist, potentially.

#### SYNGNATHUS ACUS

In a 115-mm. specimen of this fish the myodome and the fenestra ventralis myodomus are both limited to the prootic region. Posterior to the hind end of this fenestra is a shallow median groove on the ventral surface of the cartilaginous basis cranii, which extends into the basioccipital region and there lodges the hind end of the parasphenoid. This bone is triangular there, in transverse section, the apex of the triangle directed dorsally. In sections passing through the posterior portion of the fenestra ventralis myodomus, the parasphenoid is still triangular, and the cartilage bounding the fenestra on either side becomes entirely enclosed in perichondrial bone which forms part of the prootic. The parasphenoid lies directly between the ventromesial edges of these prootic bones, dense connective tissue filling the space between the parasphenoid and either prootic and also extending dorsally across the parasphenoid, there filling and closing the fenestra ventralis myodomus. Proceeding anteriorly in the sections, the parasphenoid becomes flatter and wider, and the cartilage in the ventral ends of the prootics vanishes. Further forward in the sections, a little space appears in the dense connective tissue that covers the dorsal surface of the parasphenoid, and in this space the hind ends of the recti externi soon appear (fig. 23), lying directly above the parasphenoid and separated from the cavum cerebrale cranii by membrane which continues the full length of the myodome and represents the prootic bridge.

Proceeding forward from this point, the parasphenoid begins to widen and at the same time to thicken dorsoventrally, and it soon has, in sections, a median circular portion with laterally projecting flanges, each flange being formed of external and internal plates which receive the ventral end of the ventral process of the prootic between them (fig. 22). In the rounded median portion of the bone a median cavity forms, and lodges



the hind ends of the recti interni, the recti superiores arising from the lateral walls of this cavity, near its anterior end. The recti externi lie dorsal to the parasphenoid, between it and the membrane which everywhere forms the roof of the myodome.

Still further forward, the bony roof of the median cavity in the parasphenoid is gradually replaced by a horizontal myodomic membrane which separates the myodome into two compartments, a dorsal one lodging the recti externi and a ventral one lodging the recti interni and superiores, the ventral compartment forming a semicircular depression in the floor of the entire myodomic cavity (fig. 21). The hind end of the ventral compartment is thus completely enclosed in the parasphenoid, and it seems absolutely certain that that part of the bone forming the roof of this compartment is simply an ossification of the horizontal myodomic membrane.

Proceeding anteriorly, the region of the ascending processes of the parasphenoid is soon reached, these processes rising to the level of the membranous roof of the myodome and suturing with the ventromesial edges of the prootics (fig. 20). The myodome is here semicircular in transverse section, its side wall and floor being formed wholly by the parasphenoid and its roof by membrane that separates it from the cavum cerebrale cranii. A median vertical membrane here descends from the membranous roof of the myodome, and in connection with it the recti inferiores have their origins.

The course and the main branches of the internal carotid artery are as in *Scomber*, except that the artery separates into its anterior and posterior divisions while still within the canal in the median vertical myodomic membrane, and that the anterior division then immediately enters the tissues forming the floor of the cavum cerebrale cranii, thus not actually entering the latter cavity.

#### HIPPOCAMPUS GUTTULATUS

In a 20-mm. specimen of this fish the myodome begins posteriorly beneath a part of the basis cranii that is of cartilage lined, on either side, with perichondrial bone. The parasphenoid lies at a certain distance ventral to this part of the basis

cranii, the space between the two being filled with dense connective tissue which is bounded laterally at its dorsal edges by little projecting flanges of perichondrial bone developed in relation to the cartilage of the basis cranii. The hind end of the myodome lies in this tissue, and lodges the hind ends of the recti externi. Proceeding anteriorly from this point, the cartilaginous roof of the myodome soon vanishes and is replaced by a thick layer of fibrous tissue. Cartilage is, however, now found in the ventral portion of each lateral wall of the myodomic cavity, this cartilage being enclosed between projecting flanges of the parasphenoid, one of these flanges lying along the external surface of the cartilage and the other along its internal surface. The internal flange lies in the fibrous tissue that lines the myodome, and is certainly developed in relation to it.

The internal carotid artery traverses its foramen at the hind edge of the ascending process of the parasphenoid, and then immediately enters and runs upward in the median vertical myodomic membrane, its course and distribution there being as in *Sygnathus*. The recti interni, superiores and inferiores have their origins anterior to this ascending column of the artery, close together, from the dorsal surface of the parasphenoid. The ventral compartment of the myodome is thus here wholly prespinal in position, for the foramen for the internal carotid artery lies in the plane of the pituitary opening of the brain case. The relations of these two openings to each other varies considerably in different fishes, the foramen for the artery lying markedly anterior to the pituitary opening in *Scorpaena*, but posterior to that opening in *Scomber*.

#### CATOSTOMUS

In *Catostomus teres*, Sagemehl ('91) describes a myodome that is everywhere closed ventrally by the parasphenoid, is bounded dorsally by the horizontal processes of the prootics, and apparently extends posteriorly slightly into the basioccipital. The basioccipital has a large pharyngeal process, perforated by a short canal which encloses the dorsal aorta, and Sagemehl

says ('91, p. 516) that this relation to the aorta at once suggests a lower vertebral arch. He, however, says that he finds weighty reasons against the assumption that it is such an arch. One of these reasons is that, excepting in this region of the Cyprinidae and in the tail region of all fishes, the lower arches always enclose the body cavity, and not simply the aorta. A second reason is that he himself finds, in embryos of *Chondrostomus nasus*, the pharyngeal process not preformed in cartilage, as the lower arches always are. Sagemehl accordingly concludes that the pharyngeal process of the Cyprinidae is not a lower vertebral arch, and he considers it to be a bone formed by the fusion of pharyngeal bones of dermal origin with another bone formed by the ossification of a ligament which, in the Characinidae, extends from the hind end of the basis cranii to the swim-bladder, embracing the aorta in its course.

In a 57-mm. specimen of *Catostomus occidentalis* I find the pharyngeal process formed by two ventrally projecting longitudinal flanges of bone which arise from a layer of bone surrounding the notochord, and, diverging slightly and straddling the aorta, abut against and fuse with the dorsal surface of a curved and porous plate which lies parallel to the dorsal surface of the pharynx (fig. 29). The aorta is thus enclosed in a canal that corresponds strictly to the aortal groove of *Hyodon*, except in that it is closed ventrally by the formation of a horizontal floor across its outer edges, and if the one is of vertebral origin, as I consider it to be, the other certainly also is. Whether the floor of the canal has been developed in primary continuity with its lateral walls, or as an independent dermal formation, as Sagemehl suggests, cannot be told from my sections. The lateral walls of the canal are prolonged anteriorly beyond its floor, and the aorta there lies (fig. 28) in an open groove similar to that of *Hyodon*, the lateral walls of the groove gradually diminishing in height and vanishing approximately in the level of the anterior end of the persisting notochord. Anterior to the point where the vacuolated contents of the notochord can last be recognized in the sections, the notochordal space still continues a certain distance, and in sections

passing through this region the hind ends of the parasphenoid are cut, one lying on either side of a median ridge on the ventral surface of the basioccipital, the median dorsal aorta lying ventral to the ridge (fig. 27). Here, unfortunately, one or more sections are missing in my series. In the next anterior existing section (fig. 26) there is a circular space in the basioccipital, in exactly the position of the notochordal space in the next posterior section of the series, but somewhat larger than it, and this space lodges the hind ends of the recti externi. The aorta here begins to separate into a lateral dorsal aorta on either side.

Proceeding anteriorly in the sections, the myodomic cavity increases in size, and that part of the basioccipital in which it lies forms a large median, dorsally projecting, and rounded ridge. The parasphenoid now extends across the median line (fig. 25). Still farther forward the fenestra ventralis myodomi begins, the parasphenoid closing it ventrally and having a broad but low median ridge which projects upward into the fenestra. This median ridge then sends upward a longitudinal ridge on either side, and in the space between these two ridges the recti interni make their appearance, separated from the recti externi by loose connective tissue which does not form a definite membrane (fig. 24).

Farther forward, the two lateral ridges on the dorsal surface of the parasphenoid vanish, leaving a flat median ridge, and the hind end of the hypophysis is there cut in the sections. This latter organ is large, lies wholly in the myodome, and projects posteriorly ventral to the roof of the myodome, here formed by the horizontal processes of the prootics. Anterior to the anterior edges of these latter processes the hypophysis is connected with the brain by a small stalk of nervous material, which perforates the membrane which there forms the roof of the myodome and the floor of the *cavum cerebrale cranii*.

The myodome of this fish is thus, up to this point, strictly normal, except that the hind end of its dorsal compartment is enclosed in the basioccipital, and that the recti externi apparently have their origins on the anterior end of the notochord instead of ventral to it.

In sections immediately anterior to those that cut through the nervous stalk of the hypophysis, the median ridge on the dorsal surface of the parasphenoid extends upward to the membranous floor of the cavum cerebrale cranii, and so occupies the position of a basisphenoid, which bone is said by Sagemehl to be absent in all of the Cyprinidae. A slight line separates this projecting process from the remainder of the parasphenoid, vaguely suggesting a fusion of two bones.

#### BLENNIUS GATTORUGINI

In *Blennius gattorugini* I described ('09) a myodome, the roof of which was said to be formed by membrane. This is correct, but it was also said that this membrane was attached, on either side, to the dorsal edge of a groove on the ventral edge of the prootic, and that that edge which represented the horizontal process of the bone. This is incorrect, for, on reexamining my material, I find that this groove simply lodges the related portion of the lateral edge of the parasphenoid and that the membrane representing the horizontal processes of the prootics is attached to a slight ridge on the side wall of the cranial cavity at a somewhat higher level, in direct posterior continuation of the line of the horizontal portion of the basisphenoid. The cavity thus formed lodges the recti externi only, and hence represents the dorsal compartment of the myodome. Having no sections of this fish, the arteries, veins and nerves, and the myodomic membranes could not be properly traced, but the conditions are apparently similar to those in *Hippocampus*, above described. Starks ('05) says that in six genera of the Blenniidae examined by him there was no myodome.

#### ARGYROPELACUS

In *Argyropelacus* a myodome is frequently referred to by Handrick ('01), but not particularly described, and I made brief reference to it in my work on the mail-cheeked fishes. The neurocranium of this fish is said by Handrick to be wholly of cartilage, no bone being found in any part of it, and the myodome lies external to this chondrocranium. Its hind wall is

said to be formed by the anterior, external wall of the bulla acustica, and it lodges the extracranial semilunar and ciliaris ganglia. The posterior portion of its roof is evidently formed by a horizontal plate of cartilage shown, in the figures given by him (*l. c.*, figs. 7 to 9, Pl. 1), lying ventral to the hypophysis, and which must accordingly represent the prootic bridge. In a figure of a transverse section in the postfacialis region a ventrally projecting process is shown at each lateral edge of this prootic bridge, and its ventral portion has apparently been cut off in the figure. These two processes certainly represent transverse sections of ventral processes of the prootics, similar to those found in other Teleostei, and they must form the lateral walls of the so-called extracranial myodome. Each process lies mesial to the foramen faciale of its side, and lateral to this foramen and also lateral to the foramen trigeminum there is a slight ridge of cartilage which must represent a dorsal portion of the lateral wall of the pars jugularis of a trigemino-facialis chamber. The ganglion trigeminum thus probably lies in the orbital opening of this chamber and not in the dorso-lateral corner of the myodome, as Handrick concluded. The basis cranii is perforated by a so-called 'Pituitargrube,' which is said to extend from the foramen trochleare nearly to the foramen trigeminum, is shown closed by a membrane which is perforated by the nervi optici, and extends posteriorly to the anterior edge of the prootic bridge. This so-called pituitary fossa is thus simply a perforation of the primitive cranial wall which has been formed by the fusion of the pituitary opening of the brain case with the foramina optici.

Supino ('01), in a work I did not have at my disposal when my paper on the mail-cheeked fishes was sent to press, finds several bones developed in relation to the neurocranium of this fish, two of them being the prootics and one the parasphenoid. This latter bone must evidently lie ventral to the myodome, and in a figure giving a ventral view of the entire neurocranium, extensive ventral processes of the prootics are shown which must form the lateral walls of the myodome. The foramina for the nervi trigeminus and facialis are said to perforate the

prootic, but they are not shown in the figure. It is however probable that the conditions resemble those in *Hyodon*, the myodome evidently being large and having a large orbital opening on either side. Whether or not there are both dorsal and ventral compartments to the myodome cannot be told, but they are probably both present. Supino says that a basisphenoid is found, which must accordingly separate the so-called pituitary fossa of Handrick's descriptions into a pituitary opening of the brain case and a foramen formed by the fusion of the foramina optici, and he adds that: "Posteriormente l'estremità delle porzione impari del basisfenoide si congiunge, nel *Chauloides* e *Argyropelacus*, con la cartilagine che si trova nella cavità dei muscoli oculari." This, while not quite clear, would seem to mean that cartilage formed some part of the floor of the myodome.

#### ESOX

In the adult *Esox* the myodome is large and extends posteriorly into a conical excavation in the anterior end of the basioccipital, as Huxley ('71) has stated. A horizontal membrane separates it into dorsal and ventral compartments, the dorsal one being large and lodging the recti externi, while the ventral one is short, extending, posteriorly only to the hind edges of the foramina for the internal carotid arteries. From there the membrane separating the two compartments rises rapidly to the ventral surface of the relatively deep membranous pituitary sac, fuses with that surface, and then appears as two separate membranes, each having its mesial attachment on the ventrolateral surface of the sac. The recti interni have their origins beneath this membrane, on the floor of the ventral compartment of the myodome, near its hind end. The recti superiores have their origins from the anterior edge of each half of the horizontal membrane, near its dorsomesial end, and the recti inferiores from the lateral walls of the spreading dorsal end of the median vertical membrane, immediately anterior to the membranous pituitary sac. This median vertical membrane is partly fused with the median portion of the hori-

zontal membrane, and it is traversed by the internal carotid arteries. The membranous roof of the subpituitary portion of the myodome extends forward from the horizontal processes of the prootics to the hind edge of the horizontal plate of the basisphenoid. The conditions in this fish are thus wholly normal.

Starks ('05) says that the dorsal end of the basisphenoid (dichost, Starks) of this fish is 'free,' and he suggests that this should be examined in connection with a 'myodome septum', formed of connective tissues, said by him to be found in this region and to be continued forward as the interorbital septum. Just what this myodome septum is is not clear, but it would seem to be the membranous roof of the myodome. Starks further says that "the dichost (=basisphenoid of Huxley) is always absent when the myodome is." No particular cases are cited, but it is evidently assumed that there is no myodome whenever a prootic bridge (shelf) is not found in the prepared skeleton of the cranium. This is incorrect, and the statement should probably be that there is no basisphenoid whenever the roof of the myodome is wholly of membrane. Whether or not this statement is true, even in this form, I do not know, my material being too limited to permit me to form an opinion.

#### GASTEROSTEUS ACULEATUS

The early stages of the development of the myodome in *Gasterosteus aculeatus* are quite fully described, and the myodome of the adult briefly described by Swinnerton ('02). The trabecula and parachordal of either side are said by him to be, when first formed, wholly independent cartilages, and their adjoining ends are shown in the figures lying approximatively in the tranverse plane of the tip of the notochord. The posterior halves of the trabeculae are said to enclose the infundibulum and the pituitary body, and the infundibulum is shown lying posterior to the pituitary body and reaching to the tip of the notochord. The trabeculae and parachordals soon fuse with each other, and there is then a marked anterior growth of the parachordals which carries the trabeculae forward considerably



anterior to the tip of the notochord. The pituitary body still lies between the hind ends of the trabeculae, in the so-called pituitary fossa, but the infundibulum now lies dorsal to the anterior end of the notochord. The space between the anterior ends of the parachordals is now called the interparachordal fossa, and this and the pituitary fossa are not only continuous with each other in these early stages of development, but are considered to continue so to be even in the adult. As the term fossa is probably here employed strictly in the sense of fenestra, these two so-called fossae will hereafter be referred to as the fenestrae interparachordalis and hypophyseos.

In the third and fourth stages considered by Swinnerton (embryos 6.6 to 25-mm. in length) it is said that the intracranial notochord has undergone no further change beyond a slight increase in absolute length, and further, that it undergoes no actual suppression or reduction even in later stages of development. It is also said that: "The interparachordal fossa has been carried some distance in front of the notochord; and the parachordals themselves have united across the intervening space and across the end of the notochord in such a way that this projects below, but close against the basis cranii." A transverse plate of parachordal cartilage is thus formed, and a median sagittal section through it in a 14-mm. specimen is shown in one of the figures given (*l. c.*, fig. 38, pl. 30.). The parasphenoid is shown lying slightly below the parachordal plate, and the hind end of the musculus rectus externus is inserted on the dorsal surface of the parasphenoid beneath the anterior edge of the plate. Somewhat anterior to this point, a process of bone is shown projecting dorso-anteriorly from the dorsal surface of the parasphenoid, and it is called the median process of that bone. In the space between this process and the anterior edge of the plate of parachordal cartilage, a section of the basal portion of the brain is shown, and, although not index lettered, it must represent the pituitary body and infundibulum of the earlier stages, the infundibulum here slightly differentiated as the saccus vasculosus. In a sagittal section through this same region of the adult (*l. c.*, fig. 37), the rectus

externus is shown lying between the parasphenoid and the plate of parachordal cartilage, and extending posteriorly beyond the prootic region into the anterior end of the basioccipital region. The plate of parachordal cartilage now forms a prootic bridge, but how it has been developed is not explained. In the base of the median process of the parasphenoid is a block of cartilage said to represent the anterior end of the parachordal, the median process of the parasphenoid thus lying posterior to the fenestra hypophyseos. The pituitary body (hypophysis) and infundibulum (saccus vasculosus, both shown lying posterior to the median process of the parasphenoid, must then also lie posterior to the fenestra hypophyseos, and this is apparently also their position in advanced embryos and the adults of certain other, if not all fishes, as will appear later.

Swinerton does not describe the internal carotid arteries, but it seems certain, both from his figures and from the conditions in a 40-mm. specimen of this fish, described immediately below, that these arteries pass upward between the hind ends of the trabeculae and that they are never there enclosed in cartilage.

In the earlier stages considered by Swinerton the rectus externus muscles are said to be inserted into each other and into the tissues filling the hind part of the fenestra interparachordalis. In the third and fourth stages they extend posteriorly so that their hind ends lie beneath the posterior border of that fenestra, and hence along the ventral surface of the basis cranii. The eyeballs have in the mean time descended to a level relatively lower than in the earlier stages, and this is said to cause the eye-muscles to press upon the anterior prolongations of the parachordals and, depressing them, institute the beginning of the formation of the myodome. It would naturally be supposed that this depression would affect the hind ends of the trabeculae, with which the parachordals are fused, and this is what actually takes place in *Salmo*, as described by Gaupp and to be later considered. In *Gasterosteus*, on the contrary, the hind ends of the trabeculae have not been in the least depressed in the oldest stages shown by Swinerton in which

they still persist, an embryo belonging to his third stage and said to be 6.6 mm. in length (*l. c.*, fig. 8). The lateral edges of the anterior prolongations of the parachordals are also not affected, as shown in that figure, their mesial edges alone being depressed. This depression of the edges must then represent a ventral growth of the cartilage, for it is difficult to comprehend how it could have been the result of any pressure of the rectus muscles.

In Swinnerton's fourth stage, those parts of the trabeculae which border on the fenestra hypophyseos are said to have been suppressed, and it is said (*l. c.*, p. 518) that:

In the hinder or parachordal portion, the interparachordal fossa has been carried so far away in front of the notochord that the plate formed by the median union of the parachordals now furnishes a considerable portion of the basis cranii. Those parts lying immediately on either side of the fossa have now begun to undergo a movement of depression, by which they have already come to lie slightly below the level of the basis cranii.

Swinnerton says that this movement of depression is perhaps associated with a similar movement on the part of the rectus muscles, but, as just above stated, this ventral growth of the parachordal cartilage begins in earlier stages, and it seems improbable that it can there be due to any action of these muscles.

In later stages of development, it is said (*l. c.*, p. 527) that:

The process of depression of those parts bounding the interparachordal fossa laterally has continued, so that this region now appears to be a mere downward process of the prootic, with its cartilaginous extremity mortised into the sides of the parasphenoid. This appearance is enhanced by the fact that posteriorly each process is continued into a ridge running along the under surface of the hinder portion of the prootic. These two ridges are continuous with those already described under the basioccipital, and there is a channel thus formed which runs a considerable length of the basis cranii, is closed ventrally by the parasphenoid, and opens anteriorly into the cavum cranii by means of the interparachordal fossa.

It is then further said (*l. c.*, p. 528) that:

In the larval *Amia* this canal is not present, but there is a well-marked interparachordal fossa to which the eye muscles bear the same

relations as in the stickleback. It is probable, therefore, that in this fish also a process of depression and secondary growth goes on on either side of the fossa and below the prootic; but that, whereas in the other types the fossa persists and transmits the eye muscles back again out of the cranial cavity beneath the basis cranii, in *Amia* it disappears, owing to continuous cartilaginous growth. As far back as the so-called prootic bridge these muscles may be said to run in an actual derivative of the cranial cavity; behind that they run in an extracranial space secondarily enclosed.

The myodome of *Gasterosteus* is thus conceived by Swinnerton to be a space, the anterior portion of which is bounded laterally by the bent-down anterior prolongations of the parachordals, and the posterior portion by secondary ventral downgrowths of the parachordals posterior to those anterior prolongations. These two portions of the myodome are thus of totally different origin, and the anterior portion is considered, because of its relations to the parachordals, to be an actual derivative of the *cavum cerebrale cranii*. The figures given show that it lodges the pituitary body, and that it is prechordal in position, but, as the arteries and veins of the region are not shown or particularly described, it is impossible to compare the conditions here with those in the fishes that I have considered above. I have accordingly examined this region in a series of transverse sections of a 40-mm. specimen of this fish, and as the conditions there present certain new features, they will be quite fully described.

In this 40-mm. specimen of *Gasterosteus* I find the recti superiores, inferiores, and interni all arising from a thick median vertical membrane which descends from the ventral surface of the anterior portion of an unusually large membranous pituitary sac, the recti interni having their origins posteroventral to the recti superiores and inferiores. Posterior to the points of origin of these muscles, the large hypophysis projects ventrally into the membranous pituitary sac, which lies dorsal to, and in large part posterior to, the dorsoanterior edge of that transverse ridge on the dorsal surface of the parasphenoid which Swinnerton calls its median process. This process begins near the hind edges of the ascending processes of the parasphenoid,

and, projecting dorso-anteriorly, extends approximately to the transverse plane of the anterior edge of the hypophysis, where it reaches to about the middle of the height of the myodome. The large membranous pituitary sac rests upon its dorsal surface, that surface being presented dorsoposteriorly. The space beneath this ridge opens anteriorly into the subpituitary portion of the myodome.

The ascending processes of the parasphenoid have their greatest dorsal extent anterior to the transverse ridge on its dorsal surface, and Swinnerton says that these processes of *Gasterosteus* are not the homologues of the processes of the bone of *Amia*. Swinnerton based this conclusion wholly upon the fact that each process of the bone of *Gasterosteus* lies anterior to the foramen for the nervus trigeminus, while in *Amia* it lies posterior to it; but he overlooked the fact that a part of the process of *Gasterosteus*, as shown in his figure 19, plate 29, projects dorsally posterior to the foramen trigeminum, this part of the process thus corresponding to the process of *Amia*. The anterior portion of the process of *Gasterosteus* lies lateral to the oculomotorius, trochlearis, and profundus nerves, and also lateral to the vena jugularis and the rectus muscles, between them and the nervus trigeminus, thus having exactly the relations to these several structures as does the pedicel of the alisphenoid bone of *Amia*. This part of the process of *Gasterosteus* thus replaces functionally a pedicel of the alisphenoid, and it has certainly been developed in relation to tissues that represent, in this fish, that bone of *Amia*. The orbital opening of the myodome of *Gasterosteus* thus differs from the opening in all the other fishes so far considered, except *Cottus* and *Clinocottus*, in which latter fishes the pedicel of the alisphenoid of *Amia* is also represented by a process of the parasphenoid. The orbital opening of the myodome of *Gasterosteus*, and also that of *Cottus* and *Clinocottus*, does not, however, correspond strictly to that of the myodome of *Amia*, for, as will be shown later, there has been added to its ventral portion the canals traversed, in *Amia*, by the internal carotid arteries and the palatine branches of the faciales.

In my 40-mm. specimen of *Gasterosteus* the internal carotid and efferent pseudobranchial arteries of either side perforate the base of the ascending process of the parasphenoid through a single foramen, and enter the space beneath the transverse ridge on the parasphenoid. There the pseudobranchial artery is connected by a cross-commissure with its fellow of the opposite side, and then runs forward into the orbit as the *arteria ophthalmica magna*. The internal carotid gives off, before entering its foramen, its orbitonasal branch, which traverses the foramen with the internal carotid and efferent pseudobranchial arteries, and then runs forward along the floor of the myodome to enter the orbit. The internal carotid, after giving off this branch and having entered the space beneath the transverse ridge on the parasphenoid, turns upward in the median vertical myodomic membrane, and, while in that membrane, anastomoses with its fellow of the opposite side. It then separates from its fellow and, while still in the membrane, divides into two parts, one of which at once enters the *cavum cerebrale cranii*, and is the posterior cerebral artery. The other part runs forward in the thick median portion of the membranous floor of the *cavum cerebrale cranii*, and, issuing beneath it, sends two branches to the eyeball, one of them accompanying the *nervus opticus*. The remainder of the artery then enters the *cavum cerebrale cranii* through the *foramen opticum*, and is the anterior cerebral artery. No positive and definite connection between the anterior and posterior cerebral arteries was seen, the anterior branch of the latter artery, found in the other fishes, not occurring here.

The *ramus palatinus facialis* arises from the trigemino-facialis ganglionic complex, and passing lateral and then ventral to the *vena jugularis*, runs ventromesially along the internal surface of the prootic bone and perforates the dorso-anterior portion of the transverse ridge on the parasphenoid to enter the space beneath it and then to escape into the orbit. This nerve, in this fish, thus lies lateral to the *vena jugularis*, while in all others in which it was traced (*Hyodon*, *Scomber*, *Scorpaena*, *Cottus*, *Catostomus*, and *Amia*) it lies mesial to that vein. This is, how-

ever, unquestionably related to the fact that the vena jugularis lies ventral (mesial) to the nervus facialis in *Gasterosteus*, while in the other fishes mentioned above, except *Catostomus*, it lies dorsal (lateral) to that nerve. In *Catostomus* the vein lies ventral (mesial) to the nervus facialis but lateral to the nervus palatinus, this thus being a variation in the transformation of the primitive vena cardinalis anterior into a vena capitis lateralis.

A delicate median vertical membrane separates the space beneath the transverse ridge on the dorsal surface of the parasphenoid into lateral halves, this membrane being continuous anteriorly with the membrane that gives insertion to the rectus muscles. At its hind end this membrane ossifies as a short median ridge on the dorsal surface of the parasphenoid.

The space beneath the dorso-anteriorly projecting ridge on the dorsal surface of the parasphenoid thus corresponds strictly to the ventral compartment of the myodome of the other Teleostei so far considered, but the roof of that compartment, which is of membrane in those other fishes, has here been ossified as part of the parasphenoid. The recti externi and the pituitary veins run posteriorly dorsal to this ridge, and hence lie in the dorsal compartment of the myodome, the pituitary veins lying along the lateral surfaces of the pituitary sac, and forming, posterior to it, a large median sinus.

Posterior to the hind end of the ventral compartment of the myodome, and hence posterior also to the ascending processes of the parasphenoid, a tall median ridge of the latter bone, flat on its dorsal surface, projects upward between the ventral ends of the ventral processes of the prootics, its dorsal surface there forming the floor of the dorsal compartment of the myodome. Up to this point the ventral processes of the prootics are wholly of bone, but cartilage now appears in their ventral halves, as shown in Swinnerton's figure 35, plate 30. The hind end of the membranous pituitary sac is here cut in the sections. Proceeding posteriorly, the median ridge on the dorsal surface of the parasphenoid gradually becomes wider, and, arching upward, projects into the myodome between the ventral ends of the ventral processes of the prootics. The membrane which,

anterior to this point, formed the roof of the myodome, is now replaced by membrane bone which forms the anterior portion of the prootic bridge, and the nervus abducens perforates it, on either side, to enter the dorsal compartment of the myodome. Farther posterior in the sections, a median plate of cartilage appears in the prootic bridge, enclosed between dorsal and ventral plates of perichondrial bone, and in this transverse plane the cartilage in the ventral ends of the ventral processes of the prootics disappears and is replaced by membrane only. The ventral processes of the prootics are accordingly now formed by short processes of bone, partly of membrane and partly of perichondrial origin, that are prolonged ventrally by membranes, continuous ventrally with the lateral edges of the parasphenoid. Proceeding posteriorly, the median plate of cartilage expands laterally, on either side, and becomes the cartilaginous basis cranii, here still enclosed, on either side, between plates of perichondrial bone which form parts of the prootics. The myodome still continues onward, in a median groove on the ventral surface of this cartilage, there lodging the recti externi and being bounded laterally in part by membrane only and ventrally by the parasphenoid.

At the extreme hind end of the myodome a circle of bone appears in the sections, this bone forming part of the basioccipital and lying in the groove on the ventral surface of the cartilaginous basis cranii. From this shell of bone a median plate is sent downward between the diverging hind ends of the parasphenoid, and the shell of bone then fuses with perichondrial bone developed in relation to the overlying cartilage and forming part of the basioccipital. The conditions are thus here practically as described and figured by Swinnerton in his 16-mm. specimen of this fish (*l. c.*, fig. 36, pl. 30).

The myodome of *Gasterosteus* is thus strictly comparable to that in the other Teleostei described, except that it has a greater anterior extension than it has in any of them, *Cottus* and *Clinocottus* excepted, this being due to the ossification, as part of each ascending process of the parasphenoid, of tissues representing the pedicel of the alisphenoid. The parasphenoid has under-



gone special development in this fish, and the conditions here show, even more positively than in the others considered, that part of this bone may be developed in definite relations to the membrane separating the myodome into dorsal and ventral compartments. It is accordingly certain that this bone is here developed, in part, in relation to axial skeletogenous material, and is not a simple dermal bone primarily developed in relation to the mucous lining membrane of the pharynx, and which sank gradually inward to its actual position.

#### DACTYLOPTERUS VOLITANS

The conditions in *Gasterosteus*, as above explained, seeming to offer an explanation of the somewhat exceptional conditions that I described in *Dactylopterus* in my work on the mail-cheeked fishes, I have reexamined my material of that fish. In that earlier work I described a transverse ridge on the dorsal surface of the parasphenoid that was said to project dorsoposteriorly and to form the posterior wall of the myodome. Because of the position of this wall, I concluded that the post-pituitary portions of the horizontal processes of the prootics had been depressed and appressed upon the underlying ventral flanges of those bones, and that the latter flanges had undergone marked reduction. I now find that the ventral flanges of the prootics have not undergone any particular reduction, and that there has been no depression and appression of the horizontal processes of the prootics, which are represented by a well-defined membrane forming the floor of the *cavum cerebrale cranii*. The anterior end of this membrane passes over the dorsal edge of the transverse ridge on the parasphenoid, closely adherent to it, and is then continuous with the membrane that I described as closing the pituitary opening of the brain case. Beneath the part of this membrane that represents the horizontal processes of the prootics, and between it and the parasphenoid, is a space which must represent some part of the dorsal compartment of the myodome, this space being shut off from the subpituitary portion of the myodome by the transverse ridge on the parasphenoid. The hypophy-

sis lies anterior to this ridge, the cross-commissure of the pituitary veins lying ventral to the hypophysis and separated from it by the dura mater. The recti externi have their insertions on a median vertical membrane, immediately posterior to the pituitary veins and immediately anterior to the summit of the transverse ridge. They are surrounded by connective tissue that resembles the fatty tissue found abundantly in this fish, but are not otherwise separated from the other rectus muscles, the dorsal and ventral myodomic compartments thus apparently here being confluent.

#### SALMONIDAE

In *Salmo*, Parker ('73) and Stöhr ('82) found the trabeculae and parachordals primarily independent of each other. Stöhr also found the anterior portions of the parachordals—the parts corresponding to the anterior prolongations of the parachordals of Swinnerton's descriptions of *Gasterosteus*—primarily independent of the posterior portions, and he considered them to represent the 'Balkenplatten' of the Amphibia. They are said by him to fuse, first, with the posterior portions of the parachordals and then with the trabeculae. Of the adult *Salmo*, Parker says (*l. c.*, p. 102):

One remarkable change in the investing mass, as a whole, is the growth downward of a lamella on each side, thus forming a covered archway; for in front of the retiring notochord the moieties of cartilage meet, and this viaduct is floored by the submucous bone which has been removed, the parasphenoid. All the true axial parts of the skull cease at the front edge of the investing mass behind the pituitary space; all the rest has a facial foundation, is built on the trabeculae, or has a secondary character as a development of the cranial wall.

This so-called covered archway is the myodome, which is thus considered by Parker to be bounded laterally by downgrowths of the parachordal cartilage and not by those cartilages, themselves, bent down.

Schleip says ('04, pp. 355 to 359) that, in trout embryos, 12 to 14-mm. in length, the parachordals and trabeculae form the floor of the primordial cranium, and that the cartilages of

opposite sides are separated from each other by a fissure (Fissur) the posterior, interparachordal portion of which is entirely filled by the projecting anterior end of the notochord. There accordingly is, as described by Schleip, no interparachordal fenestra in these embryos. The intertrabecular portion of the fissure is called the pituitary fossa and it is said to be closed ventrally by the parasphenoid, which, at these stages, extends from the orbit only to the tip of the notochord (*l. c.*, p. 354). The rectus muscles, in running from their insertions on the bulbus to their points of origin, are said to lie, in their anterior portions, either above the trabeculae or above the fissure (so-called pituitary fossa), and farther posteriorly to lie in the fissure itself; the recti externi extending still farther posteriorly so that their hind ends lie under the notochord and hence beneath the basis cranii. That part of the space above the trabeculae, or above the fissure, thus occupied by the rectus muscles is said to form a part of the cranial cavity, but to be closed toward the brain by a membrane which, in these embryos, extends posteriorly to the tip of the notochord. Anteriorly, the edges of this transverse membrane are said to be attached to the side walls of the cranium, above its floor, the membrane thus there separating the cranial cavity into dorsal and ventral parts. Posteriorly, the membrane is said to stretch from one trabecula to the other, there closing the intertrabecular fissure, (the so-called pituitary fossa) and taking part in the formation of the basis cranii. It is, however, further said that, in later stages (embryos 18-mm. long), this same posterior portion of the membrane chondrifies, and that the cartilage so formed extends posteriorly to the tip of the notochord and there forms both the roof of the eye-muscle canal (myodome) and the floor of the cranial cavity. This cartilage is thus evidently the pro-otic bridge, and as the bridge cannot possibly have been formed by the chondrification of a membrane extending from one trabecula to the other, there is some error in the descriptions.

The myodome, as above described, is said by Schleip to present three sections: an anterior one, intracranial in position, but separated from the brain by the transverse membrane above

referred to; a middle section, "der in der Fissur der Schädelbasis, bezw. in einem nach unten offenen Sulcus liegt," and a posterior section which lies wholly beneath the basis cranii. Reference is here made by Schleip to a series of half schematic figures (*l. c.*, pp. 355 to 357), and consideration of them shows that the so-called anterior section of the myodome is what I have called, in the fishes described by me, its prespinal section. The middle section is apparently my prootic portion of the spinal section, and the posterior section what I have called the basioccipital portion of that section. A membrane is shown in these figures extending transversely between the ventral ends of the ventral processes of the prootic cartilages and separating the recti externi from the recti interni. This membrane is the horizontal myodomic membrane of my descriptions, but I cannot find that Schleip refers to it in his text, for the transverse membrane of his descriptions is said to form the roof of the myodome.

In a 25-mm. embryo of *Salmo salar* Gaupp finds conditions strikingly similar to those described by Swinnerton in *Gasterosteus*, and he arrives at practically similar conclusions regarding the development of the myodome, without, however, here making special reference either to that author's or to Schleip's conclusions regarding it. Like Schleip, Gaupp ('05 b, pp. 665 to 669) separates the myodome into anterior, middle, and posterior sections. The anterior section is said to lie in the posterior portion of the orbitotemporal region, and its floor to be formed by the two trabeculae and a membrane which extends transversely between them. The space between the two trabeculae is called by Gaupp the fenestra basicranialis anterior, or fenestra hypophyseos, and it corresponds to the intertrabecular, or pituitary fossa of Swinnerton's descriptions of *Gasterosteus*. It, however, apparently corresponds to the anterior portion only of the intertrabecular, or pituitary fossa of Schleip's description of the trout, the hind ends of the trabeculae of Schleip's account corresponding to the anterior prolongations of the parachordals of Swinnerton and Gaupp. The membrane said by Gaupp to close the fenestra hypophyseos of *Salmo* is shown by him, in a figure of a cross-section through this region

(*l. c.*, fig. 345, p. 669), lying ventral to the muscoli recti interni, and it is furthermore said that it gives attachment on its dorsal surface to the metachiasmatic (posterior) portion of the interorbital septum. The posterior portion of the interorbital septum here referred to is evidently the median vertical myodomic membrane of my account, the membrane that closes the fenestra hypophyseos then being represented in the layer of skeletogenous tissue forming the floor of what I have called the subpituitary portion of the ventral compartment of the myodome.

The roof of the anterior section of the myodome, as thus described by Gaupp, is said by him to be formed by the membranous floor of the cranial cavity, and its side walls by the ventral portions of the cartilaginous side walls of the cranium, which are said to here extend between the otic capsules and the trabeculae. The eye muscles are said to have forced the brain upward from the basis cranii, the hypophysis being carried with it and so lifted out of the fenestra hypophyseos.

The middle section of the myodome is said by Gaupp to lie, in part, in the labyrinth region and, in part, in the extreme posterior (hintersten) portion of the orbitotemporal region. Its floor is said to be formed by the anterior prolongations of the parachordals (vordere Parachordalia) which have been forced ventrally by the pressure of the muscoli recti externi, exactly as Swinnerton had previously said was the case in *Gasterosteus*. Gaupp, however, shows the hind ends of the trabeculae—the parts bounding the fenestra hypophyseos—forced ventrally to the same extent as the parachordals. Because of its relations to the anterior parachordals, this middle section of the myodome is said to lie between the primordial basis cranii and the brain, and hence to form a part of the primordial cranial cavity. Its side walls are described as formed, on either side, by two basicapsular commissures, which extend from the otic capsule of their side to the anterior prolongation of the related parachordal, and lie, one between the nervi trigeminus and facialis, and the other between the latter nerve and the otic capsule. Its roof is formed by the membranous floor of the cavum cerebrale cranii, this membrane arising, on either side,

from the side wall of the cranium, extending posteriorly dorsal to the notochord, and anteriorly passing into the supraseptal membranous floor of the *cavum cerebrale cranii* in the orbito-temporal region. In this membranous roof of this middle section of the myodome a transverse bridge of cartilage, the prootic bridge, is later developed, and it is said to lie above and anterior to the tip of the notochord. In the adult this bridge extends forward to the hind edge of the hypophysis, as shown in Parker's figure of a bisected skull ('73, fig. 4, pl. 7), and the pituitary opening of the brain case lies considerably posterior to the anterior edges of the ventral processes of the prootics. It must then be that, as in the adult *Gasterosteus*, the hypophysis of the adult *Salmo* lies dorsal to the interparachordal fenestra and not dorsal to the fenestra hypophyseos.

The middle section of Gaupp's descriptions of the myodome thus apparently corresponds to the subpituitary portion of the prespinal section, and to all of the prootic portion of the spinal section, of my descriptions. Gaupp says that, primarily, the *nervus palatinus facialis* issues from the cranial cavity along the lateral edge of the anterior parachordal, but that, as the myodome gains in height and breadth, the nerve becomes included in it, then entering it by perforating its membranous roof and leaving it through a foramen in its floor. The course of the internal carotid arteries is not given, but as there are no special perforations of the *basis cranii* for them, they must pass upward through the fenestra hypophyseos. Gaupp shows, in his figure of the entire chondrocranium, a foramen lying between the foramen for the *nervus facialis* and the *incisura prootica*, and it is said to give passage to the *vena jugularis*, coming from the anterior portion of the cranial cavity. This vein is, however, certainly not the *jugularis* of current descriptions of fishes, and is probably the encephalic vein of Allen's ('05) description of the *Loricati*. It cannot be the pituitary vein, for that vein does not extend into the anterior portion of the cranial cavity.

The posterior section of the myodome is said to lie beneath the *basis cranii*, between it and the parasphenoid, and to com-

municate with the middle section through the fenestra basicranialis posterior, which lies between the anterior ends of the parachordals and apparently corresponds to the posterior portion of the intertrabecular fissure of Scheip's descriptions. The recti externi pass through this fenestra, and, beyond it, lie beneath the basis cranii. There, as they increase in size, they are said to push both the middle portion of the basis cranii upward and the parasphenoid downward. The basal plate, formed by the parachordals and the enclosed notochord, then thickens along each lateral surface of these muscles, and so forms the lateral walls of this section of the myodome.

Comparing the conditions in this fish with those in *Gasterosteus*, it is seen that, in both fishes, the anterior portions of the parachordals lie, when first formed, at a certain distance lateral to the anterior end of the notochord, which projects anteriorly between them. In later stages of both fishes these projecting portions of the parachordals are said, by both Gaupp and Swinnerton, to be depressed, but the figures given by both show that this depression effects only the mesial edges of the parachordals, their lateral portions retaining their primitive positions in the level of the notochord. Between these higher lying portions of the cartilages, the prootic bridge is later developed. How this bridge is developed in *Gasterosteus* is not stated by Swinnerton. In *Salmo* Gaupp says it is formed by the chondrification of a part of the membrane forming the roof of the middle section of the myodome and also the floor of the *cavum cerebrale cranii*. Gaupp says it lies, when first formed, anterior to and above the tip of the notochord, and it is shown, in one of his figures, separated from that tip by the anterior portion of an open space that is prolonged posteriorly on either side of the anterior end of the notochord. The posterior portion of this space may possibly form part of the fenestra basicranialis posterior of Gaupp, but its anterior portion certainly does not, for Gaupp says that this fenestra lies between the edges of the bent-down parachordals and gives passage to the recti externi from the middle to the posterior section of the myodome. There are, then, four distinctly different fenestrae in this myodome.

region. One of them is the fenestra hypophyseos of Gaupp, which lies between the hind ends of the trabeculae and hence in the floor of the anterior section of the myodome; and this must be, in early embryos, traversed by the internal carotid arteries, for Parker ('73) shows those arteries, in this fish, running upward anterior to the hypophysis, and I so find them in all the Teleostei I have examined. A second fenestra is the fenestra basicranialis posterior of Gaupp, which lies partly in the floor of the middle section of the myodome and partly between that section and the posterior section. A third fenestra, not described by Gaupp, lies in the floor of the posterior section of the myodome, and this, together with that part of the second fenestra that lies in the floor of the middle section of the myodome, forms the fenestra ventralis myodomus, the so-called hypophysial fenestra of Sagemehl. The remainder of the second fenestra—the part leading from the middle section of the myodome into the posterior one—is simply a transverse section of the continuous cavity of the myodome and does not open on to the ventral surface of the cranium. The fourth fenestra lies in the roof of the middle section of the myodome, and this alone is the homologue of the fenestra basicranialis posterior of the Sauropsida. This is evident from Sonies's ('07) description of this fenestra in the chick and duck, to be discussed later, and from Gaupp's ('00) account of it in *Lacerta*. In *Lacerta* the fenestra is said by Gaupp to be bounded anteriorly by the crista sellaris, and to be closed by a membrane (Gewebe) everywhere continuous with the perichondrium of the bounding cartilages, and that represents an unchondrified portion of the primordial cranium. The anterior end of the notochord is enclosed in this membrane, and lies, in part of its course, so close to its ventral surface that it forms a longitudinal ridge along it. The fenestra accordingly lies in what corresponds to the roof of the myodome of fishes, and not to its floor, and hence cannot be the homologue of the similarly named fenestra of Gaupp's descriptions of *Salmo*. In the Urodela, also, the fenestra basicranialis posterior is said by Gaupp ('05 b, p. 692) to be a perforation of the basal plate, traversed by the notochord, and lies posterior to its tip, as it does in *Lacerta*.



## AMIURUS

In the adult *Amiurus* the myodome was briefly considered by me in my work on the mail-cheeked fishes, and I there said (Allis, '09, p. 200) that;

In the anterior three-fifths, approximately, of its length, the ventral edge of the prootic does not meet its fellow of the opposite side, a wide hypophysial fenestra, closed ventrally by the parasphenoid, being left between the two bones. Posterior to this fenestra, the ventral edges of the prootics meet in the middle line, and the two bones there form, on the floor of the cranial cavity, a prominent transverse bolster which has closely the position of the cross-canal of *Lepidosteus*; and it is certainly in this bolster that McMurrich found the small cavity that he considered to be a rudimentary myodome.

In the specimens that I examined at that time I found but slight indication of this cavity, but I nevertheless considered it to have existed previously in the transverse bolster and to have been suppressed by invading growth of the surrounding cartilage.

In my work on the pseudobranchial and carotid arteries of this fish, I said (Allis, '08 b, p. 259) that the external carotid artery

does not apparently traverse a trigemino-facialis chamber, for although it would seem as if that chamber must be present in some form, there is no proper indication of but one cranial wall in this region, and that one wall would seem to be the inner wall of the chamber; for both the external carotid and the jugular vein lie external to it.

It was further said (p. 259) that:

The parasphenoid of *Ameiurus* is peculiar in that the base of the ascending process of the bone, which begins immediately posterior to the so-called orbitosphenoid, is formed of two plates which enclose within them the hind end of the subopticus (trabecular?) bar of cartilage. The bone is here apparently not of perichondrial origin, but the inner plate nevertheless lies internal to the cartilage of the skull and there forms part of the immediate bounding wall of the cranial cavity. Posterior to the hind end of the trabecular (?) cartilage there is, for a few sections, a vacant space between the two plates of the process of the parasphenoid, and then those plates, the inner one of which gradually diminishes in height, enclose the anterior portion of the prootic (parachordal?) cartilage. It is perhaps this portion of the bone of the adult that led Mc Murrich to conclude that the basisphenoid was here anchylosed with the parasphenoid.

I have now reexamined my sections of young specimens of this fish, but the material was evidently not in a good state of preservation when sectioned, for the membranes in the myodomic region are all more or less disintegrated. The cartilages I tentatively identified in my earlier work as trabecular and parachordal are certainly those cartilages, as currently conceived, for the one lies wholly anterior to the hypophysis and the other along the lateral wall of, and posterior to, that organ. The anterior end of the parachordal cartilage is, as I stated, enclosed between external and internal plates of the parasphenoid, but neither plate is adherent to it, and, in the adult, the cartilage lies in a little pocket on the dorsal surface of the parasphenoid and can be easily withdrawn from it without breakage. Posterior to this pocket, the cartilage, in embryos, gradually becomes enclosed between plates of perichondrial bone which form part of the prootic, the internal plate of the parasphenoid gradually diminishing in height and finally vanishing. The ventral edges of the prootics form the lateral boundaries of the fenestra ventralis myodomi. The hypophysis is large, lies directly above this fenestra, upon the dorsal surface of the parasphenoid, and extends posteriorly to the anterior surface of the transverse bolster described in my earlier work. This bolster is but slightly developed in my young specimens, but it is evidently formed either by the fusion of the horizontal and ventral processes of the prootics or by the horizontal processes alone, the ventral processes of the prootics, in the latter case, here vanishing. The cavity described by McMurich ('84) in this bolster would then seem to represent the prootic portion of the dorsal compartment of a myodomic cavity. A ventral myodomic compartment is wholly wanting, for that part of the parasphenoid lying in the prootic region has certainly been developed in the skeletogenous tissue which, in the other Teleostei described, forms the horizontal myodomic membrane, this part of the parasphenoid of *Amiurus* thus corresponding to the transverse ridge on the dorsal surface of the bone of *Gasterosteus*. This, then, accounts for the fact that both the internal carotid artery and the ramus palatinus facialis of *Amiurus* lie everywhere external to the para-

sphenoid instead of passing internal to the ascending process of that bone. Whether or not there is a subpituitary portion of the dorsal myodomic cavity I cannot determine, the membranes being in a more or less disintegrated condition. It is, however, apparently wanting, for there are no veins comparable to the pituitary veins of the other Teleostei considered, the pituitary region being drained by veins definitely in the *cavum cerebrale cranii*. Furthermore, the membranous pituitary sac apparently forms the perichondrial lining of the pituitary fossa, as it also does of the larger part of that fossa in the *Selachii*. There is no *pars jugularis* of a *trigemino-facialis* chamber.

The internal carotid artery gives off, as described earlier (Allis, '08 b), an orbitonasal artery, sends two branches to the eyeball, and then enters the cranial cavity through the *foramen opticum*, behind the *nervus opticus*. This latter nerve certainly lies dorsal to the trabecula. The internal carotid artery of this fish must then also have that relation to that cartilage, the artery accordingly entering the cranial cavity by passing, first lateral and then dorsal to the trabecula.

#### AMIA CALVA

In *Amia* (Allis, '97, etc.) the myodome lodges the external rectus muscles and the pituitary veins, and corresponds to the dorsal compartment only of the myodome of Teleosts. It has no basioccipital extension, being limited to the subpituitary and prootic regions. The *hypophysis* and *saccus vasculosus*, both enclosed in the membranous pituitary sac, project ventrally into this myodomic cavity, the *hypophysis* lying immediately posterior to the presphenoid bolster and the *saccus* projecting posteriorly beneath the prootic bridge. The other rectus muscles have their origins on the lateral surface of the presphenoid bolster. The myodome has a large orbital opening, bounded laterally by the pedicel of the *alisphenoid*, and the *nervus profundus* and *vena jugularis* traverse this opening to enter the *trigemino-facialis* chamber, the *recti externi* traversing it to enter the myodome, and the *oculomotor* and *trochlearis* nerves traversing it to reach their primary foramina,

which lie in the membranous wall of the *cavum cerebrale cranii*. All of these structures thus pass mesial to the pedicel of the alisphenoid, as do also, morphologically, the pituitary vein and the abducens nerve. The *arteria carotis externa* and the *nervi maxillaris* and *mandibularis trigemini*, on the contrary, pass lateral to this pedicel to enter the trigemino-facialis chamber.

The trigemino-facialis chamber is not separated by a wall of bone into ganglionaris and jugularis parts, as in most of the Teleostei, and, because of the absence of a bony floor, the chamber is in direct communication with the myodomic cavity.

A ventral compartment of the myodome, as a functional myodomic cavity, is wholly wanting in this fish, but is represented in certain canals traversed by the internal carotid and efferent pseudobranchial arteries, the internal carotid artery of either side being accompanied, in part of its course through its canal, by the palatine branch of the facialis and the pharyngeal branch of the glossopharyngeus. These several canals were fully described in an earlier work (Allis, '97, p. 496) and were there called the palatine, internal carotid, and efferent pseudobranchial canals. The palatine canal of either side, as there described, lies between the parasphenoid and the ventrolateral surface of the chondrocranium, and the *nervus palatinus facialis* enters it at a certain distance anterior to its hind end, the posterior portion of the canal lodging only the internal carotid artery and the pharyngeal branch of the *nervus glossopharyngeus*. The internal carotid canal arises from this palatine canal and, running upward, traverses the cartilaginous presphenoid bolster to enter the *cavum cerebrale cranii*. The efferent pseudobranchial canal is in two sections, one of which traverses the lateral bounding wall of the orbital opening of the myodome, while the other penetrates the presphenoid bolster to fall into the internal carotid canal. My palatine canal is the *canalis parabasalis* of Gaupp's ('05 a) account of *Lacerta*, and conditions in other vertebrates, to be later considered, show that it should be considered as formed by the fusion of two canals, one traversed by the *nervus palatinus facialis* and the other by the internal carotid artery.

In the adult *Amia* the efferent pseudobranchial artery gives off its ophthalmica magna branch as it traverses the orbital opening of the myodome, the artery and this branch thus both appearing to here lie dorsal to the trabecula. In 8-mm. and 10-mm. embryos I, however, find the artery passing ventral to the trabecula and there falling into the internal carotid as it turns upward to pass between the trabeculae. From the artery so formed the arteria ophthalmica magna arises, and runs outward, dorsal to the trabecula, thus lying, in *Amia*, on the opposite side of the trabecula to that in which it is shown by Dohrn in a 10-mm. embryo of the trout (Dohrn, '86, fig. 2). The development of these arteries and their relations to the trabeculae need further investigation.

The prootic bridge, which forms the roof of the prootic portion of the myodome of the adult *Amia*, is of relatively late formation, for it is not found in a 40-mm. specimen. In a 43-mm specimen it has been formed, and, as in *Salmo*, lies at a certain distance dorsal to the fenestra ventralis myodome and separated from the tip of the notochord by an open space, closed by membrane, which is the homologue of the fenestra basicranialis posterior of the Sauropsida. The saccus vasculosus lies, in this specimen, wholly anterior to the anterior edge of the prootic bridge, directly in line with it and embedded in the dorsal surface of loose stringy connective tissue which fills this posterior portion of the myodome. The recti externi, which, in the adult, extend to the hind end of the myodome, do not, at this age, extend posteriorly even as far as the hind end of the saccus vasculosus, having their origins approximately in the transverse plane of the posterior opening of the trigemino-facialis chamber.

From these conditions in *Amia*, it is evident that the pre-spinal and prootic portions of the normal teleostean myodome would arise if the cartilage which, in *Amia*, separates the myodome from the canals for the internal carotid and efferent pseudobranchial arteries were to be resorbed, leaving more or less developed membranes in its place. This cartilage is known to undergo resorption during the ontogenetic development of cer-

tain of the Teleostei (*Salmo*, *Gasterosteus*), and skeletogenous tissues capable of taking a membranous form would certainly be left in its place. The membranous tissues that would then represent the presphenoid bolster would not offer a firm point of attachment for the rectus muscles, and it would be wholly natural for certain of them to seek more solid points of origin, and one of them actually has, in most of the Teleostei, acquired such an origin by first creeping downward on to the dorsal surface of the parasphenoid and then pushing posteriorly in the open end of the persisting remnant of the palatine canal of my descriptions. This muscle actually is the rectus internus, but it is possible that it was primarily the rectus inferior, that muscle and the rectus internus undergoing an exchange of function and so giving rise to that manner of innervation of these muscles that I have described in several of these fishes (Allis, '03, '09), and which I now find to be apparently definitely related to the presence of a functional ventral myodomic compartment. Where that compartment is wanting, as in *Amiurus*, or present but non-functional, as in *Lepidosteus*, *Polypterus*, *Polyodon*, *Acipenser*, and higher vertebrates, these muscles are innervated approximately as they are in *Amia* (Allis, '08 b).

The definitive rectus internus of the Teleostei, in thus shifting its point of origin, passed dorsal to the efferent pseudobranchial artery and dorsolateral to the internal carotid. The membranous tissues representing the presphenoid bolster were then pressed together in the median line by these muscles, and became the median vertical myodomic membrane, the internal carotid arteries still being enclosed in it, in a membranous canal, the homologue of the cartilaginous canals of *Amia* fused to form a single canal. The floor of the myodome of *Amia* became the horizontal myodomic membrane, which becomes adherent to the ventral surface of the membranous pituitary sac and seems to end there. It, however, certainly continued, primarily, beyond that point and was continuous with the ventral end of the interorbital septum. The efferent pseudobranchial arteries were necessarily pressed ventrally by the recti interni, and, losing their connections with the internal carotids,

acquired a cross-commissural connection with each other. A basioccipital portion of the dorsal compartment of the teleostean myodome would then be added to the prootic portion, developed as above set forth, whenever an aortal groove similar to that in *Hyodon* had been developed and retained; and a posterior extension of the ventral compartment would be acquired by the recti interni pushing posteriorly between the floor of that compartment and the underlying parasphenoid. The many variations that I have described above in the myodome of the non-siluroid Teleostei would then all arise by different degrees of ossification of the several membranes in this region.

As already stated, the internal carotid arteries of *Amia* traverse the presphenoid bolster in order to enter the cavum cerebrale cranii, and, although the development of this bolster has not yet been worked out, there seems no question that it is formed by the hind ends of the trabeculae. The median vertical myodomic membrane of the Teleostei, which in those fishes represents the presphenoid bolster of *Amia*, would then also represent the hind ends of the trabeculae. The basisphenoid of the Teleostei cannot then be the exact homologue of the presphenoid bolster of *Amia*. The fenestra ventralis myodomus of the adult *Amia* lies posterior to the presphenoid bolster; it must then be bounded laterally by the so-called anterior prolongations of the parachordals, and hence correspond to Gaupp's fenestra basicranialis posterior in embryos of *Salmo*, the fenestra hypophyseos of these embryos apparently being represented in the internal carotid canals of *Amia*. The fenestra hypophyseos is said by Gaupp ('05 b, p. 585) to be a persisting portion of the large fenestra basicranialis anterior of early embryos, and it is said by him to be always traversed by the ectodermal stalk of the hypophysis. The hypophysis must then lie, in these early embryos, dorsal to this fenestra, and as the internal carotid arteries, in the Holostei and Teleostei, run upward anterior to the hypophysis, they must traverse the fenestra. The hypophysis must then have later shifted posteriorly to a position dorsal to the fenestra interparachordalis.

(fenestra basiscranialis posterior, Gaupp), leaving the carotid arteries behind it, in persisting remnants of the fenestra hypophyseos which I have called, in *Amia*, the internal carotid canals.

The carotid arteries do not, in either *Amia* or the Teleostei, enter any part of the dorsal myodomic cavity. In certain other fishes and in higher vertebrates they become included in that cavity. The arteries must accordingly there have either shifted posteriorly, with the hypophysis, out of the fenestra intertrabecularis into the fenestra interparachordalis, or the inner walls of the canals traversed by them in *Amia*, both the carotid canals through the presphenoid bolster and those parts of the parbasal canals which lodge those arteries, must have been resorbed, the canals thus being added to the dorsal myodomic cavity. The arteries would then lie dorsal to the cartilaginous floor of the myodomic cavity, instead of, as in *Amia*, ventral to it; their foramina would lie near the hind end of the subpituitary portion of the pituitary fossa, instead of anterior to it; and a part of the ventral compartment of the teleostean myodome would be added to the definitive myodomic cavity.

The septum interorbitale may now be considered, for it forms a direct anterior prolongation of the median vertical myodomic membrane and hence must be of similar origin. This septum is said by Gaupp ('05 b, p. 585) to characterize the tropibasic cranium, and to be found in many of the Selachii (Plagiostomi?), in the Ganoidei, the Teleostei, excepting the Siluridae and Homaloptera, and the Amniota. The platybasic cranium, in which this septum is wanting, is said to be found in many of the Selachii and in all of the Amphibia. In the Teleostei the septum is said to lie above the trabeculae (Gaupp, '05 b, pp. 667 and 762), between them and the cavum cerebrale cranii. The septum must then be formed by the ventral portions of the side walls of the primordial cranium pressed together in the median line, and this is in accord with Gaupp's conclusion in his work on *Lacerta*, where he says ('00, p. 553) that this septum must either be a wholly new formation of the tropibasic (tropidobasic) cranium or be formed from material derived from the side walls and floor of the platybasic (homalobasic) cranium,



and he definitely decides in favor of the latter supposition. Fuchs, however, decides just as definitely in favor of the first-mentioned supposition, for he says ('12, p. 104) that, in *Che-lone*, the trabeculae take no part in the formation of the septum; that the septum is a new formation, peculiar to the tropibasic cranium; that it first appears as a keel-shaped outgrowth (*Vorwölbung*) on the ventral surface of the primordial basis cranii, and that it increases in height by growing upward. How a ridge on the ventral surface of the basis cranii could increase in height by growing upward is not at first quite clear, but in certain of the figures given by Fuchs the fundament of the septum is shown lying between the trabeculae, and hence capable of growing upward between them. This would of course leave the trabeculae near the ventral end of the septum, and this is the position in which they are shown in one of the figures given by Fuchs (*l. c.*, fig. 16 b). It is further said that, in later stages of development than that shown in the above-mentioned figure, the trabeculae are no longer recognizable in the optic region, but persist in the region of the hypophysis and from there run forward and fuse with the lower, thickened portion of the septum interorbitale. It is, however, particularly said by Fuchs that the ventral portions of the side walls of the cranium are here formed by the trabeculae, and that, in the embryo shown in his figures 16 a and 16 b, the trabeculae, in the region anterior to the nervus opticus, are reduced to connective tissue cords which lie near the upper end of the septum.

There is thus a difference of opinion as to the manner in which this septum arises, and there would also seem to be some confusion in Fuchs's statements regarding it. My own work leads me to suggest that the epichordal and hypochordal bands of skeletogenous material, known to be developed in the spinal region of embryos, are continued forward into the prespinal region, and that the trabeculae are there developed from them. These two morphologically distinct portions of the trabeculae are fused to form the basis cranii in the orbital region of the platybasic cranium, just as they are always fused, in embryos, to form the parachordal plate in the prootic region, and usually

so fused in the basioccipital region also. In the tropibasic cranium they have been forced apart, doubtless by pressure of the eyeballs, and the interorbital septum is formed from the material of the hypochordal bands and the tissues between them and the epichordal bands, the latter bands forming the floor and side walls of this part of the cranial cavity. The trabeculae might then be said by certain authors to lie at the ventral end of the interorbital septum, and by others to lie at its dorsal end. This would also explain how, in fishes where the interorbital and internasal septa are directly continuous with each other, the trabeculae are said by certain authors to form the ventral edge of the internasal septum, and by certain others to form its dorsal edge (Allis, '13).

#### LEPIDOSTEUS OSSEUS

In *Lepidosteus* there is no functional myodome, but the pre-existing spaces which correspond to both its dorsal and ventral compartments occur and were fully described by me in my work on the mail-cheeked fishes. The space representing the dorsal compartment lies, as does the functional myodome of *Amia*, dorsal to the cartilage which actually forms the basis cranii, the space that represents the ventral compartment lying ventral to that cartilage, between it and the underlying parasphenoid, and lodging, as in *Amia*, the internal carotid arteries and the palatine branches of the facialis nerves. Veit ('07), in a work that did not appear until after my own was sent to press, had previously described, in a 150-mm. specimen of this fish, the space representing the prootic portion of the dorsal compartment, calling it the *cavum saccivasculosi*, and he later ('11), described, in younger specimens, the development of the cartilages that bound that space.

In 8 to 16-mm. embryos of this fish, Veit ('11) says that the notochord is the only recognizable skeletal element; and it ends with a blunt point against the hind wall of the infundibulum, its extreme tip turning slightly ventrally. In embryos 10 to 11 mm. in length the notochord is in similar position, but three cartilaginous elements have now developed on either side of

the brain: a parachordal cartilage which extends from the transverse plane of the root of the nervus glossopharyngeus to that of the root of the nervus trigeminus; a polar (*Pol*) cartilage, which lies lateral to the anterior end of the notochord and extends, in a direct anterior prolongation of the line of the parachordal, from the root of the trigeminus to about the middle of the length of the hypophysis; and a trabecular cartilage, which, lying in the line prolonged of the other two cartilages, extends from about the middle of the length of the hypophysis to a point in front of the nervus opticus. The fundament of the musculus rectus externus of either side lies directly against the related polar cartilage.

In embryos of this fish 11 to 12-mm. in length the adjoining ends of the parachordal polar, and trabecular cartilages of either side have fused with each other to form a continuous cartilage, the part formed by the polar and trabecular cartilages lying, as shown in the figures, slightly dorsal to the level of the anterior end of the notochord. The trabeculae of opposite sides have fused with each other anterior to the recessus preopticus, thus enclosing a large fenestra basiscranialis, into the hind end of which the anterior end of the notochord projects. The polar cartilages now occupy the positions of the so-called anterior prolongations of the parachordals of Swinnerton's and Gaupp's descriptions of *Gasterosteus* and *Salmo*, and hence of the 'Balkenplatten' of Stöhr's descriptions of *Salmo*. The recti externi have now become inserted on the polar cartilages, and, because of this or for some other reason, the fenestra basiscranialis is there slightly constricted. The fenestra encloses the ventral portions of the infundibulum and recessus preopticus, and in later stages the hypophysis and saccus vasculosus come to lie, respectively, in the interpolar and interparachordal portions of it.

In embryos 14 to 20-mm. long the region under consideration has not changed in any important respect. The planum orbitonasale, formed by the fusion of the anterior ends of the trabeculae, begins immediately anterior to the recessus preopticus and extends forward beyond that part of the lamina terminalis

which forms part of the actual ventral surface of the brain, this lamina being bent at nearly a right angle and presenting surfaces that are the one actually ventral and the other anterior. A prootic bridge has not yet begun to be formed, but it is shown by Parker ('82) in somewhat older embryos, and is there at first separated from the otic portion of the parachordal basal plate by a large fenestra basicranialis posterior similar to the one in *Amia* and *Salmo*.

Veit does not give the relations of the internal carotid and efferent pseudobranchial arteries to the cartilages bounding the fenestra basicranialis of his descriptions, but in small embryos of this fish (size not given) I found ('09) the internal carotid running forward beneath the basis cranii, being there joined by the efferent pseudobranchial artery, and the artery so formed then turning upward through the fenestra basicranialis. Whether the part of the fenestra so traversed lies between the polar or trabecular cartilages cannot be definitely told by comparison with Veit's figures, but it would seem as if it must be between the hind ends of the trabeculae, the membranous pituitary sac lying dorsal to the polar cartilages. The conditions in this fish thus differ from those in the adult *Amia* only in that the efferent pseudobranchial artery does not traverse a foramen and canal in the cartilage of the basis cranii before falling into the internal carotid, and in that the recti externi have not invaded the myodomic space.

#### POLYPTERUS

In the neurocranium of the adult *Polypterus* there is a large pituitary fossa, the posterior portion of which is roofed by a horizontal bridge of the so-called sphenoid bone. The hind end of the pituitary body projects posteriorly beneath this bridge, and Waldschmidt ('87) shows it there surrounded by what he calls 'maschiges, fettartiges Gewebe.' This tissue apparently fills the space between the membranous pituitary sac and the walls of the cartilaginous pituitary fossa, the space thus corresponding to the prootic portion of the functional myodome of *Amia*. In his text figure 8, Waldschmidt shows the side wall of the

pituitary fossa perforated by a cord of tissue. It is not said what this cord of tissue is, but it is undoubtedly the pituitary vein described by me (Allis, '08a) in a 75-mm. specimen of *Polyp-terus senegalus*. This pituitary vein falls into a vein that I called the internal jugular, but which is more appropriately called the vena orbitalis inferior. This vein comes from the orbit, accompanied by the internal carotid artery and the nervus palatinus facialis, and after receiving the pituitary vein, is joined by a vein that I called the external jugular, but which is a vena orbitalis superior and is accompanied by the external carotid artery. The vein formed by the fusion of these two is the vena jugularis of the present descriptions. Running posteriorly, it traverses a short canal in the cartilaginous portion of the lateral wall of the chondrocranium, between the foramina by which the nervi trigeminus and facialis traverse that wall, and issues from the cranium, with the nervus facialis, at the hind edge of the ascending process of the parasphenoid. The external carotid artery unites with the internal carotid, and the artery so formed continues posteriorly in a canal through the ascending process of the parasphenoid, accompanied by a sympathetic nerve. At the hind end of this canal it receives the efferent artery of the hyoid arch, and then, becoming the lateral dorsal aorta, enters the aortal canal in the basioccipital, already referred to when describing the conditions in *Hyodon*.

The conditions in this fish are thus markedly different from, but nevertheless strictly homologous to, those in the other fishes so far considered. There is a dorsal myodomic cavity strictly similar to that in the *Holostei*, and a ventral compartment represented by the canals through the ascending processes of the parasphenoid. The median portion of the parasphenoid and the lateral walls of the canals through the ascending processes of that bone must then, together, correspond to the parasphenoid of *Amia*, the mesial walls of the latter canals corresponding to the ascending processes of the parasphenoid of *Amiurus*. The canal traversed by the vena jugularis, which lies partly in the lateral wall of the chondrocranium and partly between that wall and the lateral wall of the ascending process of the parasphenoid, is the pars jugularis of a trigemino-facialis chamber.

## CHONDROSTEI

The descriptions that I find of the pituitary region of the cranium of the Chondrostei are incomplete, and but little can be said about it. A slight pituitary fossa is shown by Bridge ('79) in the chondrocranium of *Polyodon*, and both I ('11) and Danforth ('12) have described the arteries in this fish. In embryos of from 150-mm. to 170-mm. in length the internal carotid runs forward along the ventral surface of the neurocranium, at first ventral to a short lateral process of the parasphenoid, and then, anterior to that process, in a groove on the ventral surface of the lateral edge of the basis cranii, lateral to the lateral edge of the parasphenoid. The artery there becomes enclosed in dense fibrous tissues which are attached to the cranial wall, and while in the canal thus formed, it is joined by the *nervus palatinus facialis*, which issues from the cranial cavity through a special perforation of the cranial wall. The internal carotid then enters a canal in the cranial wall, receiving while in it, the efferent pseudobranchial artery, and then immediately gives off the *arteria ophthalmica magna*. A small pituitary vein is sent outward from the pituitary fossa, through a special foramen in the cranial wall, and falls into the *vena jugularis*. The *nervus abducens* traverses a short canal in the cartilage of the basis cranii and, issuing from it, apparently again lies in the *cavum cerebrale cranii*, from which it definitely issues with the main root of the *nervus trigeminus*.

There is thus evidently, in *Polyodon*, a subpituitary space corresponding to the myodomic cavity of *Amia*, but the conditions need further investigation. The ventral compartment of the teleostean myodome is represented in the canal of fibrous tissue traversed by the internal carotid artery and the *nervus palatinus facialis*, this apparently corresponding to the canal through the ascending process of the parasphenoid of *Polypterus*.

## PLAGIOSTOMI

Gegenbaur ('72) describes, in the Selachii, a large pituitary fossa (Sattelgrube), which extends from the postclinoid wall (Satellehne) to a traverse presphenoid bolster (Praesphenoidvorsprung) which lies slightly anterior to the foramina optica, and is said to lodge the lobi inferiores anteriorly and the pituitary body posteriorly. The presphenoid bolster is said to vary greatly in importance in different species of the Selachii and to be wholly wanting in some of them, the Scylliidae being included among the latter. The pituitary fossa is, in certain of these fishes, everywhere lined with the dura mater, this membrane forming both the perichondrial lining of the fossa and the sac which encloses the pituitary body. In others of these fishes there is a deeper, posterior portion of the fossa, shut off from the cavum cerebrale cranii by a portion of the dura mater which extends dorsoposteriorly from its anterior edge to the summit of the postclinoid wall. This subdural portion of the fossa is said to be traversed by the arteria carotis interna (vordere Carotis), by a vein, and by a lymph canal which Gegenbaur calls the canalis transversus. When this subdural space is wanting, the canalis transversus and the internal carotid arteries are separately enclosed in the cartilage of the basis cranii.

Parker ('76) later described the conditions in *Scyllium canicula*, and in his figures of embryos of that fish he shows conditions in the pituitary region strictly similar to those described and figured by Gegenbaur in the adult of *Scyllium catulus*. In two figures of the adult, Parker, however, shows a small pituitary fossa which lodges the pituitary body and is separated from the so-called infundibulum by a tall preclinoid wall. I have heretofore always considered this condition in this fish to be either an abnormality in the particular specimen examined by Parker, or a condition due to great age, for Parker shows both the preclinoid and postclinoid walls strongly calcified. I have, however, now examined two small adults of this fish, and I find the canalis transversus of Gegenbaur's descriptions occupying exactly the position of Parker's pituitary fossa,

and it is unusually large in both these specimens. It therefore seems certain that, if Parker's figures and descriptions be not wholly wrong in this particular respect, the specimen examined by him must have been exceptional and abnormal.

In my work on *Mustelus* ('01), I found the *canalis transversus* of Gegenbaur's descriptions traversed by the pituitary veins, and not by a lymph vessel, and this was later confirmed by work on other *Selachii* (Allis, '14 a). In this latter work I found the deeper, posterior portion of Gegenbaur's descriptions of the pituitary fossa particularly well developed in *Chlamydoselachus*, and I said of it that it had "the appearance of being a somewhat separate and independent fossa." It is sub-pituitary, as well as subdural in position, and is filled with tissues that seem to be in part tough connective tissues and in part of a different character.

In all the *Selachii* I have examined or can find described, the internal carotid arteries always lie anteroventral to the pituitary veins, as they do in the *Teleostei* and *Holostei*, and they are always separated from those veins by either membrane or cartilage. They always either fuse with each other in the median line, or are there connected by cross-commissure, and this fusion of the arteries is certainly not due, as it apparently is in the *Teleostei*, to any pressure of the muscles of the eyeball. In *Heptanchus*, *Mustelus*, and *Acanthias* I found these arteries joined by the efferent pseudobranchial arteries, either while still in the cartilage of the basis cranii or while lying between that cartilage and the lining membrane of the *cavum cerebrale cranii*. The internal carotids of these fishes thus do not enter the *cavum cerebrale cranii* until after they have received the efferent pseudobranchial arteries, which perforate the side walls of the pituitary fossa slightly anterior to the internal carotid canals, approximately in the region between the hind ends of the *lobi inferiores* and the pituitary body. In *Chlamydoselachus* I found the internal carotids entering the *cavum cerebrale cranii* before they received the efferent pseudobranchial arteries, but I now think this may be an error. The *nervus palatinus facialis* does not, in any of these fishes, come into any relation



to any part of the pituitary fossa, running forward, after issuing from the cranial cavity, ventral to the chondrocranium.

The early development of the cartilages in this region of these fishes differs somewhat from that in the Teleostei and Holostei. According to Sewertzoff ('99), the trabeculae, when first formed, are independent cartilages, which lie oral, and hence morphologically ventral, to the hypophysis, and because of the marked cranial flexure at this stage of development, these cartilages lie ventral to the parachordal plate and perpendicular to it, slightly posterior to its anterior edge. In later stages of development the anterior portions of the trabeculae are said by him to fuse with each other, their hind ends still remaining separate, but having now fused with the ventral surface of the parachordal plate. An opening is thus enclosed between the trabeculae and the parachordal plate, and the hypophysis is said to traverse it. It is called by Sewertzoff the intertrabecular basal fontanelle, and, as shown by Parker in *Scyllium* ('76, fig. 6, pl. 35), has approximately the extent of the pituitary fossa of the adult fish. In later stages this large fontanelle is greatly reduced by progressive fusion of the trabeculae, both anterior (ventral) and posterior (dorsal) to the hypophysis, but Sewertzoff says that the hypophysis still projects through it, and he so shows it in transverse sections of embryos of *Acanthias* (*l. c.*, figs. 14 and 15, pl. 30). The stalk of the hypophysis is said to run forward from this point and to end blindly, and it apparently does not traverse the persisting portion of the basal fontanelle in *Acanthias*, but it does in *Pristiurus* (*l. c.*, figs. 23 to 25, pl. 31).

The course of the internal carotid and efferent pseudo-branchial arteries is not given by Sewertzoff, but the internal carotids must certainly have traversed the posterior portion of the large primitive fontanelle, and hence that part of that fontanelle which persists in the oldest embryos of *Acanthias* described by him. It would, however, seem as if they could not have traversed that part of the fontanelle that persists in *Pristiurus*, for that part lies considerably anterior to the hypophysis, between the hind edges of the fenestrae opticae (*l. c.*,

fig. 27, pl. 31), and hence at the anterior end of the pituitary fossa of the adult.

The pituitary veins, also, are not described by Sewertzoff, and neither they nor their foramina are indicated in his figures. They are, however, apparently shown by Baumgartner ('15) in sagittal sections through this region in embryos of *Acanthias*. In that author's figures 2 to 9, he shows a vessel ventral to the anterior end of the notochord, and morphologically posterior to the hypophysis. This vessel is not lettered in the figures, but it must certainly be a cross-section of the venous commissure formed by the pituitary veins. In Baumgartner's figure 9, it is shown lying between the parachordal plate above and a ventro-anteriorly directed process of cartilage that is apparently considered by Baumgartner to be of parachordal origin, but which must represent a section through that part of the trabecular cartilage of Sewertzoff's descriptions which is formed by the fusion of the trabeculae of opposite sides dorsal (posterior) to the hypophysis. This commissural vein would then pass dorsal to the trabeculae, as it normally should. The process shown by Baumgartner forms the posterior boundary of an opening between it and the hind end of the trabecular cartilage, and is hence the intertrabecular basal fontanelle of Sewertzoff's descriptions, and a vessel, possibly the internal carotid artery, is shown lying directly in it.

The so-called intertrabecular basal fontanelle of these embryos of the Selachii would then seem to correspond to the fused anterior and posterior basicranial fenestrae of *Salmo* and *Gasterosteus*, the definitive fenestra of *Pristiurus* corresponding to the fenestra hypophyseos of *Salmo* and *Gasterosteus*, and the definitive fenestra of *Acanthias* corresponding to the fenestra basicranialis posterior of those fishes. This latter fenestra is, as will be later shown, the fenestra hypophyseos of the Dipnoi, Amphibia, and Sauropsida, in which the internal carotid arteries traverse the fenestra along its posterior border, sometimes separated by a median cartilage called the intertrabecula.

Neither Sewertzoff nor Baumgartner describe polar cartilages in these fishes, but van Wijhe ('05) describes them in early

embryos of *Acanthias*, between the trabeculae and parachordals and primarily independent of those cartilages, thus corresponding to the hind ends of the trabeculae of Sewertzoff's descriptions, and apparently also to the median, ventro-anteriorly directed process of the parachordal of Baumgartner's description.

The conditions in these fishes thus show that chondrification has taken place to such an extent in the prootic and subpituitary regions that the dorsal compartment of the teleostean myodome has been reduced, either to canals traversed by the pituitary veins or to some part of a deeper, posterior portion of the pituitary fossa of the chondrocranium. The remainder of the deeper portion of the fossa represents an anterior extension of the dorsal myodomic cavity which has been developed in some relation to the enclosure of the internal carotid arteries in it. The subdural canals traversed by those arteries after they leave this subpituitary space evidently form anterior prolongations of it, and were they to be added to it, and the pituitary fossa reduced to the proportions in *Ceratodus* and higher vertebrates, the arteries would traverse a peripituitary space separated from the *cavum cerebrale cranii* by the *dura mater*. The conditions here thus seem to indicate that the *fenestra hypophyseos* of these fishes is the homologue of the *fenestra interparachordalis* of the *Holostei* and *Teleostei*, and not of the *fenestra hypophyseos* of those fishes. The *foramina carotica* of *Amia* and the *Selachii* are then not homologous.

No ventral myodomic cavity is found in these fishes, except as it may be represented in a part of the canals traversed by the internal carotid arteries. The cross-commissure between these arteries has a position which suggests that it may have been utilized, in the *Teleostei*, to form the cross-commissure between the efferent pseudobranchial arteries.

In certain of these fishes, a canal in the lateral wall of the chondrocranium, traversed by the *vena jugularis*, represents, as in *Polypterus*, a *pars jugularis* of a *trigemino-facialis* chamber (Allis, '14b).

In the *Batoidei*, the pituitary fossa, as shown in Gegenbaur's figures, is but slightly developed, but as he says that a *canalis*

transversus is found in these fishes, as in the Selachii, the conditions are probably strictly similar.

#### DIPNOI

In *Ceratodus*, the so-called *pars ascendens* of the anterior process of the palatoquadrate of Greil's ('13) descriptions forms the lateral wall of a space which, in an earlier work (Allis, '14 c), I showed to be the homologue of the trigemino-facialis chamber of the Holostei. In early embryos of *Ceratodus* this chamber has anterior and posterior openings which Greil calls, respectively, the foramen sphenoticum commune and the foramen praeoticum basicraniale. In older embryos the foramen sphenoticum commune becomes separated into four parts by bars of cartilage developed in the connective tissues surrounding the nerves and vessels which traverse the foramen. One of these parts, called by Greil the foramen sphenoticum majus, transmits all the branches of the nervi maxillo-mandibularis and lateralis trigemini and the vena and arteria temporalis, the latter artery being the carotis externa of my descriptions of other fishes. A second foramen, called the foramen sphenoticum minus, transmits the nervus profundus and the vena capitis media, this latter vein being also called the vena pterygoidea. A third foramen, called the foramen hypoticum, transmits the nervus oticus trigemini; the fourth foramen transmitting the nervus abducens. The posterior opening of the chamber, the foramen praeoticum basicraniale, does not undergo subdivision in the oldest embryos considered by Greil, and it is traversed by the nervus facialis, the ramus palatinus facialis, the arteria temporalis (carotis externa), and the vena capitis lateralis; the latter vein being a posterior continuation of the vena capitis media (pterygoidea), and the two together forming the vena jugularis of my descriptions of other fishes. The floor of the trigemino-facialis chamber is formed by the processus basalis of the palatoquadrate, and the palatinus facialis, after issuing through the posterior opening of the chamber, runs forward ventral to this floor, between it and the underlying parasphenoid.

In these embryos the hypophysis lies at the hind end of a large fenestra basicranialis, and even projects posteriorly slightly beyond and beneath the tip of the notochord. The fenestra basicranialis is bounded laterally by cartilages which Greil considers of trabecular origin, the parachordal cartilage not extending anteriorly beyond the tip of the notochord. A vena hypophyseos is said to arise in the neighborhood of the hypophysis and to issue from the cranial cavity through a foramen sphenolaterale, which lies dorsal to the trabecula and anterior to the foramen sphenoticum minus. This vein falls into the vena pterygoidea (jugularis), and although it is not said to be connected with its fellow of the opposite side by a cross-commissural vessel, it is certainly the pituitary vein of my descriptions. There is no indication, in the figures given, of a membrane separating this vein from the cavum cerebrale cranii, but this membrane must certainly exist, for it occurs in all other fishes so far considered.

In early embryos the arteria carotis interna is connected with its fellow of the opposite side by a cross-commissural vessel, immediately posterior to the hypophysis and immediately ventral to the tip of the notochord, but Greil says this cross-commissure has aborted in the oldest embryos examined by him. Anterior to this cross-commissure, the artery gives off an arteria palatina, which runs forward ventral and mesial to the trabecula. The artery itself then runs upward mesial to the trabecula of its side and is distributed mainly to the brain, one branch, however, the arteria orbitalis, being sent outward through the foramen sphenolaterale with the pituitary vein, and a second branch, the arteria ophthalmica sent outward with the nervus opticus through the foramen opticum. Before passing upward through the fenestra basicranialis, the internal carotids are said to lie between the ventral surface of the chondrocranium and the underlying parasphenoid.

In the adult, the large fenestra basicranialis of the embryo is shown entirely closed by cartilage in the median vertical sections given by Günther ('71), Huxley ('76), and Bing ('05), and each of these authors shows a deep pituitary fossa with

pronounced postclinoid and preclinoid walls. Bing says the hypophysis lies in the posterior portion of this fossa, the anterior portion being filled with arachnoidal tissue (*Arachnoideal-maschen*). The postclinoid wall is evidently formed by growth of the epichordal and hypochordal bands of parachordal cartilage said by Greil to enclose the tip of the notochord in embryos. The preclinoid wall had not begun to be developed in the oldest embryos described by Greil. No foramina leading into the pituitary fossa are shown or described by any of these three authors.

I find, in an old and somewhat dissected skull of this fish, a perforation of the cartilage of the basis cranii at the bottom of the posterior portion of the pituitary fossa, and it is closed by tough membrane. A small canal in the cartilage leads from either orbit to the edge of this membrane and must certainly have transmitted a vein which either traversed the membrane or passed dorsal to it, in order to reach and drain the hypophysis. The space traversed by this vein, wherever it may be, is a dorsal myodomic cavity. The internal carotid artery of either side passes internal to the parasphenoid, is there joined by the efferent pseudobranchial artery (mandibular aortic arch of Greil's descriptions), and then becomes embedded in the cartilage of the basis cranii and covered externally by membrane. The arteries of opposite sides are connected by a cross-commisural vessel which lies posterior to the median perforation in the floor of the pituitary fossa, the canal traversed by this cross-commissure representing part of a ventral myodomic cavity. Anterior to this cross-commissure each artery runs forward ventral to the pituitary vein, sends forward the *arteria palatina*, and then certainly enters the pituitary fossa through a foramen that I find lying anterolateral to the median perforation in the floor of the fossa, but, as my skull had been cleaned and the arteries removed, I cannot definitely establish this. If it traverse this foramen, as seems certain, it must enter and traverse that anterior portion of the pituitary fossa which Bing says is filled with arachnoidal tissue, this part of the fossa then representing the internal carotid canals of *Amia*, fused with each

other and become part of the pituitary fossa of the chondrocranium. Whether this part of the fossa is separated from the *cavum cerebrale cranii* by the *dura mater* or not cannot be told from my specimen, but comparison with other fishes and with higher vertebrates show that it must be.

There are thus, certainly, in this fish, both dorsal and ventral myodomic cavities, and the dorsal cavity has apparently fused with the prepituitary portions of the canals traversed by the internal carotid arteries to form a single peripituitary space similar to that found in higher vertebrates and represented in the cavernous and intercavernous sinuses of man, as will be explained later. The *foramina carotica* lie at the hind edge of the pituitary fossa, as they do in higher vertebrates. The cross-commissure connecting the internal carotids is evidently the homologue of the cross-commissure in the *Selachii*, and probably not the homologue of the anastomosis of the arteries of opposite sides in the *Teleostei*.

The bar of cartilage separating the *foramina sphenoida majus* and *minus* is the homologue of the pedicel of the *alisphenoid* of *Amia*, and if the anterior edge of this bar of cartilage were to grow forward so as to pass beyond the *foramina* for the pituitary vein and the *oculomotorius* and *trochlearis* nerves, it would give rise to the orbital opening of the *myodome* of *Amia*.

#### AMPHIBIA

In the *Amphibia* there apparently is no vein comparable to the pituitary vein of fishes, for I find no such vein described, and the pituitary region is said to be drained, in certain of these vertebrates, by branches of intracranial veins. It might be assumed that the myodomic conditions here were as in *Amiurus*, where the pituitary veins are also wanting, but it seems much more probable that the ventral processes of the *prootics* have here been wholly suppressed, and that the *basis cranii* corresponds to the roof of the dorsal compartment of the *myodome* of fishes, and hence represents the primary *basis cranii*. The course of the internal carotid artery in *Rana*, and that of the *nervus abducens* both in *Rana* and *Salamandra*, favor this interpretation.

The internal carotid artery of *Rana* is said by Gaupp ('93 b), p. 403) to pass upward, in early embryos, mesial to the trabecula of its side, but, because of enveloping growth of the trabecular cartilage, soon to become enclosed in a primary foramen caroticum. Having traversed this foramen and entered the cranial cavity, the artery gives off the *arteria carotis cerebialis* and then itself issues from the cranial cavity through the foramen oculomotorium as the *arteria ophthalmica*. In later stages, that part of the trabecula between the foramina caroticum and oculomotorium is resorbed, and the internal carotid is said then to lie in the orbit and to send its cerebral branch inward through the foramen oculomotorium. Comparing these conditions in *Rana* with those I have described in the Teleostei, it is evident that the primary foramen caroticum of *Rana* must lie in what corresponds to the floor of the *cavum cerebrale cranii* of *Amia* and the Teleostei, for that floor, alone, is continuous with that part of the cranial wall which is perforated by the foramen oculomotorium.

The *nervus abducens* of *Rana* is said by Gaupp to issue from the cranial cavity in the sheath of the *ramus orbitonasalis trigemini*, and to pass, with that nerve, under, and hence morphologically anterior to, the *processus ascendens quadrati*. In fishes the corresponding branch of the trigeminus (*nervus profundus*) passes mesial and anterior to the pedicel of the alisphenoid, and always lies dorsolateral to the myodome, never traversing it. Comparison of these conditions would accordingly indicate that the dorsal myodomic cavity is wanting in *Rana*. In *Salamandra*, Fuchs ('10) shows the *nervus abducens* perforating the basis cranii and then lying mesial to the *arteria carotis interna* in a canal between the basis cranii and the parasphenoid, the *nervus palatinus facialis* lying lateral to the *carotis interna*. The hypophysis lies in a perforation of the basis cranii, and even projects ventrally slightly beyond it, lying in a slight concavity on the dorsal surface of the parasphenoid. The dorsal myodomic cavity must accordingly be wholly suppressed here by failure of the ventral processes of the prootics to develop, the canal which lodges the internal carotid artery and the *nervus*



palatinus lying directly beneath the floor of the cavum cerebrale cranii. Thus this canal is, as Fuchs says, not the homologue of the canalis parabasalis of reptiles, and also not the homologue of that same canal in fishes.

The fenestra hypophyseos of the Amphibia is then the homologue of the pituitary opening of the brain case of fishes, and not of either the fenestra hypophyseos or the fenestra ventralis myodonomus.

The antrum petrosus laterale of Drüner's ('01) descriptions of the Urodela represents some part of a trigemino-facialis chamber, and quite certainly its pars jugularis only (Allis, '14 d), the pars ganglionaris of the chamber then being enclosed within the cranial wall. The lateral wall of the pars jugularis of the chamber is formed by that part of the palatoquadrate terminating in the processus oticus, the processus ascendens quadrati, which is the homologue of the pedicel of the alisphenoid of fishes, forming the lateral wall of a space which corresponds to the orbital opening of the myodome of *Amia*. There, however, apparently is, in these vertebrates, no cartilage corresponding to the floor of that opening of *Amia*.

In the *Anura* the conditions are apparently similar to those in the *Urodela*, for, in embryos of *Rana*, Gaupp ('93 b) shows the trigemino-facialis ganglion lying within the chondrocranium.

#### REPTILIA

In my work on the mail-cheeked fishes, I came to the conclusion that there was, in the pituitary region of the chondrocranium of *Lacerta*, a 'space of uncertain dimensions' which corresponded to a part, if not the whole, of the myodome of fishes. This space was between the cartilaginous floor of the cranial cavity and a membrane which was assumed to overlie it and to form the actual floor of the cavum cerebrale cranii, but I could not then find this membrane described. It is, however, shown by Gaupp ('02, fig. 6, p. 172), well developed, in a figure of a cross-section through the prootic region of a 32-mm. embryo of *Lacerta*, and in the space between it and the cartilaginous basis cranii the hypophysis and the nervi abducentes are shown.

The foramina for the internal carotid arteries are cut in the section, lying in the floor of this space and separated from each other by a median piece of cartilage which lies at a slightly lower level than the cartilage on either side of it. The internal carotid arteries are shown lying ventral to the basis cranii, each artery accompanied by, and lying mesial to, the nervus palatinus facialis of its side. No parasphenoid bone is shown, but comparison with a figure of a 47-mm. embryo (Gaupp, '05 b, p. 763) shows that that bone lies ventral to the nerve and artery and forms the floor of the canalis parabasalis of Gaupp's later descriptions ('05 a, p. 292), this canal of *Lacerta* thus being the homologue of the palatine canal of my descriptions of *Amia*. The piece of cartilage between the foramina carotica is the intertrabecula of Fuchs's ('12) descriptions of *Chelone*, and, as it forms part of the floor of the little space here under consideration, it cannot be part of the crista sellaris, as the lettering in Gaupp's figure of the entire chondrocranium of *Lacerta* ('00, fig. 1) would lead one to suppose. The nervus abducens enters the space here under consideration by traversing a foramen which perforates the cartilage of the chondrocranium, lateral to the lateral end of the crista sellaris, and issues from it into the orbit.

No pituitary veins are shown in Gaupp's figure of a cross-section through this region in *Lacerta*, but in an earlier work ('93, p. 571) he fully describes them. A vein lies along each lateral surface of the middle lobe of the hypophysis and is connected with its fellow of the opposite side by several cross-commissures, the largest of which lies posterior to the hypophysis. From either end of this posterior cross-commissure an important vein leads into a large vein which drains the blood from the orbital venous sinus, and the vessel so formed falls posteriorly into the vena jugularis interna. These veins thus must traverse the space of uncertain dimensions mentioned in my earlier work, which is a dorsal myodomic cavity. The internal carotid arteries run upward through the fenestra hypophyseos, and then along the lateral surfaces of the lateral lobes of the hypophysis, lying, in their course, anteroventral to the pituitary veins.

A ventral myodomic cavity is represented in those parts of the canales parabasales posterior to the foramina carotica.

The antipterygoid is said by Gaupp ('00, pp. 541 and 542) to be the homologue of the ascending process of the quadrate of the Amphibia and to be wholly wanting in the cranium of mammals. The ala temporalis of the mammalian cranium is considered by him to be represented, in reptiles, by the processus basipterygoideus. Fuchs ('12, pp. 91 to 95), on the contrary, maintains that the antipterygoid (epipterygoid, Fuchs) is the homologue of the mammalian ala temporalis, and that the processus basipterygoideus is the homologue of the processus alaris of the ala temporalis. To explain the difference in the relations of the nervus maxillaris trigemini to the antipterygoid and ala temporalis, he assumes that the nerve has, in mammals, slipped over the top of the antipterygoid in early stages of development.

I formerly concluded ('14 d) that the antipterygoid of *Lacerta* was the homologue of the pedicel of the alisphenoid of *Amia*, and the processus basipterygoideus the homologue of the floor of the orbital opening of the myodome of *Amia*. The pars ascendens of the quadrate formed the lateral wall of the post-trigeminal portion of a trigemino-facialis chamber, as in the Amphibia. My present work leads me to consider these conclusions correct, but to consider the trigemino-facialis chamber of these vertebrates to be the homologue of that chamber of *Ceratodus* and the Holostei, and not of the chamber of the Amphibia and Teleostei; for the lateral wall of the chondrocranium, both of *Lacerta* and *Crocodylus* (Shiino, '14), is certainly the primitive cranial wall and not the outer wall of a trigemino-facialis recess. The processus basitrabecularis of *Crocodylus* would then represent a part of the floor of that chamber, and the processus pterygoideus quadrati a part of its lateral wall.

The vena cardinalis anterior of *Lacerta* is said by Gaupp ('00, pp. 547 and 548) to run posteriorly dorsal to the processus basipterygoideus and then along the external surface of the chondrocranium, thus lying wholly external to that cranium. This is exactly as it should be under my interpretation of the conditions, for this vein is the vena jugularis of my descriptions of

fishes, and in *Amia* it enters the orbital opening of the myodome and then traverses the trigemino-facialis chamber, lying always external to the wall of the *cavum cerebrale cranii*. Gaupp considers this vein to be the homologue of the sinus cavernosus of mammals, and as that sinus is intracranial in position, he concludes that the space traversed by the vein in *Lacerta*, which is actually extracranial, has been added to the cranial cavity in mammals. The sinus cavernosus is, however, a branch of the *vena cardinalis anterior (capitis media)*, and not that vein itself, as will be later explained.

#### MAMMALIA

Properly to explain the conditions in mammals it is necessary first to consider the *ala temporalis*. This element of the cranial wall has been considered by many authors to have its homologue in the antipterygoid of reptiles, but Gaupp considers it, as stated above, the homologue of the *processus basipterygoideus* of those vertebrates. A well-recognized objection to its being the homologue of the antipterygoid of the *Reptilia* is that the *nervus maxillaris trigemini* (second branch of the trigeminus) lies posterior to that element of the reptilian cranium, but anterior to the *ala temporalis* of mammals. Gaupp accounts for this by saying that, because of the absence of an antipterygoid in mammals, there was no intervening skeletal element, and the nerve has simply joined the first branch of the trigeminus instead of remaining with the third. Other authors have suggested that the nerve has either cut through or slipped over the top of the antipterygoid, or simply, for some unknown reason, chosen a presumably more direct or advantageous course on the other side of it. My work leads me to quite a different conclusion, and I look for the homologue of the *ala temporalis* in a part of the lateral wall of the trigemino-facialis recess of fishes.

In all of the lower vertebrates there is apparently always either a trigemino-facialis chamber, a *pars ganglionaris* of that chamber (trigemino-facialis recess), or both *partes ganglionaris* and *jugularis* separated from each other by a wall of bone. The outer

wall of the pars jugularis of this chamber of fishes, and the pedicel of the alisphenoid are represented, respectively, in the Amphibia by the otic and ascending processes of the quadrate, the latter process being the homologue of the antipterygoid of the Reptilia (Allis, '14 c). These two portions of the neurocranium of fishes are thus secondarily acquired additions to it, and one or the other, or even both of them, is frequently wanting. In the Selachii, the pars ganglionaris of the trigemino-facialis chamber may be separated, by a partition of membrane or cartilage, into trigeminus and facialis portions, the latter portion then fusing with an acusticus recess to form an acustico-facialis recess.

Assume that, in a piscine skull, the pedicel of the alisphenoid and the lateral wall of the pars jugularis of the trigemino-facialis chamber are both wanting, as is actually the case in certain of the Teleostei; that independent trigeminus and acustico-facialis recesses have been formed, as in certain of the Selachii; that the muscles of the eyeballs have not acquired entrance into the preexisting myodomic cavities, as in many fishes; that these cavities have been reduced to the conditions found in *Ceratodus*; and that the trigeminus recess has been enlarged to such an extent that its floor projects ventrally below the level of the pituitary fossa (*sella turcica*), as it actually does in many of the Mammalia. If the wall separating the trigeminus and acustico-facialis recesses were then to be perforated, the facialis portion of the latter would be in communication with the trigeminus recess, and conditions would arise similar to those described by Voit ('09) in rabbit embryos, where the *cavum epiptericum* (trigeminus recess) and the *cavum supracochleare* (facialis recess) form a continuous cavity which communicates with the *meatus acusticus internus* (acusticus recess) through a *foramen faciale primitivum*. The facialis nerve would then issue from the facialis portion of this continuous cavity through a *foramen faciale secundarium*, the profundus nerve (first branch of the trigeminus) and trigeminus issuing from the trigeminus portion of the cavity, and their foramina of exit lying at the hind end of the orbit and not far from the foramina of the pituitary vein

and the oculomotorius, trochlearis, and abducens nerves. In the Teleostei and Selachii these several last mentioned foramina may lie relatively close together, and the chondrification or ossification of the tissues of the cranial wall may actually give rise to marked variations in the number and arrangement of the definitive foramina. Assume that the tissues surrounding the nervi maxillaris and mandibularis trigemini, as they issue from the trigeminus recess, chondrify to form a vertical bar of cartilage; that this bar grows forward so as to shut in the other foramina mentioned above, as the pedicel of the alisphenoid actually does in *Amia*; and that the tissues separating these other foramina from each other and from the nervus maxillaris persist as membrane. This would give rise, in this hypothetical cranium, to three fenestrations of the cranial wall which would be strictly similar, so far as the nerves traversing them are concerned, to the fissura orbitalis superior and the foramina ovale and faciale secundarium of Voit's description of embryos of the rabbit. If, then, the venous and arterial vessels of the region also have the same relations to these foramina that they do to the foramina in the rabbit, there would seem to be no reasonable doubt that the foramina, and hence their bounding walls, are strictly homologous.

In fishes the vena jugularis always runs posteriorly mesial to the pedicel of the alisphenoid, when the pedicel exists, and then always traverses the pars jugularis of the trigemino-facialis chamber, when it is present and independent of the pars ganglionaris. When the pars jugularis of the chamber is wanting, the vein passes along the lateral wall of the neurocranium, whether that wall be formed by the primary wall of the cranial cavity or by the lateral wall of a trigemino-facialis recess, never entering either the recess or the cavum cerebrale cranii. The pituitary vein arises from this vena jugularis and perforates the cranial wall, anterior to the trigemino-facialis chamber, to enter the dorsal myodomic cavity, never itself entering either the cavum cerebrale cranii or any part of the trigemino-facialis chamber. A branch is, however, sent into the cavum cerebrale cranii to drain the hypophysis, and, in certain Teleostei, this branch

is connected with an intracranial vein, the encephalic vein of Allen ('05), which enters the trigemino-facialis recess, perforates its lateral wall posterior to the nervus trigeminus, and falls into the vena jugularis. In other Teleostei the pituitary vein is connected with intracranial veins which issue through the foramen vagum there to fall into the vena jugularis. If either of these two connections were to become important, the flow of blood in the pituitary vein would be reversed, and a vein would be formed which would drain the hypophysial region and would issue, in the one case, through a foramen jugulare spurium, and, in the other, through a foramen jugulare.

In the Amphibia and Reptilia the vena jugularis always passes mesial to the ascending process of the palatoquadrate, or its homologue, the antipterygoid, and then, in each case, traverses the pars jugularis of the trigemino-facialis chamber, never there traversing any portion of the lateral wall of the neurocranium.

The arteria carotis externa of fishes, like the vena jugularis, always traverses the pars jugularis of the trigemino-facialis chamber, when that part of the chamber has been separated from the pars ganglionaris, never traversing the pars ganglionaris. On issuing from the chamber into the orbit, it always runs outward, posterior and lateral to the pedicel of the alisphenoid. In the Amphibia and Reptilia it traverses the pars jugularis of the trigemino-facialis chamber, always lying lateral to the lateral wall of the neurocranium, and issues from the chamber, posterior to the ascending process of the palatoquadrate in the Amphibia, or to the antipterygoid in the Reptilia, thus lying lateral to that element of the cranial wall.

In embryos of the porpoise the vena jugularis of fishes is represented in the vena capitis media plus the vena capitis lateralis, and, as described by Salzer ('95), all the cerebral veins empty into it, some anterior, some posterior to the nervus trigeminus, between it and the nervus facialis, and some in the region of the nervus vagus. The anterior of these three connections with the primitive vena jugularis loses its importance in later stages of development, the other two increasing, but varying in relative importance at different stages of development, and appar-

ently also in different species of the Mammalia, this giving rise to a vena jugularis interna which issues, either through a foramen jugulare spurium or a foramen jugulare, or even through both those foramina; these two connections with the primitive vein thus evidently corresponding to those referred to above in the Teleostei. The sinus cavernosus is said by Salzer (l. c., p. 252) to be formed from the veins which primarily collected the blood from the eyeball and the orbit, and which acquire a secondary connection with the sinus petrosus. This secondary connection must certainly be formed by a vein, the homologue of the pituitary vein of fishes, which has become important because of the abortion of the short vertical venous commissure which primarily connected the venae capites media and lateralis between the trigeminus and facialis ganglia. I do not find that Salzer mentions the abortion of this connection, but his figures show that it is absent in older embryos. Thus the sinus cavernosus of mammals is the pituitary vein of fishes, and it is said by Salzer (l. c., p. 242) primarily to have delivered the blood from the orbital veins into the sinus petrosus. Later, the flow of blood is reversed, in the porpoise, and the sinus cavernosus and the orbital veins are drained by the facial vein, the flow of the blood in the sinus cavernosus thus now being in the same direction as in the pituitary vein of fishes.

The sinus cavernosus of mammals thus certainly contains no part of the primitive vena jugularis, but a persisting portion of that vein forms the connection between it and the orbital veins. In the Sauria the sinus cavernosus is said by Grosser and Brezina ('95, p. 323) to be perhaps a remnant of the vena cardinalis anterior, and there to be extracranial in position (l. c., p. 321); neither of which statements is correct, for the conditions are here certainly as in the Mammalia. Gaupp ('00, p. 548) quotes Grosser and Brezina as here saying that the sinus cavernosus is actually (wohl) a part of the vena cardinalis, and adds that he has himself confirmed this, as well as its extracranial position, in embryos of *Chelone*.

These statements regarding this sinus led me formerly to conclude (Allis, '09, p. 193) that the venous vessel which tra-



verses the sinus cavernosus of man was the homologue of the vena jugularis of fishes; that the intercavernous sinuses represented the pituitary veins of fishes; and that the cavernous and intercavernous sinuses and the cava Meckelii together represented the myodome of *Amia* together with its so-called upper lateral, or trigemino-facialis chamber. This is, however, an error, for the so-called cavernous and intercavernous sinuses together represent a dorsal myodomic cavity plus the internal carotid canals, and the venous vessels traversing this cavity are, together, the homologues simply of the pituitary veins of fishes. The cavum Meckelii is then simply a trigeminus recess and not a trigemino-facialis chamber.

In Thane's figure ('94, fig. 405, p. 523) of a transverse section through the sinus cavernosus of the adult man, the outer wall of the sinus, formed by the dura mater, is thickened and is traversed by the oculomotorius, trochlearis, profundus (first branch of the trigeminus), abducens and maxillaris trigemini nerves. The inner wall of the sinus is continued across the dorsal surface of the sella turcica, and is there separated by a narrow space from the membranous pituitary sac, this space being traversed, on either side of that sac, by the intercavernous sinuses. The internal carotid artery enters this sinus through the inner part of the foramen lacerum, runs forward in the carotid groove on the lateral surface of the body of the sphenoid, and turns upward in a semicircular notch on the posterior surface of the preclinoid wall, this notch representing a remnant of the internal carotid canal of *Amia*. The artery lies lateral to the pituitary vein, but if the myodomic cavity were convex on its ventral surface, as it is in fishes, instead of concave, as in man, the artery would lie ventral and internal to the loop formed by the veins of opposite sides, as it does in fishes. The external carotid artery lies everywhere external to the cranial wall, as does also the vena jugularis externa, terminal branches only being sent into the cranial cavity.

The relations of the veins and arteries of man to the cranial wall are thus, like those of the nerves, strictly similar to those in the hypothetical piscine cranium here under consideration,

and no suppositions have been made in regard to the latter that are not warranted by conditions actually found in fishes, excepting only the formation of a bar of cartilage between the nervi maxillaris and mandibularis trigemini and the fusion of the foramen for the nervus maxillaris with certain other foramina to form a single large fenestra; and, as already stated, marked variations in the fusions and groupings of the foramina in this region are of constant occurrence in fishes. It thus seems certain that the foramina in this region in the two crania are homologous, and it follows that the lamina ascendens of the ala temporalis of mammals is a bar of cartilage formed between the nervi maxillaris and mandibularis trigemini as they issue from a trigemino-facialis recess, and this element of the cranium is apparently characteristic of these vertebrates. The processus alaris of the ala temporalis must then be represented in some ventral portion of the basicapsular commissures of fishes, and apparently in that part which, in *Amia*, lies between the palatine foramen and the floor of the orbital opening of the myodome. If it includes the latter floor, it must include the processus basipterygoideus of reptiles, which seems improbable.

Certain other features of the region, which favor this interpretation of the conditions, may now be considered.

The myodomic cavity of the mammalian cranium, corresponding to the so-called cavernous and intercavernous sinuses of man, must necessarily extend, on either side, beyond the lateral edge of the foramen caroticum, and its roof is thus formed by what Terry ('17) has recently described as the spreading basal portion of his membrana limitans. The carotid foramen accordingly lies in the floor of this myodomic cavity and not, as Voit ('09) concluded was the case in rabbit embryos, in the floor of the cavum epiptericum. The nervus petrosus superficialis major (nervus palatinus facialis) of the rabbit does, however, perforate the floor of the cavum epiptericum, as Voit concluded, this being in accord with its course in the Teleostei, where it usually perforates the floor of the pars ganglionaris of the trigemino-facialis chamber, but may occasionally perforate the floor of the pars jugularis.

The arteria carotis interna of the rabbit is said by Voit to run upward through the foramen caroticum into the cavum epiptericum, which, as explained above, is certainly incorrect. The artery is said then to run forward dorsal to the processus alaris of the ala temporalis, which is in accord with my interpretation of the conditions, for that process forms part of the floor of the dorsal myodomic cavity. The artery is said by Voit to lie lateral to a cartilage 'c,' which Voit considers to form part of the lateral wall of the cavum cerebrale cranii. This cartilage is, however, certainly a chondrification of a membrane shown, in one of Arai's figures of this animal ('07, fig. 6, p. 432), running upward between the hypophysis mesially and the arteria carotis interna and the pituitary vein (so-called sinus cavernosus) laterally. This membrane is continued mesially between the hypophysis and the dorsal surface of the sella turcica, and is shown as a single membrane, but it must necessarily be formed by the fusion of two membranes, one forming the floor and the other the roof of the subpituitary myodomic cavity. The cartilage 'c' is evidently a chondrification of some part of this membrane, and may therefore represent a chondrification of either one of its two components; and its position and its coalescence with the floor of the sella turcica seem to indicate that its basal portion belongs to both membranes while its dorsal portion belongs to the dorsal membrane only and forms part of the roof of the myodomic cavity and hence of the wall of the cavum cerebrale cranii. The internal carotid accordingly here lies in a lateral portion of the myodomic cavity which has been separated from the median portion of the cavity by this wall of cartilage. The cartilages 'a' and 'b' of Voit are, as he concluded, remnants of the mesial wall of the cavum epiptericum (trigemini recess).

Because of the passage of the internal carotid through what Voit considered to be a part of the cavum epiptericum, he concludes ('09, p. 551) that this artery of the rabbit, and hence also that of others of the Mammalia ditremata, must run upward lateral to the trabecula, the internal carotid of these animals thus not being the homologue of the similarly named artery of

the Mammalia monotremata and of lower vertebrates. Gaupp had previously suggested that the trabecula had here simply 'cut through' the artery, but Voit is not inclined to accept this suggestion. The bounding walls of this foramen are, however, under my interpretation of the conditions, of parachordal (polar) and not of trabecular origin, and there is, accordingly, no question here of its lying on one side or the other of the trabecula. It does, however, apparently lie lateral to the polar cartilage, and hence morphologically lateral, instead of mesial, to the trabecula, and a possible explanation of this will be given when the polar cartilages are considered later.

The processus pterygoideus arises from the ala temporalis at the base of its lamina ascendens, and hence, under my interpretation of the conditions, from the ventral edge of the lateral wall of the trigemino-facialis recess. Its position, alone, thus indicates that it is a remnant of the lateral wall of the pars jugularis of a trigemino-facialis chamber, and its relations to the nerves, arteries, and veins are in accord with this conclusion. The several branches of the nervus trigeminus all lie dorsal to it, as they should; the nervus petrosus superficialis major runs forward ventral to it; and the vena capitis media of embryos must necessarily have passed dorsal to the place where the process later develops, for that vein lies directly ventral to the nervus trigeminus. The relations of the arteria maxillaris interna (carotis externa of fishes) to the process vary. In embryos of the rabbit the artery perforates the process (Voit). In embryos of the dog it is said by Olmstead ('11) to traverse a canalis alaris s. alisphenoideum, which begins on the external surface of the lamina ascendens of the ala temporalis and issues on its anterior edge. The foramen rotundum opens into this canal, and the second branch of the trigeminus, passing through this foramen, enters the canalis alaris and, accompanying the arteria maxillaris interna, issues through its anterior opening into the orbit. In *Vespertilio* the artery is said by Grosser ('01) to enter the cranial cavity through the foramen ovale, then to run forward ventral to the second branch of the trigeminus, and to issue from the cranial cavity through an opening which corresponds to the

fissura orbitalis superior of man plus the foramina rotundum and opticum. In the Macrochiroptera the artery traverses a canalis pterygoideus in the basis cranii of this region (Grosser), while in *Rhinolopas* it lies, as in man, wholly free along the lateral wall of the cranium. This is, then, wholly in accord with the varying relations of this artery to the lateral wall of the cranium in fishes, the artery traversing the pars jugularis of the trigemino-facialis chamber in all of the Teleostei in which that part of the chamber occurs, traversing a foramen in its lateral wall in *Amia*, entering it with the nervus palatinus facialis in *Lepidosteus*, and lying wholly external to the lateral wall of the cranium in those fishes (*Cottus*, *Amiurus*) in which the pars jugularis of the trigemino-facialis chamber is not enclosed. It is thus evident that, both in the dog and in the Macrochiroptera, the processus pterygoideus has fused with the lamina ascendens of the ala temporalis and so has enclosed the external carotid in a canal which corresponds to a part of the pars jugularis of a trigemino-facialis chamber, and that, in *Vespertilio*, the mesial wall of this canal has been resorbed, the artery then lying in a part of a trigemino-facialis chamber.

The fovea epitympanica of rabbit embryos is a depression on the lateral surface of the chondrocranium, said by Voit ('09, p. 450) to lie between the crista facialis and the tegmen tympani. The tegmen tympani is said to arch over the upper edge of the fovea, and it is so shown in his figures, the tegmen apparently forming the dorsal portion of the lateral wall to the fovea. It is, however, said (*l. c.*, p. 449) that the tegmen is perforated by the foramen faciale externum s. secundarium, but as that foramen lies in the plane of the mesial wall of the fovea epitympanica, it would seem as if there must be some error in the descriptions. But however this may be, the fovea lodges the upper ends of the malleus and incus, and these two cartilages lie external to the nervus facialis, to the posttrigeminus portion of the vena capitis lateralis, and to the arteria stapediales (maxillaris interna, carotis externa). The fovea and the space traversed by this nerve, vein, and artery thus together form a cavity which has the relations to the cranial wall of the pars jugularis of a tri-

geminio-facialis chamber, the tympanic cavity of mammals thus being a derivative of this chamber of fishes. The tegmen tympani and the malleus, incus, and stapes are then quite certainly parts of the outer wall of this cavity, and hence derived from the quadrate, this being as Drüner ('04) has maintained for the malleus, incus, and stapes. It would also seem as if the annulus tympanicus must have the same origin, thus completing the outer wall of the cavity and encircling the part that was broken up to form the auditory ossicles. The fact that the stapes may be traversed by the arteria stapediales is in accord with the perforation, in *Amia*, of the lateral wall of the trigemino-facialis chamber by the external carotid.<sup>1</sup>

The tympanic cavity is traversed, in mammals, by the chorda tympani, and Jacobson's nerve and sympathetic fibers enter it. In fishes the pars jugularis of the trigemino-facialis chamber is traversed by a sympathetic nerve and frequently (always ?) also by a communicating branch from the nervus facialis to the nervus trigeminus, and Jacobson's nerve enters it as a part of the truncus facialis. The communicating branch from the nervus facialis to the nervus trigeminus must then be the chorda tympani, and that nerve must be a prespiracular one, for in fishes it certainly is prespiracular. The chorda tympani must then be represented, in fishes, in the ramus mandibularis internus trigemini of my descriptions of *Amia* (Allis, '01, p. 188).

In fishes the spiracular canal or a diverticulum of it may lie along the lateral wall of the trigemino-facialis chamber. If a diverticulum of either of those canals were to expand into the pars jugularis of the chamber, it would evidently give rise to a tympanic cavity connected with the pharynx by an eustachian tube, or the same result would be obtained by the expansion in-

<sup>1</sup>Later work has somewhat modified this opinion and convinced me that the incus, alone, corresponds to the lateral wall of the trigemino-facialis chamber of fishes, both structures being derived from the posterior branchial-ray bar of the mandibular arch. The malleus and the teleostean quadrate both represent the epal element of the mandibular arch. The styloid and mastoid processes are, respectively, the anterior and posterior branchial-ray bars of the hyal arch, and the stapes probably the pharyngohyal. The chorda tympani is a posttrematic nerve.

to the chamber of a diverticulum of a plica hyomandibularis (Drüner, '03).

The conditions in *Echidna* remain to be considered. In an earlier work (Allis, '14 b) I came to the conclusion that the cavum epiptericum of Gaupp's descriptions of embryos of this animal was the strict equivalent of the trigemino-facialis chamber of *Amia* less its pars facialis, this conclusion being based on my interpretation of Gaupp's descriptions of the venous vessels of the region. According to him ('08, p. 598), there is, in the cavum cerebrale cranii of this animal, a large cross-commisural venous vessel, anterior to the hypophysis and issuing on either side through the fenestra pseudo-optica into the cavum epiptericum. There, one part of this vessel turns forward and passes into the orbit, the other turning posteriorly in the cavum epiptericum and becoming the sinus cavernosus. This so-called sinus cavernosus is said to pass ventral to the ganglion trigeminum, and it is shown, in a figure of a transverse section through this region, lying ventrolateral to the base of the taenia clino-orbitalis, the hypophysis lying mesial to the taenia. Posterior to this point, and hence apparently posterior to the sella turcica, the sinus cavernosus turns laterally and falls into the sinus transversus, the latter sinus descending almost vertically in front of the otic capsule. The fusion of these two veins is said to form the vena capitis lateralis, which issues from the cranial cavity through the hindermost corner of the fenestra sphenoparietalis and immediately enters the sulcus facialis on the external surface of the chondrocranium. In a slightly older embryo the sinus cavernosus is said (*l. c.*, p. 629) still to be connected with the sinus transversus, but to be now also prolonged posteriorly as the sinus petrobasilaris, which runs posteriorly in the cavum cerebrale cranii, sends a branch outward through the foramen jugulare, and then itself issues through the foramen occipitale magnum.

From these descriptions I concluded ('14 b) that the so-called sinus cavernosus, plus the vena capitis lateralis, must form a vein the homologue of the vena jugularis of fishes. That vein could not then enter the cavum cerebrale cranii, as Gaupp says it does,

and I concluded that there must be some error in the descriptions, for I did not question the identification of the veins. Because of the position of this vein, I concluded that the *cavum epiptericum* was a trigemino-facialis chamber. This is, however, wrong, for the so-called *sinus cavernosus* is, in reality, the homologue of the pituitary vein of fishes, and not of the *vena jugularis*. This vein of *Echidna* must then traverse a myodomic cavity, as it does in the *Mammalia ditremata*, and there must be a membrane separating it from the *cavum epiptericum*, that membrane being a part of the *membrana limitans* of Terry's ('17) descriptions of the cat and forming the roof of a myodomic cavity which is the *sinus cavernosus* properly so-called. The pituitary vein then traverses this cavity, as it does in man, and that part of the so-called *sinus* which Gaupp says turns laterally and falls into the *sinus transversus*, is the *vena encephalica* of fishes, this latter vein falling into the *vena capitis lateralis* (*vena jugularis* of fishes) after and not before, it issues from the *cavum epiptericum*. The *vena capitis lateralis* has here, as in the *Mammalia ditremata*, lost its primitive continuity with the *vena capitis media*; the persisting portions of these veins both lie external to the cranial wall; and the *cavum epiptericum* is a trigemino-facialis recess. The conditions in this animal are then strictly similar to those in the *Mammalia ditremata* except that a *taenia clino-orbitalis* has been formed, comparable to, but somewhat different from, the cartilage 'c' of Voit's descriptions of the rabbit.

In the adult *Echidna* it would seem, from Gaupp's descriptions, as if certain of the bones forming the lateral wall of the cranium were developed in the lateral wall of the *cavum epiptericum* (trigeminus recess), and certain of them in the lateral wall of the *pars jugularis* of a trigemino-facialis chamber, for certain of the bones are said (*l. c.*, p. 650) to be ossifications of the *membrana sphenobutatoria*, which is said to lie external to the *ala temporalis*. The *taenia clino-orbitalis* is said by Gaupp (*l. c.*, p. 647) to have fused, in the adult, with the lateral edge of the *sella turcica* along the full length of the *sella*, the *fissura pseudo-optica* thus being greatly reduced in size; the



development of this bar of cartilage doubtless accounting for the suppression of a posthypophysial commissure between the pituitary veins of opposite sides of the head.

The so-called parasphenoid of *Echidna* is considered by Gaupp ('05 a) to be the homologue of the ascending process of the parasphenoid of the Sauria, and also of the mammalian pterygoid, the latter bone not being the homologue of the pterygoid of reptiles. The bone of *Echidna* is said to lie, in embryos, directly upon the cartilage of the basis cranii, without intervening connective tissue, and later to fuse with the sphenoid (Keilbein) as part of its processus pterygoideus. No cartilage has been found in this bone in *Echidna*, but it is said to be found in the pterygoid of mammals. The bone lies anterior to the foramen caroticum, the internal carotid arteries accordingly not coming into any relations to it. The nervus parabasalis (palatinus facialis) is said to run forward external to the posterior portion of the bone, but, anterior to the point of exit of the nervus opticus from the cranial cavity, it perforates the bone through a foramen parabasale, and so enters the anterior portion of the cavum epiptericum. There is thus no canalis parabasalis in this animal, and the relations of the parasphenoid to the chondrocranium, to the internal carotid arteries, and to the ramus palatinus facialis all show that it corresponds to the ascending process of the parasphenoid of *Amiurus*, and to the mesial plate of that process of the parasphenoid of *Polyp-terus*, and that it is accordingly an ossification in the roof of a ventral myodome cavity and not in its floor.

#### CARTILAGINES POLARIS AND ACROCHORDALIS

Polar cartilages were, as already stated when describing the *Selachii*, first described by van Wijhe ('05) in embryos of *Acanthias*, where the cartilage of either side is said by him to lie between the trabecular and parachordal cartilages, but it soon fuses with both those cartilages and then forms, with the trabecula, the ventral border of the orbital fenestra. The posterior border of the orbital fenestra is said to be formed by the lamina antotica, which is an outgrowth of the anterior end of

the parachordal of its side. Nothing is said of the relations of the eye-muscles, arteries, and veins to these cartilages. Sewertzoff ('97, '99), in his work on embryos of this same fish (*Acanthias*), did not find these cartilages, and he says that the alisphenoid, which is van Wijhe's *antotica*, is primarily a wholly independent cartilage and hence not an outgrowth of the parachordal. He considers it to be a prechordal structure, and says that it is apparently developed in close relations to the eye-muscles, the four rectus muscles and the obliquus superior all having their insertions on it. The only other fish in which this cartilage has been described is, so far as I know, *Lepidosteus*, where it has been described by Veit and has been already referred to when considering that fish. The cartilage is there said to give insertion to the rectus externus, this cartilage of this fish thus apparently corresponding, functionally, to the base of the alisphenoid cartilage of Sewertzoff's descriptions of *Acanthias*, as it does also to the eye stalk of the adult selachian. A polar cartilage, although only described in these two fishes, has been recognized and described in certain of the *Sauropsida* and *Mammalia*.

In 5-mm. chick embryos and 8 to 9-mm. embryos of the duck, Sonies ('07) finds no cartilage as yet developed in the cranial region. The notochord is said to extend far up in the *plica encephali ventralis*, and its tip is there bent slightly ventrally and is lost in connective tissues behind the hypophysis. In slightly older stages, an unpaired cartilage, the *cartilago acrochordalis*, develops around the anterior end of the notochord, the cartilage inclining dorso-anteriorly and the notochord perforating it from its dorsal surface. The parachordals are said to then develop, posterior to this *acrochordalis* cartilage, as a simple unpaired median plate, for, although always thickest along their lateral edges, they are always continuous with each other dorsal to the notochord and, in most instances, also continuous ventral to it. These two primarily independent and unpaired cartilaginous plates, the *acrochordalis* and *parachordalis*, then become connected with each other, on either side, by a short cartilage which is called the *cartilago basiotica*, these

two paired cartilages developing as independent pieces in the duck, but in the chick in continuity with the anterior edge of the parachordal plate. The basal plate is thus completed, and it is perforated by a median space, traversed longitudinally by the notochord, which is said to be the fenestra basicranialis posterior and which has the position of that fenestra in *Lacerta* and the *Amphibia*.

The trabeculae appear as independent paired cartilages at about the same time as the cartilagine basioticae, lying rostral to the nervi optici and nearly at right angles to the basal plate. An independent cartilago polaris then develops, in the duck, on either side of the hypophysis, between the trabeculae and the ventral surface of the basal plate, and later fuses with both of those cartilages, usually first with the trabeculae, but occasionally first with the basal plate. In the chick the cartilago polaris is, from the very first, continuous with the hinder end of the trabecula of its side. The fusion of the polar cartilages with the basal plate takes place in the line of the fusion of the cartilagine acrochordalis and basioticae, and a fenestra hypophyseos is thus enclosed, which lies nearly at a right angle to the fenestra basicranialis posterior and is separated from it by the cartilago acrochordalis (*l. c.*, p. 426). The side walls of this fenestra hypophyseos are at first formed both by the polar cartilages and the hinder ends of the trabeculae, but, as the trabeculae gradually fuse with each other in the median line, that part of the fenestra which was primarily enclosed between them is gradually suppressed, the trabeculae then only forming its anterior wall, the tuberculum sellae. The cartilago acrochordalis, projecting dorsq-anteriorly, is said to form the dorsum sellae. A processus infrapolaris develops later on either side, from the posteroventral surface of the polar cartilage, and in *Sterna* projects posteriorly beneath and parallel to the basal plate, its hind end fusing with it on either side of the fenestra basicranialis posterior. A somewhat vertical, subparachordal plate is thus formed which is perforated by a large opening, traversed by the arteria carotis interna. That artery, after traversing this opening, passes through the fenestra hypo-

physeos, posterior to the hypophysis, sends a cross-commissural branch to its fellow of the opposite side, another branch, the arteria ophtalmica interna, outward dorso-anterior to the polar cartilage, and is then itself distributed to the brain. It passes mesial to the polar cartilage of its side, but lateral and dorsal to the processus infrapolaris. If this latter process were to become the only connection between the polar cartilage and the basal plate, the artery would pass lateral to the polar cartilage, and this is apparently what actually takes place in the Mammalia, as will be explained later.

Comparing these conditions in the chick and duck with those in embryos of the Teleostei and Holostei, it is at once evident that the cartilago acrochordalis of the former must be the homologue of that cartilaginous prootic bridge of the latter which forms the beginning of the definitive prootic bridge. The relations of these two cartilages to the other skeletal elements, and to the brain, are too strictly similar to leave any reasonable doubt as to this, the differing relations of the cartilages to the notochord evidently being related to the early development of the cartilage in the chick and duck and its late development in the Teleostei and Holostei. The space which, in the Teleostei and Holostei, lies between this bridge and the otic portion of the basal plate must then be the homologue of the fenestra basicranialis posterior of the chick and duck, as has already been stated, and the side walls of this fenestra the homologues of the basiotic cartilages; these latter cartilages being prolonged ventrally, in fishes, by the ventral processes of the prootics, and, in the chick and duck, by the infrapolar processes. These latter processes, together with the polar cartilages, are then the so-called anterior prolongations of the parachordals of Swinnerton's and Gaupp's descriptions of *Gasterosteus* and *Salmo*, there apparently developed in continuity with the basiotic cartilages, as they are said to be in certain of the Aves. The so-called fenestra basicranialis posterior, or fenestra interparachordalis, of Gaupp's and Swinnerton's descriptions of fishes is then the homologue of the fenestra hypophyseos of the chick and duck and not of the fenestra basicranialis posterior, and the fenes-

tra hypophyseos of embryos of fishes has been suppressed in advanced embryos of the chick and duck.

In *Talpa*, Noordenbos ('05) finds the parachordals of opposite sides, when first developed, united with each other, ventral to the notochord, and not extending to its tip. The tip of the notochord reaches, at this stage, to the hypophysis, and is said to represent, in a certain sense, the morphological anterior end, or anterior pole, of the embryo, the hypophysis being an organ at that pole. In slightly older embryos the notochord is somewhat withdrawn from the hypophysis, and its tip then doubtless lies posterior to the infundibulum. The parachordal plate has at the same time grown rostralward, and, turning upward at its anterior end, now surrounds the notochord, which traverses it from its dorsal to its ventral surface and extends anteriorly beyond it.

The trabeculae first appear as a single median plate between the nasal sacs and extending posteriorly to the recessus preopticus. In the space between the trabecular and parachordal plates, ventral to the hypophysis and at a slightly lower level than the parachordal plate, two pairs of little cartilages, the insulae polares, later appear, and soon fuse to form a polar plate which is at first perforated by a median fenestra hypophyseos, which soon becomes closed by growth of the bounding cartilage. This polar plate fuses, soon after its formation, with the trabecular plate, and in the line of fusion a slight transverse furrow is formed which lodges the chiasma opticum. The hind edge of this furrow is slightly raised, and forms the tuberculum sellae, which thus lies on the anterior end of the polar plate and not, as in the chick and duck, on the hind ends of the trabeculae. No cartilago acrochordalis has yet been formed, and the polar plate accordingly cannot fuse with the basal plate along the line of fusion of that cartilage with the cartilagine basioticae, as it does in the chick and duck. Accordingly, a direct fusion of the polar plate with the basal plate does not take place, and connection with the latter plate is acquired through the intermediation of a delicate Y-shaped mass of cartilage, the arms of which fuse with the projecting anterior ends of the

parachordal plate. This Y-shaped cartilage, probably together with the posterior pair of insulae polares, thus corresponds to the infrapolar processes of the chick and duck, and the internal carotid arteries run upward lateral to them, as they do in the chick and duck and as explained just above.

The Y-shaped cartilage of *Talpa*, by its fusion with the anterior end of the parachordal plate, encloses a circular opening which Noordenbos calls the fenestra basicranialis posterior. The anterior end of the notochord lies directly above this fenestra, which it would not do were the fenestra the homologue of the similarly named fenestra in the chick and duck. Furthermore, Noordenbos says ('05, p. 385) that the hypophysis lies in a slight fossa, bounded anteriorly by the tuberculum sellae (a ridge formed, as above stated, on the anterior end of the polar plate) and posteriorly by the anterior end of the parachordal plate, thus necessarily lying directly above the so-called fenestra basicranialis posterior, instead of, as in the chick and duck, definitely anterior to it. This fenestra of *Talpa* must then be an opening corresponding to some part of Gaupp's fenestra basicranialis posterior of *Salmo*, and apparently to that part of it which he says leads from the middle into the posterior sections of his descriptions of the myodome. The fenestra of *Talpa* is, in any event, not a perforation of the floor of the *cavum cerebrale cranii*, as it is in the chick and duck, and that perforation, and a *cartilago acrochordalis* are both wanting in these embryos. The *dorsum sellae* of these early embryos is then not the homologue of the postclinoid wall of *Amia* and the *Tel-eostei*, nor of the *dorsum sellae* of Sonies's descriptions of the chick and duck. It is, however, possible that a *cartilago acrochordalis* may be developed in later stages than those described by Noordenbos, for Voit shows this cartilage in his figures of embryos of the rabbit, there perforated by an opening, the evident homologue of the fenestra basicranialis posterior of Sonies's descriptions of the chick and duck; and Fawcett ('10), in a work I have not been able to consult, is said by Kernan ('16, p. 621) to have found the *dorsum sellae* separated from the *crista transversa* in 19-mm. and 21-mm. human embryos, the *dorsum sellae*

then there representing the cartilago acrochordalis, and the crista transversa representing the anterior end of the parachordal plate.

Sonies calls attention ('07, p. 406) to the unusual position of the fenestra basicranialis posterior in *Talpa*, and suggests that the posterior pair of insulae polares correspond to the cartilago acrochordalis of his own descriptions of the chick and duck. Terry ('17) says that this fenestra lies, in embryos of the cat, between the anterior end of the parachordal plate and the cartilago polaris (hypophyseal cartilage), thus agreeing with Noordenbos in his identification of it, and he says that it lies "not within the basal (parachordal) plate, but anterior to it, as Noordenbos insists." In his figure of a median vertical section of a 12-mm. embryo (l. c., fig. 17) he, however, shows it lying definitely beneath the turned up anterior end of the parachordal plate, in exactly the position I have assigned to it.

Polar cartilages, lying between the trabeculae and parachordals, have thus been identified in *Acanthias* and *Lepisosteus* among fishes, and in several of the *Sauropsida* and *Mammalia*, and it is probable that they form an integral element of the cranium in all of the *Gnathostomata*, though probably not always developed as wholly independent cartilages. The two cartilages embrace the ectodermal stalk of the hypophysis, the opening between them thus being the fenestra hypophyseos properly so-called, but this fenestra is continued both anteriorly and posteriorly, at certain stages of development, in most of the *Gnathostomata*. The anterior prolongation of it lies between the hind ends of the trabeculae, and although it is generally considered to persist, in the *Teleostei* and *Holostei*, as part of the fenestra ventralis myodomi of the adult, it is probable that it becomes largely, if not entirely, suppressed by fusion of the trabeculae. The posterior prolongation of it lies, in fishes, between the ventral edges of the ventral processes of the prootics, and, in the *Aves* and *Mammalia*, between the corresponding edges of the infrapolar processes. These processes must then be homologous structures, and if the ventral processes of the prootics of fishes are ventrolateral processes, as I conclude,

the intrapolar processes, and hence also the polar cartilages, must be hypochordal and not parachordal structures. This, then, is in accord with, but an extension of, Terry's conclusion ('17, pp. 344 and 396) that there seems no doubt of the presence of a cartilaginous hypochordal layer in the occipital region of mammals generally, and that the basal plate of the occipital region falls into the category of arch structures, not centra.

The notochord and trabeculae may now be considered. Swinerton says that the notochord in *Gasterosteus* undergoes no actual reduction from the earliest to the latest stages examined by him, its relatively less extensive anterior prolongation in older embryos being wholly due to an anterior prolongation of the parachordal cartilages. Froriep, however, says ('02 a, '02 b) that in *Torpedo* there is an actual disintegration of the anterior portion of the notochord. According to him, in early embryos of that fish, the notochord is separated into two definite regions, one of which he considers to be spinal and the other prespinal. The spinal region is said to begin at the dorsorostral corner of the first visceral pouch, this point coinciding with that in which the dorsal wall of the foregut, in early embryos, bends abruptly ventrally in an obtuse angle, the notochord there also bending ventrally at the same angle. Posterior to this point the notochord develops a cuticular sheath immediately after its constriction from the dorsal wall of the foregut, and is persistent throughout the life of the individual. Anterior to this point, and hence in the prespinal region, the notochord presents two different conditions, one related to the region in which the mandibular head cavities develop and the other to that in which the premandibular cavities develop. In the mandibular region a chorda entoblast is said to be constricted from the dorsal wall of the foregut exactly as in the spinal region, but it does not undergo further differentiation and later entirely disintegrates. In the premandibular region, according to Froriep ('92 b, p. 55):

Kommt es nicht einmal zur Bildung einer primitiven Chordaanlage, sondern deren Bildungsmaterial sowohl wie dasjenige des Mesoblasts bleibt ungesondert in der Wand des Vorderdarms enthalten.



Diese indifferente Urdarmmasse schnürt sich zu Ende des Stadium F von den Gebilden der Mandibularregion vollständig ab und stellt nun die Anlage der Prämandibularen Kopfhöhle Balfour's oder das I. Somit van Wijhe's dar.

The protovertebrae are said by Froriep to extend the full length of the persisting notochord, and not to extend beyond that point; the whole animal being, at this stage, vertebral column. The prespinal, or head region is said to contain the matrix in which all the visceral arches and the mandibular and premandibular head cavities are developed.

Katherine M. Parker, in the latest work I know of relating to this subject, also finds, in the Marsupialia, the notochordal tissue extending anteriorly beyond the end of the persisting notochord, for she says ('17, p. 24):

The primitive relation of the tip of the notochord is one of continuity with the protochordal plate, and in *Perameles* continuity is retained between the chorda and the derivatives of the protochordal plate (prechordal plate and Seesel's pocket). As a secondary condition, continuity may be established between the chorda and the hypophysis.

His, in a much earlier work, also came to a similar conclusion, for he says ('92, p. 348) that the notochord, in all early vertebrate embryos, ends anteriorly in a tapering point which lies immediately posterior to a transverse basal ridge (Basilarleiste) of the brain which lies at the extreme anterior end of the ventral surface of the neural tube. This basal ridge is in contact, either with the dorsal end of Seesel's pocket or with a strip of entoderm (Entodermstreife) which replaces that pocket, and His shows the tip of the notochord wedged in between his basal ridge and Seesel's pocket in two different figures, one said to be a general vertebrate schema and the other to show an actual median sagittal section of the head of an embryo of *Pristiurus* 26-mm. in length. Seesel's pocket lies at the dorsal edge of the oral plate, and is said to be not only topographically, but also genetically, an anterior continuation of the notochord (*l. c.*, p. 350), the notochordal tissue thus extending to the level of the anterior end of the ventral surface of the neural tube. This primitive topographical relation of these four structures, the basal ridge,

the tip of the notochord, Seesel's pocket, and the dorsal edge of the oral plate, is said to be subject to marked changes in later stages and in different vertebrates, Seesel's pocket shifting either anteriorly or ventrally (*rachenwärts*) relatively to the basal ridge. In the latter case an ectodermal fold is formed between it and the basal ridge, and becomes the hypophysial invagination (Rathke's pocket), which extends posteriorly beyond the basal ridge, forcing the tip of the notochord away from the ventral surface of the brain, and even forcing it upward into the *plica encephali ventralis*. The relations of the brain to the notochord, in the adult vertebrate, are accordingly said by His not always to be the primitive ones; and he (*l.c.*, p. 358) considers only those parts of the brain of the adult to be prechordal which lie anterior to the basal ridge, and which therefore formed primarily a part of the anterior surface of the neural tube. Those parts are said by him to be the regions of the recessus infundibuli, the chiasma opticum, the recessus opticus, the lamina terminalis, and the olfactory lobes. The saccus vasculosus lies posterior to the basal ridge and belongs morphologically, as well as actually, to the ventral surface of the brain, the line between the morphologically ventral and anterior surfaces of the brain thus lying between the saccus and the recessus infundibuli.

There is thus reason to believe that the notochord extended primarily to the level of the anterior end of the primitive gut, and that, accordingly, the epichordal and hypochordal bands of skeletogenous material, developed in relation to it, had a similar extent. The polar and trabecular cartilages must then be developed from some part of these anterior extensions of these bands, and the polar cartilages quite certainly, as already stated, from the hypochordal bands alone. The trabeculae, in crania of the platybasic type, would seem to be developed from both these bands of tissue. In crania of the tropibasic type the two bands seem to have been forced apart, by pressure of the eyeballs, the epichordal bands lying at the top of the interorbital septum and the hypochordal bands at the bottom of that septum.

It is furthermore to be noted that the trabeculae do not lie

along the ventral surface of the brain, as that surface is defined by His; since as, when first formed, their hind ends apparently always lie anterior to the recessus infundibuli, they must themselves lie either definitely on the anterior surface of the brain or along the lateral surface of its extreme anterior end. In the latter case they would actually have, to the neural tube, the relations of dorsal vertebral arches. It does not, however, necessarily follow that they are such arches, for their relations to the brain may be wholly due to a cranial flexure so sharp and pronounced that it has turned the anterior surface of the neural tube downward upon cartilages which primarily lay either in the line of the axis of the body, or projected ventrally beneath it.

#### SUMMARY

A functional myodome is found only in fishes, and even among them it is limited, in those I have examined, to *Amia* and the non-siluroid Teleostei.

The myodome is always separated from the cavum cerebrale cranii by membrane (*dura mater*), cartilage, or bone, and the separating wall is in part spinal and in part prespinal in position. A depression in the prespinal portion lodges the hypophysis or both the hypophysis and saccus vasculosus, and this part of the wall never undergoes either chondrification or ossification, a more or less developed pituitary sac always projecting into the myodome.

The myodome is found in its most complete form in the Teleostei, and there consists of dorsal and ventral compartments which are usually separated from each other only by membrane, but that membrane, the horizontal myodomic membrane, is capable of either chondrification or ossification. The dorsal compartment lodges the hind ends of the *musculi recti externi* and is always traversed by a cross-commissural venous vessel formed by the pituitary veins. The ventral compartment lodges the hind ends of the *musculi recti interni* and is traversed by the internal carotid and efferent pseudobranchial arteries and the palatine branches of the *facialis* nerves.

The parasphenoid forms the floor of the ventral compartment of the myodome, and whenever the horizontal myodomic membrane undergoes ossification, the bone so formed forms part of the parasphenoid. This bone is thus certainly, in some fishes, in part of axial origin, and not simply a dermal bone which has gradually sunk inward to its actual position.

In the Siluridae (*Amiurus*) there is apparently a much reduced, but non-functional, dorsal myodomic compartment, but no ventral compartment, that portion of the parasphenoid which lies in the prootic region being developed in what corresponds to the horizontal myodomic membrane of others of the Teleostei.

In *Amia* the myodome corresponds to the dorsal compartment only of the teleostean myodome, and a strictly similar, but non-functional myodomic cavity is found in *Lepidosteus* and *Polypterus*. The ventral compartment of the teleostean myodome is represented, in each of these three fishes, by a canal, on either side of the head, which is traversed by the internal carotid artery, and which corresponds to the *canalis parabasalis* of Gaupp's descriptions of higher vertebrates.

The myodomic cavity is limited, in the Holostei and Crossopterygii, to the prootic region, and is there in part subspinal and in part prespinal and subpituitary in position. In the non-siluroid Teleostei examined, the dorsal compartment of the myodome is always more or less prolonged posteriorly into the basioccipital region and the ventral compartment frequently so prolonged.

The posterior part of the basioccipital portion of the myodome lies between ventrolateral vertebral processes which are quite certainly the homologues of the haemal arches of the tail. In *Hyodon* this part of the myodome is an open groove and lodges the anterior portion of the median dorsal aorta. In the Cyprinidae part of this groove has become enclosed to form a short canal which is traversed by the median dorsal aorta, the enclosing bone forming the pharyngeal process.

The conditions in these fishes thus lead inevitably to the assumption that the entire dorsal myodomic cavity is a sub-vertebral canal similar to the haemal canal in the tail, and that

the dorsal aorta has been excluded from it because of the formation of a *circulus cephalicus*. What the primary relations of the hypophysis and pituitary veins to this preexisting canal were is problematical, but they became lodged in its anterior portion and so gave rise to the conditions actually found in *Lepidosteus* and *Polypterus*. The *musculi recti externi* then secondarily invaded this space by traversing the foramina for the pituitary veins, the other rectus muscles retaining their insertions on the external surface of the preclinoid wall, and so gave rise to the conditions found in *Amia*. The conditions in the non-siluroid Teleostei then arose as a result of the resorption of the cartilage which, in *Amia*, forms the preclinoid wall, the pedicel of the alisphenoid, and those ventral portions of the basicapsular commissures which form the lateral walls of the subpituitary portion of the myodome. Because of the resorption of the preclinoid wall, and its replacement by membrane, the *musculi recti interni*, which in *Amia* have their points of insertion on either lateral edge of that wall, have first sought firmer attachment on the dorsal surface of the parasphenoid, and have later pushed posteriorly in the open ends of the persisting portions of the canales parabasales. The fusion of these two canals with each other has formed a ventral myodomic compartment which, in early embryos, is separated from the dorsal and primary compartment by membrane only; but this membrane may undergo either partial chondrification (*Hyodon*) or ossification (*Gasterosteus*), the bone, in the latter case, forming a transverse and inclined ridge on the dorsal surface of the parasphenoid. The membranes resulting from the resorption of the preclinoid wall were then pressed together in the median line by the *recti interni*, and form a median vertical myodomic membrane which encloses the internal carotid arteries in a membranous canal, the homologue of the cartilaginous canals of *Amia*. The efferent pseudobranchial arteries, pressed downward by the *recti interni*, lost their connections with the internal carotids and acquired a cross-commissural connection with each other. The membrane resulting from the resorption of the anterior portions of the basicapsular commissures of either side ossified as part of the

ascending process of the parasphenoid, and the tissues resulting from the resorption of the pedicel of the alisphenoid ossified, in certain fishes (*Cottus*, *Gasterosteus*), to form an anterior portion of that process.

The myodomic cavities of the *Holostei* and *Teleostei* are represented in the *Selachii* either by canals in the basis cranii which are traversed by the pituitary veins and the internal carotid and efferent pseudobranchial arteries or by a posterior and deeper portion of the large pituitary fossa of the chondrocranium which is shut off from the cavum cerebrale cranii by the dura mater, and is traversed by the pituitary veins and the internal carotid arteries.

In embryos of *Ceratodus* there is a subpituitary space, traversed by the pituitary veins, which corresponds to the dorsal compartment of the teleostean myodome, and the internal carotid canals of *Amia* have been added to it. This fusion of these canals with the dorsal myodomic cavity is due, either to the resorption of the cartilage that separates them in *Amia* or to a shifting posteriorly of both the hypophysis and the internal carotids from a position between the hind ends of the trabeculae to one between the so-called anterior prolongations of the parachordals.

In the *Amphibia* the basis cranii apparently corresponds to the roof, and not to the floor, of the dorsal myodomic cavity of *Amia* and the *Teleostei*. The fenestra hypophyseos of these animals is then the homologue of the pituitary opening of the brain case of fishes.

The *Reptilia* and *Mammalia* have a dorsal myodomic cavity similar to that in *Ceratodus*. In man it is represented in the cavernous and intercavernous sinuses, and the venous vessels that traverse the sinuses are the homologues of the pituitary veins of fishes.

The cartilago acrochordalis of *Sonies'* and *Noordenbos'* descriptions of birds and mammals, respectively, is the homologue of the cartilaginous prootic bridge of embryos of fishes. The open space between this cartilage, or bridge, and the anterior end of the parachordal plate is the fenestra basicranialis poste-

rior proper. This fenestra is a perforation of the roof of the myodomic cavity, and hence is not the homologue of the so-called fenestra basicranialis posterior of embryos of fishes, which is a perforation of the floor of that cavity. This latter fenestra of embryos of fishes is the homologue of the fenestra hypophyseos of birds and mammals, the so-called anterior prolongations of the parachordals of fishes being the homologues of the polar cartilages of birds and mammals.

In certain of the Selachii there is an acustico-trigemino-facialis recess, and there may be certain canals in the cranial wall traversed by the vena jugularis and the external carotid artery.

In *Amia* the trigemino-facialis portion of this recess has fused with the canals for the vena jugularis and the external carotid artery to form a trigemino-facialis chamber; this chamber has become continuous with the myodome, and the large chamber so formed has been prolonged anteriorly by a space between the pedicel of the alisphenoid and the primitive side wall of the neurocranium. The foramina for the pituitary vein and the oculomotor and trochlear nerves open into this anterior prolongation of the chamber, and through its orbital opening into the orbit. The vena jugularis traverses this opening to enter and traverse the trigemino-facialis chamber; the musculus rectus externus traverses it to enter the myodome, and the nervus profundus traverses it to join the ganglion, or root of the nervus trigeminus. The nervus trigeminus and the external carotid artery issue from the trigemino-facialis chamber posterior to the pedicel of the alisphenoid and run forward lateral to it.

In the non-siluroid Teleostei the trigemino-facialis chamber is not continuous with the myodome, and it has been separated by a wall of bone into ganglionaris and jugularis parts which correspond, respectively, to the trigemino-facialis recess and the jugular and external carotid canals of the Selachii. The pedicel of the alisphenoid is incomplete or wholly wanting, but it may be replaced by an anterior prolongation of the ascending process of the parasphenoid. In the latter case the nerves, arteries, veins, and muscles all have the same relations to this process that they have to the pedicel of the alisphenoid of *Amia*. The

lateral wall of the pars jugularis of the trigemino-facialis chamber is always less extensive than in *Amia* and may be wholly wanting.

In *Ceratodus* there is a trigemino-facialis chamber similar to that in *Amia*, and there is a bar of cartilage which corresponds to the pedicel of the alisphenoid of that fish.

In the Amphibia there is a trigemino-facialis recess, and the pars ascendens of the quadrate forms the lateral wall of a space corresponding to the pars jugularis of the chamber of the Teleostei. The ascending process of the palatoquadrate is the homologue of the pedicel of the alisphenoid of fishes.

In the Reptilia there apparently is no trigemino-facialis recess, the lateral wall of the neurocranium being the primitive cranial wall. The pars ascendens of the quadrate forms the lateral wall of a trigemino-facialis chamber. The antipterygoid (columella) is the homologue of the pedicel of the alisphenoid of fishes, and the processus basipterygoideus the homologue of the floor of the orbital opening of the myodome of *Amia*.

In the Mammalia there is a trigemino-facialis\*recess formed by the cava epiptericum and supracochleare. The ala temporalis is peculiar to mammals; it is a bar of cartilage formed between the nervi maxillaris and mandibularis trigemini as they issue from the trigemino-facialis recess, the processus alaris corresponding to some part of the side wall of the prespinal portion of the myodome of *Amia*. The ala temporalis has been prolonged anteriorly so as to enclose a space anterior to the trigemino-facialis recess, and the foramina for the pituitary vein (sinus cavernosus) and the nervi oculomotorius, trochlearis and profundus (first branch of trigeminus) open into this space and from it into the orbit. The cavum tympanicum is the pars jugularis of the trigemino-facialis chamber, and the processus pterygoideus, the malleus, incus, and stapes, and probably also the annulus tympanicus, are quite certainly portions of the lateral wall of that part of the chamber. A diverticulum of the spiracular canal, or an independent evagination of the pharynx, has expanded into this part of the chamber and so formed the middle ear. The chorda tympani must then correspond to that communicating branch from the nervus facialis to the nervus



trigeminus which, in fishes, traverses the trigemino-facialis chamber, and hence must be a prespiracular nerve.

The internal carotid artery enters the cranial cavity, in most vertebrates, by passing upward mesial to the related trabecula, or mesial to the posterior prolongation of the trabecula formed by the polar cartilage, but in *Amiurus* it enters the cranial cavity through the foramen opticum, and hence would there seem to pass lateral and then dorsal to the trabecula. In embryos of the *Mammalia ditremata* this artery is said to also pass upward lateral to the trabecula, but it is probable that it here simply passes lateral to the infrapolar process of the polar cartilage, the latter cartilage not itself fusing directly with the parachordal plate, and its direct relations to the artery thus being obscured.

Palais de Carnolès, Menton, France,  
May 1, 1918

#### LITERATURE CITED

- ALLEN, W. F. 1905 The blood-vascular system of the Loricati, the mail-cheeked fishes. •Proc. Washington Acad. Sci., vol. 7.
- ALLIS, E. P., JR. 1897 The cranial muscles and cranial and first spinal nerves in *Amia calva*. Jour. Morph., vol. 12.
- 1901 The lateral sensory canals, the eye-muscles, and the peripheral distribution of certain of the cranial nerves of *Mustelus laevis*. Quart. Jour. Microsc. Sci., vol. 45.
- 1903 The skull, and the cranial and first spinal muscles and nerves in *Scomber scomber*. Jour. Morph., vol. 18.
- 1908 a The pseudobranchial and carotid arteries in *Polypterus*. Anat. Anz., Bd. 33.
- 1908 b The pseudobranchial and carotid arteries in *Ameiurus*. Anat. Anz., Bd. 33.
- 1909 The cranial anatomy of the mail-cheeked fishes. Zoologica, Hft. 57.
- 1911 The pseudobranchial and carotid arteries in *Polyodon spathula*. Anat. Anz., Bd. 39.
- 1913 The homologies of the ethmoidal region of the selachian skull. Anat. Anz., Bd. 44.
- 1914 a Certain homologies of the palato-quadrate of Selachians. Anat. Anz., Bd. 45.
- 1914 b The pituitary fossa and trigemino-facialis chamber in Selachians. Anat. Anz., Bd. 46.
- 1914 c The pituitary fossa and trigemino-facialis chamber in *Ceratodus forsteri*. Anat. Anz., Bd. 46.
- 1914 d The trigemino-facialis chamber in Amphibians and Reptiles. Anat. Anz., Bd. 47.

- ARAI, H. 1907 Der Inhalt des Canalis cranio-pharyngeus. Anat. Hefte, Bd. 33.
- BAUMGARTNER, E. A. 1915 The development of the hypophysis in *Squalus acanthias*. Jour. Morph., vol. 26.
- BING, R., AND BURCKHARDT, R. 1905 Das Centralnervensystem von *Ceratodus forsteri*. Jenaische Denkschriften, Bd. 4.
- BRIDGE, T. W. 1879 The osteology of *Polyodon folium*. Phil. Trans. Royal Soc. London, vol. 169.
- 1899 The air-bladder and its connection with the auditory organ in *Notopterus borneensis*. Jour. Linn. Soc. Zool., vol. 27.
- 1904 Fishes, Cambridge Nat. Hist., vol. 7.
- BUDGETT, J. S. 1902 On the structure of the larval *Polypterus*. Trans. Zool. Soc., vol. 16.
- DANFORTH, C. H. 1912 The heart and arteries of *Polyodon*. Jour. Morph., vol. 23.
- DOHRN, A. 1886 Studien zur Urgeschichte des Wirbeltierkörpers. XI. Mittheil. Stat. Neapel, Bd. 7.
- DRÜNER, L. 1901 Studien zur Anatomie der Zungenbein-, Kiemenbogen- und Kehlkopfmuskeln der Urodelen, I. Teil. Zoolog. Jahrb. Abt. f. Anat., Bd. 15.
- 1903 Über die Muskulatur des Visceralskelettes der Urodelen. Anat. Anz., Bd. 23.
- 1904 Über die Anatomie und Entwicklungsgeschichte des Mittelohres beim Menschen und bei der Maus. Anat. Anz., Bd. 24.
- FAWCETT, E. 1910 Notes on the development of the human sphenoid. Jour. Anat. and Physiology, vol. 44.
- FRORIEP, A. 1902 a Zur Entwicklungsgeschichte des Wirbeltierkopfes. Anat. Anz. Ergän. zum 21. Band.
- 1902 b Einige Bemerkungen zur Kopffrage. Anat. Anz., Bd. 21.
- FUCHS, H. 1910 Über das Pterygoid, Palatinum und Parasphenoid der Quadrupeden, insbesondere der Reptilien und Säugetiere, nebst einigen Betrachtungen über die Beziehungen zwischen Nerven und Skeletteilen. Anat. Anz., Bd. 36.
- 1912 Über einige Ergebnisse meiner Untersuchungen über die Entwicklung des Kopfskelettes von *Chelone imbricata*. Anat. Anz. Ergän. zum 41. Band.
- GAUPP, E. 1893 a Über die Anlage der Hypophyse bei Sauriern. Archiv mikros. Anatom., Bd. 42.
- 1893 b Beiträge zur Morphologie des Schädels. 1. Primordial-Cranium und Kieferbogen von *Rana fusca*. Morphol. Arbeiten, Bd. 2.
- 1900 Das Chondrocranium von *Lacerta agilis*. Ein Beitrag zum Verständnis des Amniotenschädels. Anat. Hefte, Bd. 14.
- 1902 Über die Ala temporalis des Säugerschädels und die Regio orbitalis einiger anderer Wirbeltierschädel. Anat. Hefte, Bd. 19.
- 1905 a Neue Deutungen auf dem Gebiete der Lehre vom Säugetierschädel. Anat. Anz., Bd. 27.
- 1905 b Die Entwicklung des Kopfskelets. Handbuch d. vergl. u. experim. Entwickel. d. Wirbeltiere von O. Hertwig. Bd. 3.

- GAUPP, E. 1908 Zur Entwicklungsgeschichte und vergleichenden Morphologie des Schädels von *Echidna aculeata* var. *typica*. Jenaische Denkschriften, Bd. 6, Teil 2.
- GEGENBAUR, C. 1872 Das Kopfskelet der Selachier. Untersuchungen zur Vergleichenden anatomie der Wirbeltiere. H. 3., Leipzig.
- GREIL, A. 1913 Entwicklungsgeschichte des Kopfes und des Blutgefäßsystemes von *Ceratodus forsteri*. Zweiter Teil: Die epigenetischen Erwerbungen während der Stadien 39-48. Jenaische Denkschriften, Bd. 4.
- GROSSER, O. 1901 Zur Anatomie und Entwicklungsgeschichte des Gefäßsystemes der Chiropteren. Anat. Hefte, Bd. 17.
- GROSSER, O., AND BREZINA, E. 1895 Über die Entwicklung der Venen des Kopfes und Halses bei Reptilien. Morphol. Jahrb., Bd. 23.
- GÜNTHER, A. C. L. G. 1871 Description of *Ceratodus*, a genus of ganoid fishes recently discovered in Queensland, Australia. Phil. Trans. Royal Soc. Lond.
- HANDRICK, K. 1901 Zur Kenntnis des Nervensystems und der Leuchtorgane von *Argyrolepeus hemigymnus*. Zoologica, Heft 32.
- HAY, O. P. 1895 On the structure and development of the vertebral column of *Amia*. Field Columbian Museum, Chicago vol. 1, no. 1, Zool. Ser.
- HIS, W. 1892 Die Entwicklung der menschlichen und thierischer Physiognomien. Archiv Anatom. u. Entwickel.
- HUXLEY, T. B. 1871 A manual of the anatomy of vertebrated animals. London. 1876 On *Ceratodus forsteri*, with observations on the classification of fishes. Proc. Zool. Soc. London.
- KERNAN, J. D., JR. 1916 The chondrocranium of a 20-mm. human embryo. Jour. Morph., vol. 27.
- McMURRICH, J. P. 1884 The osteology of *Amiurus catus* (L.) Gill. Proc. Canadian Instit. vol. 2, Toronto.
- NOORDENBOS, W. 1905 Über die Entwicklung des Chondrocraniums der Säugetiere. Petrus Camper. Deel. 3.
- OLMSTEAD, M. P. 1911 Das Primordialcranium eines Hundeembryo. Ein Beitrag zur Morphologie des Säugetierschädels. Anat. Hefte, Bd. 43.
- PARKER, K. M. 1917 The development of the hypophysis cerebri, pre-oral gut and related structures in the Marsupalia. Jour. Anatomy, vol. 51, pt. 3. London.
- PARKER, W. K. 1873 On the structure and development of the skull in the salmon (*Salmo salar*). Phil. Trans. London. 1876 On the structure and development of the skull in sharks and skates. Trans. Zool. Soc. London, vol. 10. 1882 On the development of the skull in *Lepidosteus osseus*. Philos. Trans. Royal Soc. London, vol. 173.
- RIDEWOOD, W. G. 1904 On the cranial osteology of the fishes of the families Mormyridae, Notopteridae, and Hyodontidae. Journ. Linn. Soc. London, Zoology, vol. 29.
- SAGEMEHL, M. 1883 Beiträge zur vergleichenden Anatomie der Fische. 1. Das Cranium von *Amia calva* (L.) Morph. Jahrb., Bd. 9. 1891 Beiträge zur vergleichenden Anatomie der Fische: IV. Das Cranium der Cyprinoiden. Morph. Jahrb., Bd. 17.

- SALZER, H. 1895 Über die Entwicklung der Kopfvenen des Meerschweinchens. *Morph. Jahrb.*, Bd. 23.
- SCHÄFER, E. A. 1894 *Organs of the senses*. Quain's *Anatomy*, vol. 3, pt. 3, 10th edition, London.
- SCHAUINSLAND, H. 1905 Die Entwicklung der Wirbelsäule nebst Rippen und Brustbein. *Handb. Entw. Wirbelth.* O. Hertwig 1906, Bd. 3, Abth. 2, Jena.
- SCHLEIP, W. 1904 Die Entwicklung der Kopfknochen bei dem Lachs und der Forelle. *Anat. Hefte*, Bd. 23.
- SCHREINER, K. E. 1902 Einige Ergebnisse über den Bau und die Entwicklung der Occipitalregion von *Amia* und *Lepidosteus*. *Zeit. wiss. Zool.*, Bd. 72.
- SEWERTZOFF, A. N. 1897 Beitrag zur Entwicklungsgeschichte des Wirbeltierschädels. *Anat. Anz.*, Bd. 13.  
1899 Die Entwicklungsgeschichte des Selachierschädels. *Festschrift C. von Kupffer*, Jena.
- SHIINO, K. 1914 Studien zur Kenntnis des Wirbeltierkopfes. 1. Das Chondrocranium von *Crocodylus* mit Berücksichtigung der Gehirnnerven und der Kopfgefäße. *Anat. Hefte*, Bd. 50.
- SONIES, F. 1907 Über die Entwicklung des Chondrocraniums und der knorpeligen Wirbelsäule bei den Vögeln. *Petrus Camper*, Deel. 4.
- STARKS, E. C. 1905 Some notes on the myodome of the fish cranium. *Science*, vol. 21, pp. 754, 755.
- STÖHR, P. 1882 Zur Entwicklungsgeschichte des Kopfskeletes der Teleostier. *Festschr. der Julius-Maximilians-Universität zu Würzburg*. Leipzig.  
1895 Über die Entwicklung der Hypochorda und des dorsalen Pankreas bei *Rana temporaria*. *Morph. Jahrb.*, Bd. 23.
- SUPINO, F. 1901 Ricerche sul cranio dei Teleostei. 1. *Scopelus*, *Chauliodus*, *Argyrolepeceus*. *Ricerche Lab. Anat. Roma*, T. 8.
- SWINNERTON, H. H. 1902 A contribution to the morphology of the teleostean head skeleton, based upon a study of the developing skull of the three-spined stickleback (*Gasterosteus aculeatus*). *Quart. Jour. Mic. Sci.*, vol. 45.
- TERRY, R. J. 1917 The primordial cranium of the cat. *Jour. Morph.*, vol. 29.
- THANE, G. D. 1894 *Arthrology—Myology—Angiology*. Quain's *Elements of Anatomy*, vol. 2, pt. 2, London.
- VEIT, O. 1907 Über einige Besonderheiten am Primordialcranium von *Lepidosteus osseus*. *Anat. Hefte*, Bd. 33.  
1911 Beiträge zur Kenntnis des Kopfes der Wirbeltiere. 1. Die Entwicklung des Primordialcranium von *Lepidosteus osseus*. *Anat. Hefte*, Bd. 44.
- VOIT, M. 1909 Das Primordialcranium des Kaninchens unter Berücksichtigung der Deckknochen. Ein Beitrag zur Morphologie des Säugertierschädels. *Anat. Hefte*, Bd. 38.
- WALDSCHMIDT, J. 1887 Beitrag zur Anatomie des Centralnervensystems und des Geruchsorgans von *Polypterus bichir*. *Anat. Anz.*, Bd. 2.
- VAN WIJHE, J. W. 1905 Über die Entwicklung des Kopfskelets bei Selachiern. *Compte Rendu, 6ieme Congrès Internat Berne, 1904*, published Geneva.

Figs. 1 to 12. Semidiagrammatic figures of transverse sections through a 51-mm. specimen of *Hyodon tergisus*, showing the myodomic cavities and adjacent regions, and selected at intervals between the hind end of the interorbital septum and the hind end of the basioccipital.

Figs. 13 to 18. Similar sections of a 20-mm. specimen of *Cottus scorpius*.

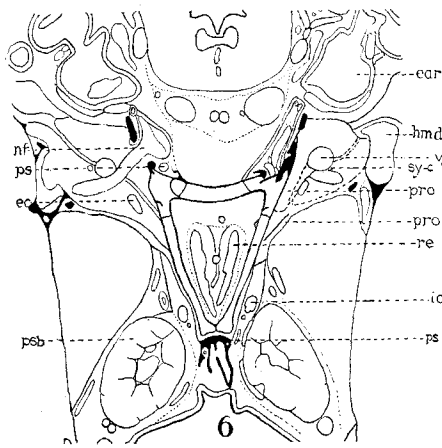
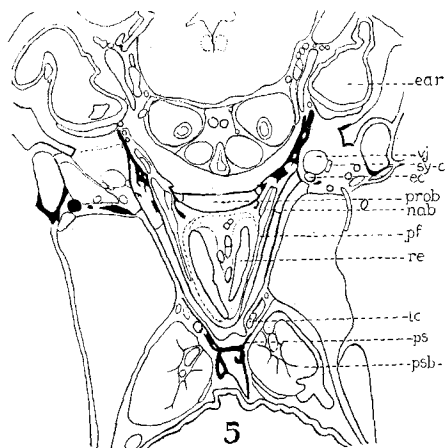
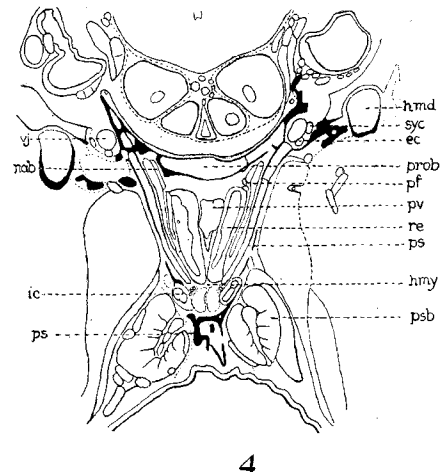
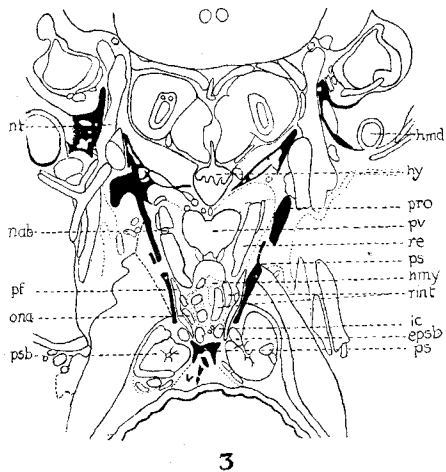
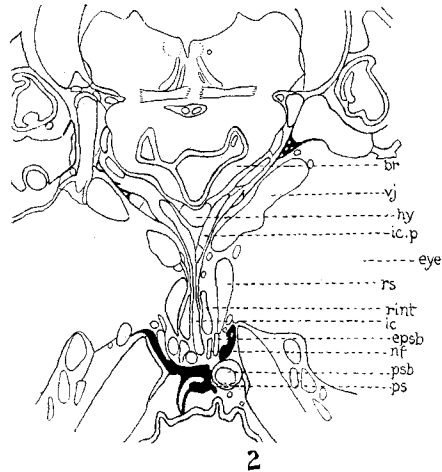
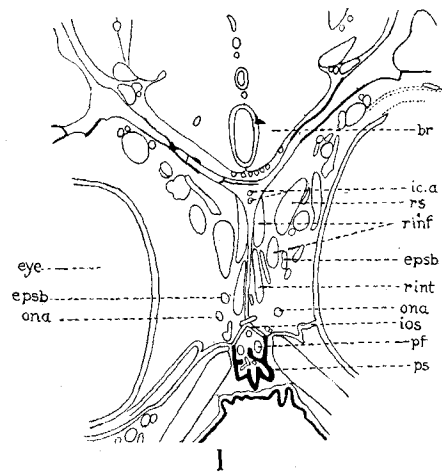
Fig. 19. Similar sections of a 31-mm. specimen of *Clinocottus analis*.

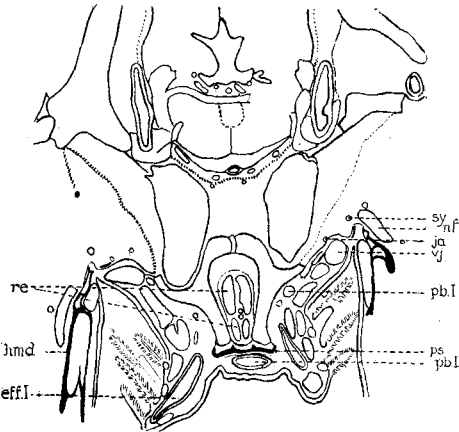
Figs. 20 to 23. Similar sections of a 113-mm. specimen of *Syngnathus acus*.

Figs. 24 to 29. Similar sections of a 57-mm. specimen of *Catostomus occidentalis*.

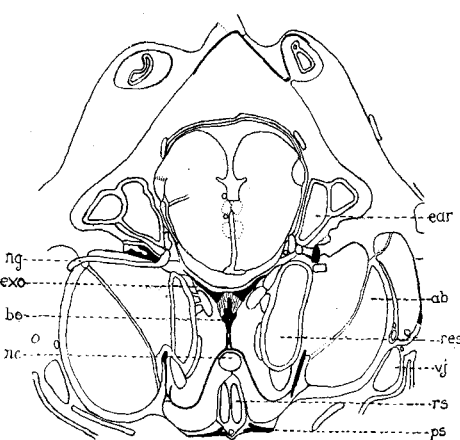
#### ABBREVIATIONS

<i>ab</i> , air-bladder	<i>ng</i> , nervus glossopharyngeus
<i>as</i> , aortal support	<i>nocm</i> , nervus oculomotorius
<i>ba</i> , basioccipital	<i>nl</i> , nervus trigeminus
<i>br</i> , brain	<i>ona</i> , orbitonasal artery
<i>dlp</i> , dorsolateral vertebral process	<i>pb. I</i> , pharyngobranchial of first branchial arch
<i>ear</i> , parts of membranous ear	<i>pb. II</i> , pharyngobranchial of second branchial arch
<i>ec</i> , external carotid artery	<i>pf</i> , ramus palatinus facialis
<i>eff, I</i> , efferent artery of first branchial arch	<i>php</i> , pharyngeal process
<i>epsb</i> , efferent pseudobranchial artery	<i>pro</i> , prootic
<i>exo</i> , exoccipital	<i>prob</i> , prootic bridge
<i>hmd</i> , hyomandibula	<i>ps</i> , parasphenoid
<i>hmy</i> , horizontal myodomic membrane	<i>psb</i> , pseudobranch
<i>hy</i> , hypophysis	<i>pv</i> , pituitary vein
<i>ic</i> , internal carotid artery	<i>re</i> , musculus rectus externus
<i>ic. a</i> , anterior division of internal carotid artery	<i>res</i> , recessus sacculus
<i>ic. p</i> , posterior division of internal carotid artery	<i>rinf</i> , musculus rectus inferior
<i>ios</i> , interorbital septum	<i>rint</i> , musculus rectus internus
<i>ja</i> , Jacobson's anastomosis	<i>rs</i> , musculus rectus superior
<i>l</i> , ligament	<i>sv</i> , saccus vasculosus
<i>lda</i> , lateral dorsal aorta	<i>syc</i> and <i>sy-c</i> , sympathetic nerve and communicating branch from N. trigeminus to N. facialis
<i>mda</i> , median dorsal aorta	<i>vj</i> , vena jugularis
<i>nab</i> , nervus abducens	<i>vlp</i> , ventro-lateral vertebral process
<i>nc</i> , notochord or notochordal space	
<i>nf</i> , nervus facialis	

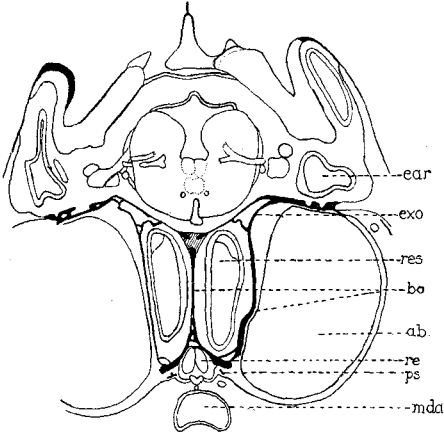




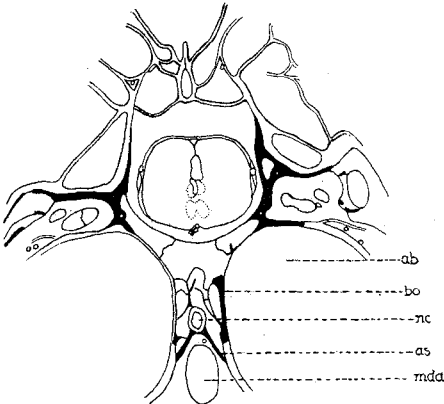
7



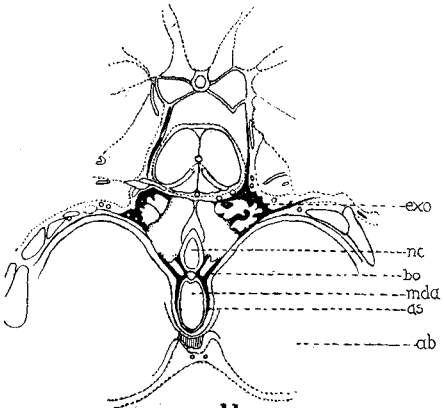
8



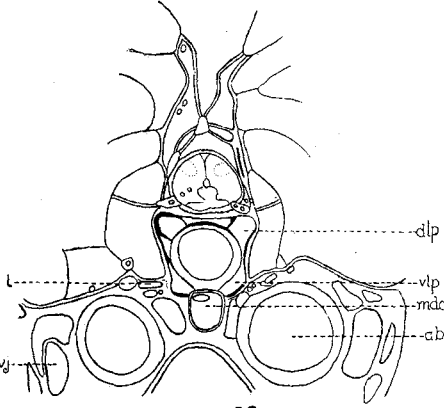
9



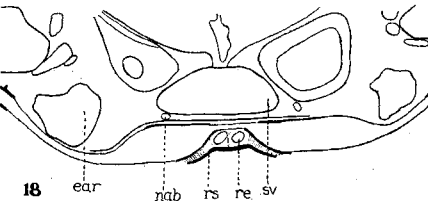
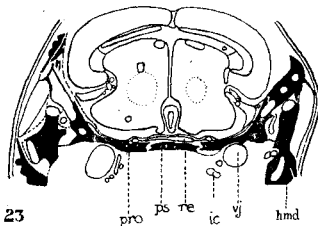
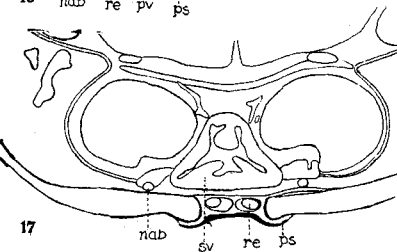
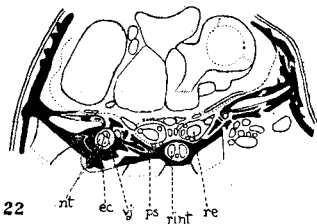
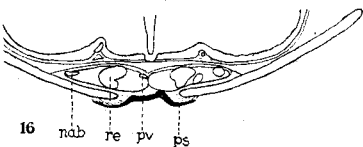
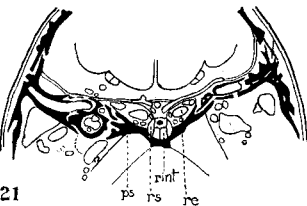
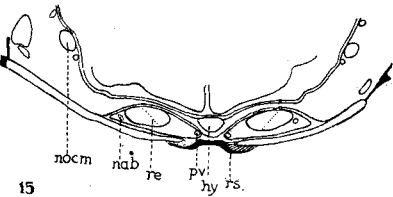
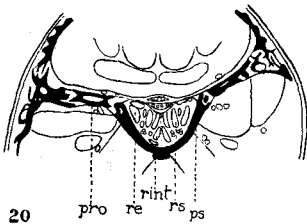
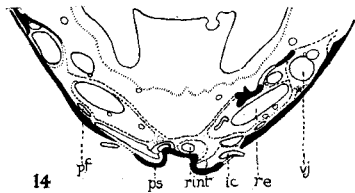
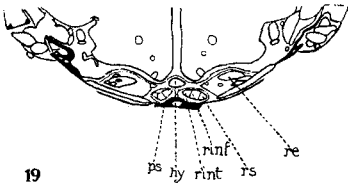
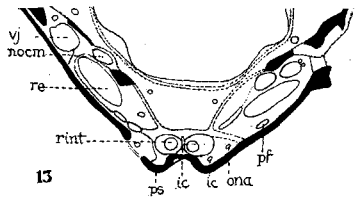
10



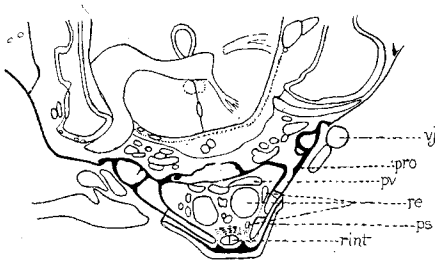
11



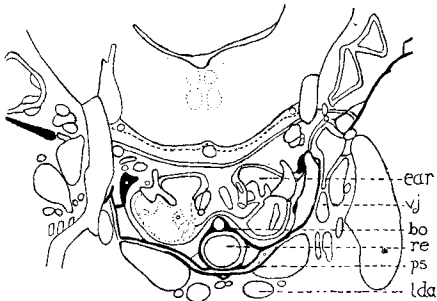
12



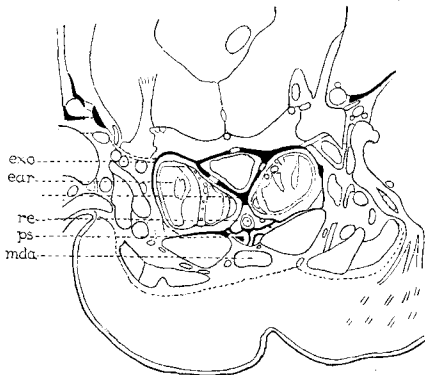




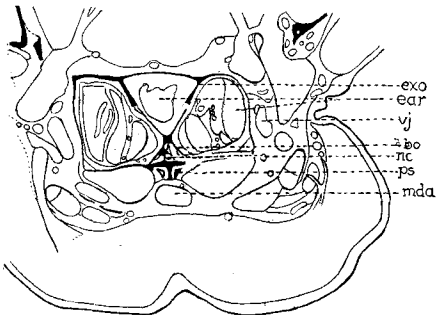
24



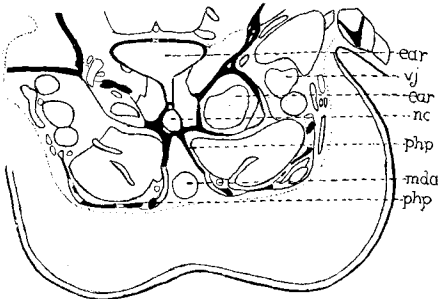
25



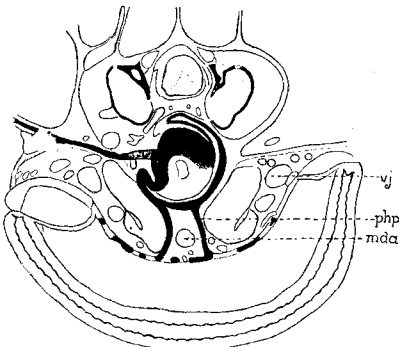
26



27



28



29